ALLIGATORINE PHYLOGENY AND THE STATUS OF *ALLOGNATHOSUCHUS* MOOK, 1921

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ABSTRACT—Whether the extinct crocodylians given the name *Allognathosuchus* represent a monophyletic assemblage remains controversial, and some have argued that *Wannaganosuchus brachymanus* Erickson, 1982 is a form of *Allognathosuchus*. A revised phylogenetic analysis supports a set of relationships in which the type species of *Allognathosuchus* (*A. polyodon*) is closer to *Alligator* than it is to European "*Allognathosuchus*" or "*Allognathosuchus*" from the North American Paleocene, and a close relationship between *Allognathosuchus* and *Wannaganosuchus* is not supported. One European fossil assigned to *Allognathosuchus*, *A. woutersi*, is similar (and possibly referable) to *Diplocynodon*. *Chrysochampsa mlynarskii* can be distinguished from all other Early Tertiary alligatoroids, but its relationships to other members of the clade (and whether it should be placed within *Allognathosuchus*) are unclear. These results support multiple dispersal events of alligatorines from North America to Eurasia, and suggest that the cranial anatomy thought to distinguish forms such as *Allognathosuchus* is plesiomorphic at the level of Alligatoridae. The name *Allognathosuchus* should be applied in a restricted sense to *Allognathosuchus polyodon* and its closest relatives, with alternative generic names applied to distantly related "*Allognathosuchus*."

INTRODUCTION

Like most modern crocodylians, the American alligator (*Alligator mississippiensis*) has a long, broad snout and is regarded as an ecological generalist, eating any animal matter it can swallow (Ross, 1998). But most Paleogene alligatorids from North America had relatively short snouts and large, blunt teeth toward the back of the maxilla and dentary. Many were probably small relative to their living relatives, perhaps not exceeding 1.5 meters in total body length. These animals are sometimes viewed as specialists for a durophagous diet (e.g., Abel, 1928; Carpenter and Lindsey, 1980). We cannot know if these animals were ecological specialists, but the morphology of the skull suggests a difference in feeding behavior from modern *Alligator*.

Recent phylogenetic analyses suggest a complicated evolutionary history for Alligatoridae. Most pre-cladistic studies clustered the presumably specialized short-snouted fossils together, sharing a common ancestor with modern alligators, but not ancestral to them (e.g., Case, 1925; Simpson, 1930; Kälin, 1936; Mook, 1941). But recent analyses do not support such groups—rather, some of these specialists may be more closely related to extant *Alligator* than to other blunt-snouted fossil taxa (Wu et al., 1996; Williamson, 1996; Brochu, 1997; Fig. 1). The most common name applied to these animals, *Allognathosuchus*, may itself be paraphyletic as used in the literature; and fossil European alligatorids do not form a clade (Brochu, 1999). The characters thought to be derived specializations in some taxa may actually diagnose more inclusive clades within Alligatoroidea.

This pattern has several implications. First, these analyses imply multiple dispersal events from North America to Eurasia during the Cretaceous and Cenozoic (Buscalioni et al., 1997; Brochu, 1999), and so these alligatorids may prove important for studies of vertebrate paleobiogeography during the Paleogene. Second, the nesting of *Alligator* within clades of ancestrally blunt-snouted alligatorids with crushing teeth suggests that the generalized morphology of extant *Alligator* is derived from a potentially more specialized morphology seen in extinct relatives (Clark and Norell, 1992; Brochu, 2001). This lies in apparent contradiction of the commonly-held assumption that specialized morphologies or ecologies are derived from generalized ancestors, but not vice versa—the so-called "Law of the Unspecialized" (Cope, 1896).

Unfortunately, we are still faced with a taxonomic and phylogenetic quagmire. These small alligatorids are all very similar to each other, and the characters used to distinguish one species from another can be very subtle. This is especially problematic given the fragmentary nature of some of the holotypes. Various authors have drawn conflicting conclusions over the number of known valid taxa. The recent phylogenetic analyses have been challenged on methodological and morphological grounds, and whether *Allognathosuchus* can be treated as a clade is debated (e.g., Lucas and Estep, 2000).

This paper revisits the relationships among basal alligatorids, with emphasis on alligatorines (*Alligator mississippiensis* and crocodylians closer to it than to *Caiman crocodilus*), *Allognathosuchus*, and patterns of snout shape evolution within the group. It is conducted in light of recent alligatorid phylogenetic analyses (e.g., Wu et al., 1996; Brochu, 1997, 1999) and criticisms of the characters and nomenclatural philosophy used in these studies (Lucas and Estep, 2000; Sullivan and Lucas, 2003). The analysis is based primarily on a reconsideration of a matrix used in earlier studies by this author, with revisions made necessary by new information and restudy of material considered previously.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **CM**, Carnegie Museum of Natural History, Pittsburgh; **FMNH**, Field Museum, Chicago; **HLMD**, Hessisches Landesmuseum, Darmstadt, Germany; **IRSNB**, Institut Royal des Sciences Naturelles de Belgique, Brussels; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, MA; **MNHN**, Museum National d'Histoire Naturelle, Paris; **RTMP**, Royal Tyrell Museum of Palaeontology, Drumheller, Alberta; **SDSM**, South Dakota School of Mines and Technology, Rapid City; **SMM**, Science Museum of Minnesota, St. Paul; **SUI**, University of Iowa, Iowa City; **TMM**, Texas Memorial Museum, University of Texas at Austin; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor; **USNM**, United States National Museum, Smithsonian Institution, Washington, DC; **YPM-PU**, Yale Peabody Museum-Princeton University collection, New Haven.

PREVIOUS PHYLOGENETIC WORK

Initial Considerations

Fossil alligatoroids with unusual back teeth have been known since Harlan (1824) described what we now call *Bottosaurus har-*
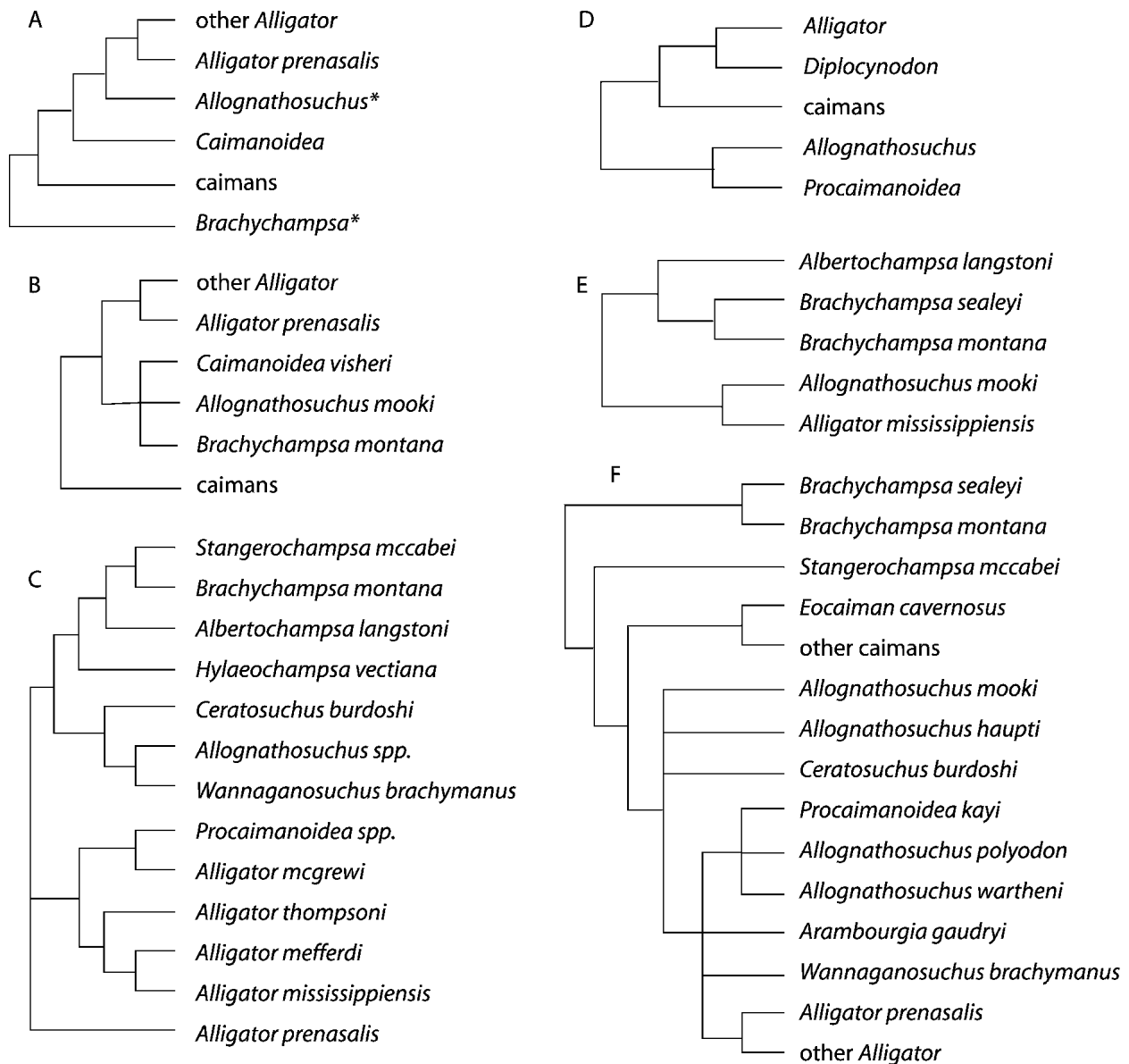
FIGURE 1. Different expressions of evolutionary relationships among fossil alligatorids. **A**, Mook, 1932. **B**, Kälin, 1936. **C**, Wu et al., 1996. **D**, Mook, 1941. **E**, Williamson, 1997. **F**, Brochu, 1999.

lani in the Late Cretaceous greensands of New Jersey. Fossil crocodyliforms were nothing new in 1824, but the specimen described by Harlan—a partial dentary with three in-place teeth—struck him as unusual. The dentary itself was stout and nearly cylindrical in cross-section, and the caudal interdental plates were very thin. Most importantly, the teeth were "exceedingly short, thick, and blunt" compared with those of modern crocodylians (Harlan, 1824:21). Harlan thought the shape of the dentary and teeth indicated an ability to crush mollusk prey—an interpretation that was widely accepted (and even amplified) by later workers (e.g., Case, 1925; Abel, 1928; Kälin, 1933, 1936, 1939; Carpenter and Lindsey, 1980).

Whether these forms are truly specialized in an ecological sense remains unknown. Indeed, the functional significance of the modified skull and dental morphology in these animals remains debated. Abel (1928) and Carpenter and Lindsey (1980) suggested that the robust mandibular rami, dentary symphysis, and teeth of *Allognathosuchus* and *Brachychampsa* were modi-

fications for crushing turtle shells. Aoki (1989) emphasized the elevated position of the jaw joint relative to the rest of the skull, concluding that it allowed a certain amount of grinding motion for the rear dentition. Other authors have expressed skepticism about the alleged dietary specializations of these animals (e.g., Bartels, 1984; Sullivan and Lucas, 2003).

Although phylogenetic hypotheses were not always clearly stated in the older literature, some authors argued that these presumably durophagous forms were somehow closely related to each other and represented some sort of "side branch" derived from a common generalized ancestor with modern alligators and caimans. This is characteristic of the ideas expressed by Kälin (1936; Fig. 1B), and although Mook (1932; Fig. 1A) initially implied a direct ancestor-descendant relationship between *Allognathosuchus* and *Alligator*, he later figured a phylogeny in which blunt-snouted alligatorids (*Allognathosuchus*, *Procaimanoidea*) were separated from the more generalized forms (Mook, 1941; Fig. 1D).

The work of Simpson (1930) provides an important exception, but his exception demonstrates the rule. He argued that Cretaceous *Brachychampsa* and Tertiary *Allognathosuchus* acquired their similarities independently because of perceived differences between the two and the amount of time separating them. But he expressed confusion when comparing *Allognathosuchus* with Oligocene *Alligator prenasalis* (*Caimanoidea visheri* in his usage—see below); *A. prenasalis* looked less specialized than *Allognathosuchus mooki*, but occurred later in time. He stated, "were *Caimanoidea* the earlier genus, one might suppose it approximately ancestral, for many of its peculiarities resemble those of *Allognathosuchus* but are less extreme" (Simpson, 1930: 9). He entertained the possibility of convergence (a conclusion he drew for the similarities between *Allognathosuchus* and *Brachychampsa*), but felt the similarities were close enough to suggest common ancestry. But although reversal was not strictly ruled out, Simpson (1930:11) felt that "a more tenable hypothesis would derive the more specialized and more quickly extinct *Allognathosuchus* line and the rather more conservative and tenacious *Caimanoidea* line from a common ancestry."

His argument amounts to an invokation of what Cope (1896) called the "Law of the Unspecialized"—the idea that specialists evolve from generalists, but because lineages that had acquired "specialized" or "adaptive" features would not revert to the ancestral (generalized) condition, generalists could not evolve from specialists. Modern discussions of specialization focus on ecology, which is unknown for fossil crocodylians, but this "law" has been a commonly-accepted theme throughout 20th century evolutionary thought, whether explicitly stated or not (e.g., Futuyma and Moreno, 1988).

Thus, to Simpson, the specializations seen in *Allognathosuchus* could be derived multiple times independently (as he thought was the case for *Allognathosuchus* and *Brachychampsa*), but complete reversals were viewed much more skeptically. Paleocene *Allognathosuchus mooki* was "more specialized" than Late Eocene or Oligocene *Alligator prenasalis*, arguing against an ancestor-descendant relationship and suggesting instead that the last common ancestor of *Allognathosuchus* and *Alligator* lacked the derived features of *Allognathosuchus*. A similar arrangement was implied by Kälin (1936), in which the more and less specialized groups both arose in the Cretaceous, with long range extensions for the less-specialized forms of the later Tertiary.

In this context, the alligatorids from the White River Group of South Dakota were a source of confusion, because they seemed to lie morphologically between the highly derived Eocene forms and comparatively generalized modern *Alligator*. Some authors took this at face value and thought the White River alligatorids to be intermediate evolutionarily as well as morphologically (e.g., Patterson, 1931; Mook, 1932), but Simpson (1930) found this troubling, largely because of the implied polarity of snout shape. Still others accepted different phylogenetic relationships for different named entities from the White River group—hence, *Alligator prenasalis* would be closer to *Alligator* and *Caimanoidea visheri* closer to *Allognathosuchus* (e.g., Kälin, 1936). At present, only a single species is recognized from the White River Group—*Alligator prenasalis* (Higgins, 1972; Malone, 1979), but it is telling that incomplete specimens formed the basis of different species thought to be somehow closer to the blunt-snouted assemblage than to living species of *Alligator* (Mehl, 1916; Patterson, 1931).

Parsimony-Based Work

The earliest comprehensive cladistic study of fossil and recent alligatorids was that of Wu et al. (1996). Their results were broadly congruent with the suspicions expressed by Kälin and Mook—alligatoroids from the Cretaceous (*Stangerochampsa*,

Albertochampsa, *Brachychampsa*) and the Paleocene or Eocene (*Ceratosuchus*, *Allognathosuchus*, *Wannaganosuchus*) formed subclades within a monophyletic blunt-snouted group (Fig. 1C). A close relationship between *Albertochampsa* and *Brachychampsa* had also been proposed previously (e.g., Norell et al., 1994). *Alligator*, as used in the literature, was not monophyletic—*Alligator mcgrewi* was closer to *Procaimanoidea*, and *A. prenasalis* was either the sister taxon of the blunt-snouted assemblage or of the group including *Procaimanoidea* and other *Alligator*.

An analysis by Williamson (1996; Fig. 1E) included fewer ingroup taxa, but some of his results were congruent with those of Wu et al. (1996). Alligatorids formed a monophyletic group, and there was a clade exclusively including *Brachychampsa* and *Albertochampsa*. But Williamson's analysis argued for a closer relationship between *Allognathosuchus mooki* and *Alligator mississippiensis*.

The most comprehensive phylogenetic analysis of basal alligatorids to date is that of Brochu (1997, 1999; Fig. 1F). At the root of Alligatorinae in these studies was a polytomy including *Allognathosuchus mooki*, *A. haupti*, *Ceratosuchus burdoshi*, and a clade including *Procaimanoidea*, *Alligator*, *Arambourgia*, *Wannaganosuchus*, and two other species of *Allognathosuchus* (*A. polyodon*, *A. wartheni*). *Alligator* was monophyletic including *A. prenasalis*, but *Allognathosuchus*—represented by only one terminal in previous analyses—was not.

All three analyses agree on one point—species of *Alligator* with long, flat, modern-looking snouts are nested within clades including blunt-snouted forms. The Wu et al. analysis comes closest to approximating pre-cladistic concepts in that the blunt-snouted forms with enlarged back teeth are clustered together. *Procaimanoidea* has a short, but dorsoventrally deep, snout resembling that of extant *Paleosuchus*; and *Alligator mcgrewi*'s snout is rather *Allognathosuchus*-like in dorsal outline (Fig. 2), but both taxa lack enlarged posterior alveoli on the dentary or maxilla. Williamson's and Brochu's analyses placed *Allognathosuchus mooki* closer to *Alligator* than to *Brachychampsa*. Indeed, in Brochu's analyses, *Brachychampsa* and *Stangerochampsa* fell outside the crown-group Alligatoridae. A stem-based group name, Globidonta, was erected to include *Alligator mississippiensis* and forms closer to it than to *Diplocynodon*, and all basal lineages within this group are blunt-snouted animals with enlarged dentition.

INGROUP SAMPLING—*ALLOGNATHOSUCHUS*, *CHRYSOCHAMPSA*, AND *WANNAGANOSUCHUS*

Brochu's analyses argued not only for nonmonophyly of the blunt-snouted alligatorids, but of *Allognathosuchus*. This was criticized by Lucas and Estep (2000), who challenged some of the character codings and questioned the philosophical basis for concluding that the taxon as used in the literature was paraphyletic. They also disputed Brochu's acceptance of *Wannaganosuchus brachymanus* Erickson 1982 as a valid species.

A separate discussion of this controversy is warranted because it impinges on the ingroup taxa used in this study. Furthermore, *Allognathosuchus* is an important name in the literature, and we need a clarified meaning for it to be anything more than an opinion.

Allognathosuchus

Allognathosuchus was originally based on fossils from the Eocene of Wyoming (Mook, 1921), but has since been applied to Late Cretaceous through Oligocene material from North and South America, Eurasia, and Africa (e.g., Dorr, 1952; Berg, 1966; Wassersug and Hecht, 1967; Estes, 1975; Godinot, et al., 1978; Estes and Hutchison, 1980; Groessens-Van Dyck, 1986; West-
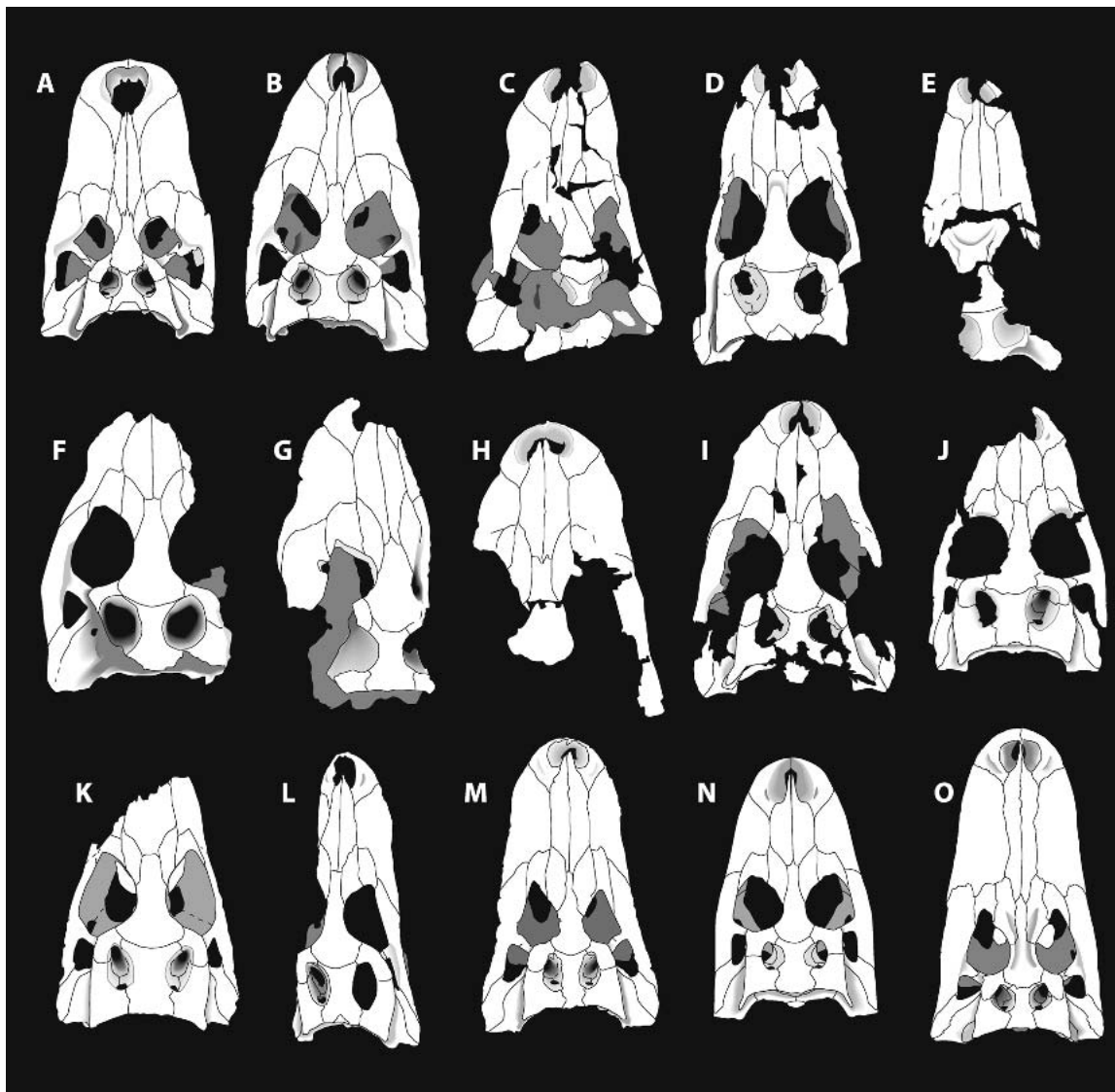
FIGURE 2.   Skulls of fossil and living globidontan alligatoroids, dorsal view, with sutural boundaries indicated. **A**, UCMP 133901, *Brachychampsa montana*; **B**, RTMP 86.61.1, holotype, *Stangerochampsa mccabei*; **C**, AMNH 6780, holotype, *Allognathosuchus mooki*; **D**, MCZ 8381, cf. *Allognathosuchus mooki*; **E**, AMNH 5186, holotype, *Navajosuchus novomexicanus*; **F**, HLMD 4415, holotype, *Allognathosuchus haupti*; **G**, YPM-PU 16989, Willwood alligatorid (identified as *Allognathosuchus wartheni* in Brochu, 1999); **H**, AMNH 6049, *Allognathosuchus polyodon*; **I**, SMM p.76.28.247, holotype, *Wannaganosuchus brachymanus*; **J**, MNHN QU17155, holotype, *Arambourgia gaudryi*; **K**, CM 9600, holotype, *Procaimanoidea kayi*; **L**, USNM 15996, holotype, *Procaimanoidea utahensis*; **M**, SDSM 243, *Alligator prenasalis*; **N**, *Alligator mcgrewi*, composite reconstruction based on the holotype (FMNH p26242) and AMNH 7905; **O**, TMM m-7487, *Alligator mississippiensis*.

gate, 1989; Rauhe, 1990, 1995; Pascual and Ortiz Jaureguizar, 1991; Lucas, 1992; Gallagher, 1993; Rauhe and Rossmann, 1995; Cifelli, et al., 1999; Lillegraven and Eberle, 1999; Zonneveld, et al., 2000; Rossmann, et al., 2000; Kotsakis et al., 2000; Rana and Sati, 2000). As of this writing, fifteen species have been referred to *Allognathosuchus* by different authors (Table 1). Bartels (1988) accepted five and mentioned three additional undescribed species, but other authors accept fewer (e.g., Lucas and Estep, 2000). Some referrals are based on relatively complete and well-preserved material, others on considerably less.

Many literature references to *Allognathosuchus* pertain to isolated bulbous teeth. That the posterior dentary and maxillary teeth of *Allognathosuchus* bear rounded crowns was regarded as a diagnostic feature for the taxon by Mook (1921), and to this day the name *Allognathosuchus* is frequently treated as a formtaxon for these teeth when found in the field, especially in Pa-

leogene deposits. The problem is that teeth like this occur in several crocodyliform lineages (Buffetaut, 1975; Buffetaut and Ford, 1979; Aoki, 1989; Brinkmann, 1992; Eaton, et al., 1997, 1999), and they may not be distinguishable from those referred to *Allognathosuchus* (Hutchinson and Kues, 1985).

Type Species—Cope (1873:614) first recognized *Diplocynodus* (= *Diplocynodon*) *polyodon* on the basis of "portions of cranium and teeth, with probably some vertebrae found close to them." The "cranium" (now catalogued as USNM 4112) consists of a partial left mandibular ramus (Fig. 3). His description noted that the splenials met at the midline and that a series of eight or nine very small alveoli separated the anteriormost large alveolus (presumably the fourth) and another large alveolus in the middle of the toothrow. He later reassigned *D. polyodon* to *Crocodilus* on the recognition that the double dentary canines characteristic of *Diplocynodon* could not be observed (Cope, 1884).

TABLE 1.   List of fossil alligatorids previously referred to *Allognathosuchus*. Notes: 1, Rauhe (1990) synonymized *Arambourgia gaudryi* with *Allognathosuchus haupti*; 2, *Allognathosuchus mooki* includes *Navajosuchus novomexicanus*; 3, *A. riggsi* is now regarded as a junior synonym of *Alligator prenasalis*; 4, Rauhe (1995) regards *E. weigelti* and *C. brevirostris* as synonymous. Asterisks denote taxa based on material not viewed by this author and not considered in the present study.

Taxon	Referral to *Allognathosuchus*
Crocodilus polyodon Cope, 1872	Mook, 1921
Alligator heterodon Cope, 1872	Mook, 1921
Alligator prenasalis (Loomis, 1904)	Bartels, 1988
Arambourgia gaudryi (de Stefano, 1905)	Rauhe, 1990[1]
Allognathosuchus wartheni Case, 1925	Case, 1925
Allognathosuchus mooki Simpson, 1930[2]	Simpson, 1930
Allognathosuchus riggsi Patterson, 1931[3]	Patterson, 1931
Hassiacosuchus haupti Weitzel, 1935	Berg, 1966
Caimanosuchus brevirostris Kuhn, 1938	Rauhe, 1995
Eocenosuchus weigelti Kuhn, 1938[4]	Rauhe, 1995
Albertochampsa langstoni Erickson, 1972	Lucas, 1992
Wannaganosuchus brachymanus Erickson, 1982	Sullivan et al., 1988
Allognathosuchus woutersi Buffetaut, 1985	Buffetaut, 1985
Chrysochampsa mlynarskii Estes, 1988	Lucas and Sullivan, 2003
Allognathosuchus gracilis Rauhe and Rossmann, 1995	Rauhe and Rossmann, 1995

When figured by Cope (1884:plate 23a; Fig. 3A,B), the type jaw comprised two parts: a left dentary lacking the anteriormost tip and anything behind the toothrow; and the left postdentary bones. These had been cemented together before Mook (1921) redescribed them, and in the plate in Mook's description, the plaster was white and easily distinguishable from the bone. This plaster has since been tinted and is nearly the same color as the bone; in Figure 3C, I digitally darkened the plaster to make it distinguishable. The original pieces may not have fit together as reconstructed; indeed, we cannot know if they belonged to the same individual in the first place.

Mook (1921) stated that the dentary bears a "superior process" toward the rear of the toothrow, with the posteriormost alveoli elevated dorsally above the level of the small fifth through twelfth alveoli (assuming that the anteriormost large alveolus preserved is the fourth). The fifth through twelfth alveoli thus lie within a deep concavity on the dentary's dorsal surface. Most crocodylian dentaries are depressed in this general region of the toothrow, but the depth of the depression is much greater in *Allognathosuchus polyodon* (and in most other taxa referred to *Allognathosuchus*). This feature was coded in the phylogenetic analysis of Brochu (1997, 1999; character 68), but the character was based on the depression, not the posterior dorsal expansion noted by Mook.

Mook noticed that the dentary alveoli are very close together, with very thin interalveolar walls. Had this taxon been referable to *Crocodylus*, he reasoned, the teeth should have been spaced further apart. He also noticed that the posterior alveoli are very large in diameter, and that the alveoli within the dentary depression are *much* smaller than the fourth alveolus. Ironically, the bulbous teeth considered so characteristic of *Allognathosuchus* are not preserved in this specimen.

Mook (1961) later referred a partial skull and jaw (AMNH 6049; Fig. 2H) to *A. polyodon*. This specimen was not associated with the type jaw—indeed, the specimens may not derive from the same locality. The features used to make the referral to *A. polyodon* were never specified. The characters most diagnostic of the *A. polyodon* jaw—the "superior process" and small, closely spaced array of alveoli—cannot be seen on this specimen because the jaw is firmly attached to the skull. Mook's description of *A. heterodon* (see below) included cranial material, and by 1961 some European Eocene alligatorids (with cranial mate-

rial known) were referred to *Allognathosuchus*. His reasoning may thus have been partly stratigraphic—AMNH 6049 could be referred to *Allognathosuchus*, and the only named species of *Allognathosuchus* from the Bridger Formation was *A. polyodon*.

The other species referred to *Allognathosuchus* by Mook (1921) was originally described as *Alligator heterodon* by Cope (1872) on the basis of a disarticulated skull and jaw, along with various postcranial elements. The specimen is currently catalogued as USNM 4115 and is from the Wasatch Formation of Wyoming. The figure published by Cope (1884; Fig. 4P,Q) shows a deceptively complete specimen; the preserved fragments do not articulate (Fig. 4A–O), and the shape of the skull as restored by Cope is pure speculation.

Mook's description of *Allognathosuchus heterodon* was based on additional Wasatchian material in the AMNH collections beyond the type described by Cope. There are several complete skulls and jaws in the AMNH and USNM collections, but most are coated in hematite, and little can be said about them aside from the general shape of the skull and the presence of enlarged, spherical teeth at the back of the maxillary and dentary toothrows. Cranial sutures can be traced in a few of them. The features listed in the "summary of specific characters" either occur in *A. polyodon* (e.g. seven or eight small alveoli in front of superior process) or are cranial or dental characters unknown in *A. polyodon*.

Other Species—The validity of *Allognathosuchus mooki* is not disputed. *Allognathosuchus mooki* is based on a nearly complete skeleton and skull from the Puerco Formation of New Mexico, and specimens from the overlying Torrejon Formation (including the type of *Navajosuchus novomexicanus*) have subsequently been referred to this taxon (Sullivan, et al., 1988; Lucas, 1992). Codings herein are based on all of this material, as discussed in Brochu (1999).

Allognathosuchus haupti is based on a well-preserved skull from Messel (Weitzel, 1935; Berg, 1966), with several additional skeletons subsequently collected. Well-preserved material from correlative beds in Geiseltal (Kuhn, 1938; Rauhe, 1995) is very similar and might pertain to this species, but it was not involved in codings for this analysis.

Allognathosuchus wartheni is a problem. The type, from the Wasatchian Willwood Formation, is fragmentary (Case, 1925) and, as pointed out by Lucas (1992) and Lucas and Estep (2000), cannot be readily distinguished from other species assigned to *Allognathosuchus*. But small alligatorids are abundant in the Willwood Formation (Bartels, 1983; Fig. 2G), and extensive collections are held in the UMMP and YPM-PU. Bartels (1983) and Brochu (1997, 1999) applied the name *A. wartheni* to that assemblage, and catalogue numbers for the specimens involved were listed in Appendix 1 of Brochu (1999; *contra* Lucas and Estep, 2000). However, I acknowledge that "Willwood alligatorid" might have been a more appropriate term.

Brochu (1997, 1999) explicitly assumed that these specimens represent a single taxon. Bartels (1980, 1988) has argued that at least two species are involved. The differences were not apparent to this author, but more detailed study of this material, including morphometric analysis, may reveal multiple species. Until this is done, I continue to treat it as a single taxon.

Allognathosuchus woutersi is based on incomplete material from the Early Eocene of Belgium (Buffetaut, 1985) and was viewed as a primitive member of the genus. The rear teeth are not as large relative to those in front of them as in *A. polyodon* or *A. mooki*, and although the alveolar diameter patterns are somewhat different (Buffetaut, 1985), the holotype dentary shows similarities to a more complete *Diplocynodon* dentary from the same locality, especially in the geometry of the splenial attachment scar and lateral outline of the bone. Because of its incompleteness, *A. woutersi* was not included in this phylogenetic analysis.
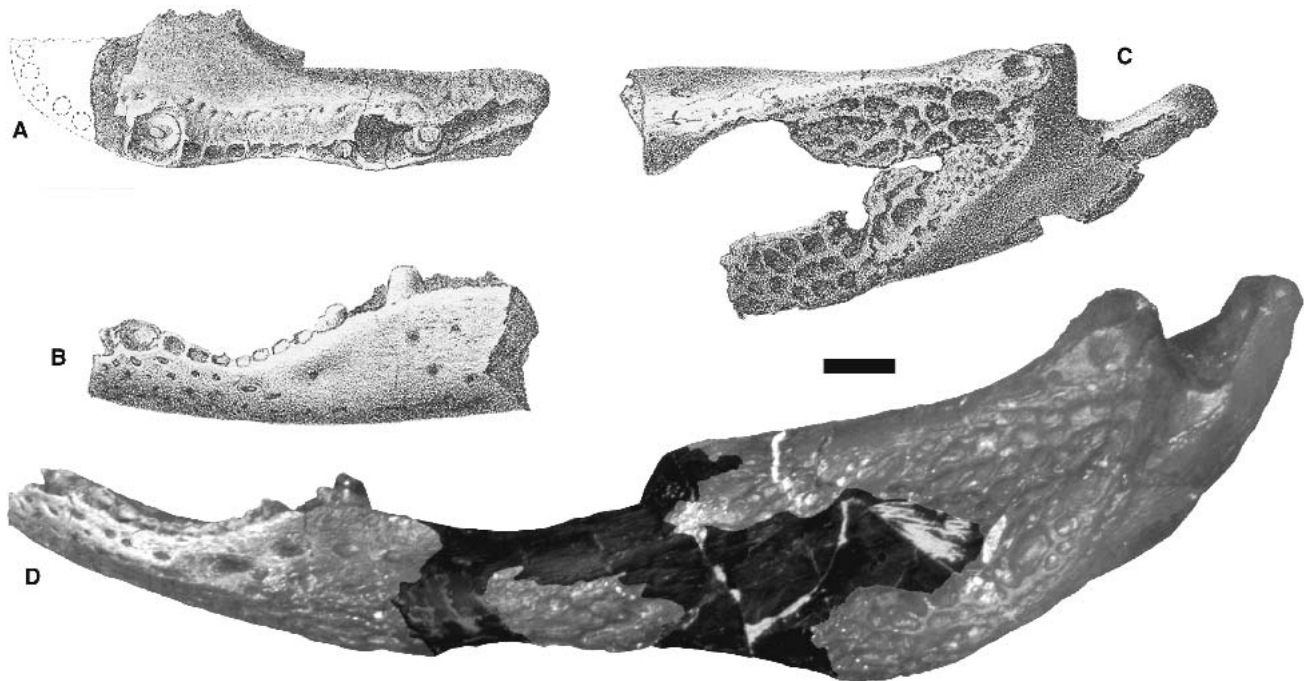
FIGURE 3. USNM 4112, holotype, *Allognathosuchus polyodon* (Cope, 1873). **A**, **B**, **C**, specimen as originally figured by Cope (1884:plate 23). **D**, lateral view. Scale equals 1 cm.

Summary—This analysis continues to use four ingroup taxa with the name *Allognathosuchus*—*A. mooki*, *A. haupti*, Willwood alligatorid, and *A. polyodon*. The Willwood form is virtually identical to specimens from the Wasatch Formation possibly referable to *A. heterodon*, suggesting that a single Clarkforkian through Bridgerian assemblage can be recognized, but the Bridgerian material is kept separate here.

Whether *A. polyodon* and *A. heterodon* can be distinguished from each other is an open question. Bartels (1983:369) called them the "ill-defined *Allognathosuchus heterodonpolyodon* complex," and stated that the quality of description prevented assignment of Early Eocene fossils to either taxon. The quality of the types may be a greater limitation. The available material simply does not allow us to distinguish them—anatomical overlap is minimal, and where homologous elements are preserved, they are virtually identical. The same is true if AMNH 6049 is included—systematic differences with any of the skulls from the Wasatch Formation cannot be identified. Indeed, the type material may not allow us to distinguish *A. polyodon* or *A. heterodon* from many other Paleogene alligatorids. *Allognathosuchus polyodon* and *A. mooki* can be separated if AMNH 6049 is accepted as an *A. polyodon* skull, but if we only consider type material, this is not the case.

Chrysochampsa

Lucas and Sullivan (2003) referred *Chrysochampsa mlynarskii* Estes 1988, based on a poorly preserved skull and associated osteoderms from the Wasatchian of North Dakota, to *Allognathosuchus*. They further argued that it might be synonymous with *A. mooki*. This would extend the stratigraphic range of *A. mooki* from the base of the Paleocene into the Eocene.

The skull is dorsoventrally crushed, and few sutures can be traced with certainty. It was placed on a phylogenetic diagram by Brochu (2003:368) based on its stratigraphic and geographic position, and this author is no longer confident of this arrangement.

It was not included in the parsimony analysis presented below. As such, although this author strongly suspects *Chrysochampsa* is not a junior synonym of *Allognathosuchus*, this study does not address the question of *Chrysochampsa*'s relationships to other alligatoroids.

Nevertheless, the type of *Chrysochampsa mlynarskii* can be distinguished from all other Tertiary alligatoroids and clearly represents a distinct species. The dentary symphysis extends back only to the fourth dentary alveolus. It extends to or beyond the sixth alveolus in *Allognathosuchus mooki*, *A. polyodon*, and most other fossil alligatorines (see below). The splenial symphysis was either absent or extremely slight and, if the splenials contacted each other, they did so only dorsal to the Meckelian groove. In contrast, the splenial symphyses of all other Paleogene alligatorines are more robust with contact made dorsal and ventral to the Meckelian groove. The posterior premaxillary process is very slender and resembles those of *Brachychampsa* and *Stangerochampsa* (Norell et al., 1994; Fig. 5). The anterior end of the nasals on the specimen preserves the actual terminus of these bones, and they do not extend as far into the narial opening as in most other alligatorines, including *A. mooki* and *A. polyodon* (Estes, 1988). The shape of the skull and external naris (approximated from the distorted type) and anterior geometry of the splenial are similar to those of *Brachychampsa*, but unlike *Brachychampsa*, the largest maxillary alveolus of *C. mlynarskii* is the fourth.

Wannaganosuchus

Another controversial name is *Wannaganosuchus brachymanus* Erickson 1982 from the Tiffanian Tongue River Formation of North Dakota. Though known from one of the most complete Paleocene alligatorid skeletons ever collected, opinion on the status of this form varies—it was held to be a valid species by Wu et al. (1996) and Brochu (1997, 1999), although Brochu's analysis left open the possibility that *W. brachymanus* was a form of
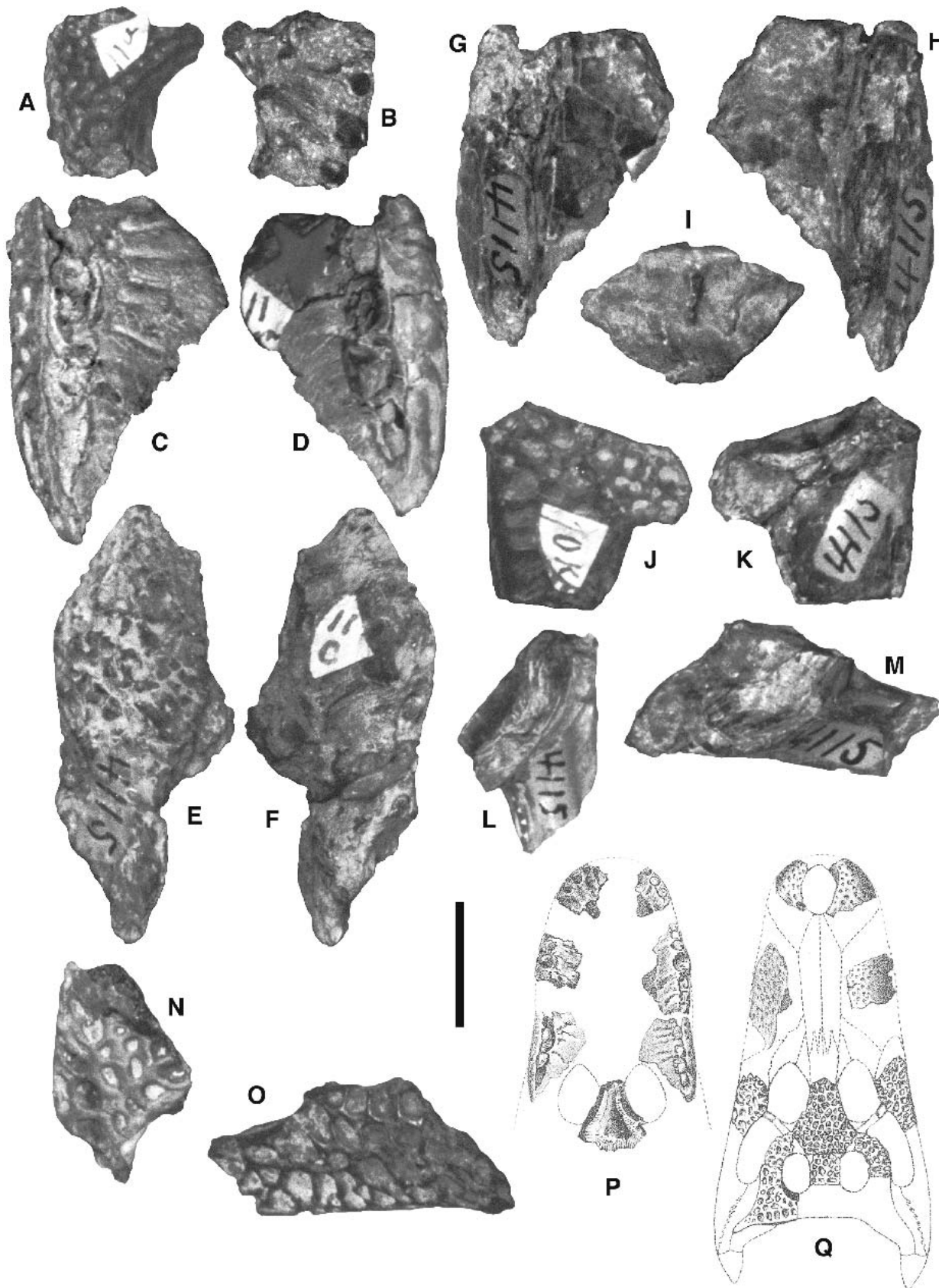
FIGURE 4. USNM 4115, holotype, *Allognathosuchus heterodon* (Cope, 1873). **A**, left premaxilla, dorsal view; **B**, left premaxilla, ventral view; **C**, Right posterior maxilla, ventral view; **D**, left posterior maxilla, ventral view; **E**, left anterior maxilla, dorsal view; **F**, right anterior maxilla, dorsal view; **G**, left posterior maxilla, dorsal view; **H**, right posterior maxilla, dorsal view; **I**, supraoccipital, posterior view; **J**, left squamosal, dorsal view; **K**, left squamosal, ventral view; **L**, left jugal, medial view (anterior up); **M**, right jugal, medial view (anterior left); **N**, left jugal, lateral view (anterior up); **O**, right jugal, lateral view (anterior right); **P**, reconstruction from Cope (1884, plate 23), ventral view; **Q**, reconstruction from Cope (1884, plate 23), dorsal view. Scale equals 1 cm.
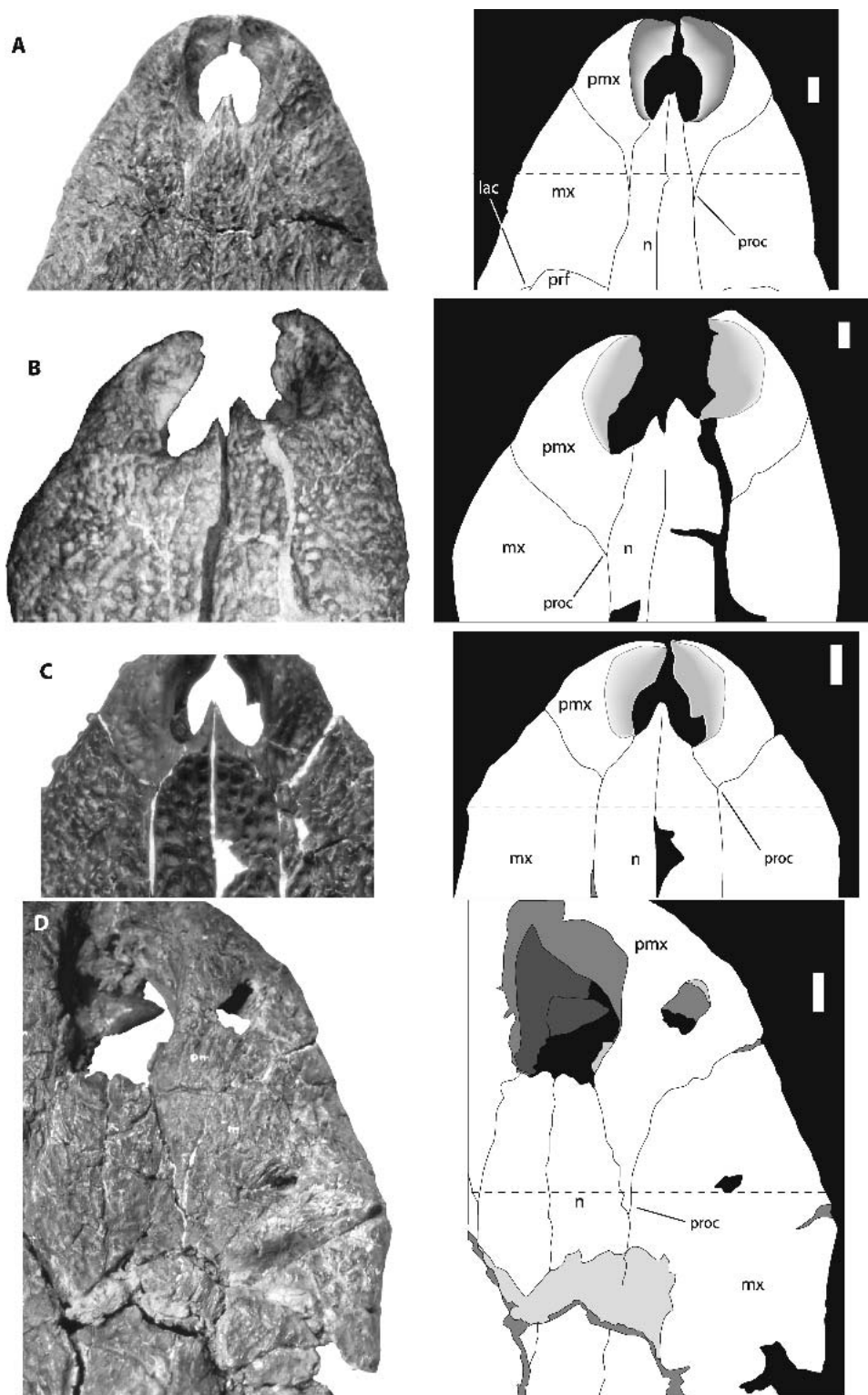
FIGURE 5.   Anterior end of skull in dorsal view showing extent of posterior premaxillary process (proc). Dashed line indicates position of third maxillary alveolus. **A**, RTMP 86.61.1, holotype, *Stangerochampsa mccabei*. **B**, AMNH 6780, holotype, *Allognathosuchus mooki*. **C**, SMM p.76.28.247, holotype, *Wannaganosuchus brachymanus*. **D**, YPM-PU 17258, holotype, *Chrysochampsa mlynarskii*. **Abbreviations**: **lac**, lacrimal; **mx**, maxilla; **n**, nasal; **pmx**, premaxilla; **prf**, prefrontal. Scale equals 1 cm.

Allognathosuchus. Bartels (1988) regarded *W. brachymanus* as a junior synonym of *Allognathosuchus wartheni*. Others consider *W. brachymanus* to be an immature specimen of *Allognathosuchus mooki* (Sullivan et al., 1988; Lucas, 1992; Lucas and Estep, 2000). This section briefly reviews the evidence that *W. brachymanus* can be distinguished from other Tertiary alligatorids (in particular, *Allognathosuchus mooki* and the Willwood alligatorid), at least at the specific level.

Osteoderms—Lucas and Estep (2000) stated that they could find no difference in the shape of the osteoderms between *A. mooki* and other related forms, including *Wannaganosuchus* and *Stangerochampsa*. But if one compares *homologous* osteoderms—i.e., osteoderms from the parasagittal rows of the dorsal shield and from the same region of the back—differences can clearly be seen. The midline dorsals are rectangular in *A. mooki* but square in *W. brachymanus* (Erickson, 1982; Fig. 6).

Incisive Foramen—The relative size of the incisive foramen was viewed as a difference between *A. mooki* and *W. brachymanus* by Brochu (1999); it was coded as large in *A. mooki* and small in *W. brachymanus*. Lucas and Estep (2000) argued for a small incisive foramen in *A. mooki*, but although the reconstruction figured by Lucas and Estep (2000:158) suggests a small foramen, the skull photo and drawing they figured (2000:156, 157) reveal a much larger feature. The premaxillae of the holotypes of *A. mooki* and N. *novomexicanus* are both damaged and open to multiple interpretations, but the *A. mooki* type strongly suggests a large foramen. This is also indicated by more complete specimens (e.g., MCZ 8381). I thus stand by my original coding of the incisive foramen of *A. mooki* as large, in contrast with the smaller incisive foramen of *W. brachymanus*.

Anterior Extent of the Lacrimal and Prefrontal—In most crocodylians, the lacrimal's anterior limit is anterior to that of the prefrontal. In derived alligatorines, the reverse is true. Although the lengths of these bones can vary within modern species (especially with respect to ontogeny), the relationship between anterior limits is invariant—the prefrontal extends further anteriorly in *Alligator mississippiensis* throughout posthatching ontogeny, and the reverse is true in all other living crocodylians at all stages. The lacrimal was coded as extending further anteriorly than the prefrontal in *A. mooki* and *A. haupti* in 1999, a feature separating these from other alligatorines (including *A. polyodon*, *A. wartheni,* and *W. brachymanus*).

Lucas and Estep (2000:155) argued that the lacrimals of the type specimen of *A. mooki* "are relatively small, trapezoidal bones in dorsal view" and that the lacrimal is shorter, not longer, than the prefrontal. In fact, the full shape of the lacrimals is not visible on either side. Only the lateralmost lacrimal margins are preserved. The anterior limit of the lacrimal can be compared with that of the prefrontal only on the right side, where the triple junction of prefrontal, nasal, and maxilla is visible. The right lacrimal's anterior limit itself cannot be seen, but the lateral margin between the lacrimal and maxilla clearly extends further forward than the prefrontal (Fig. 2C). The same is true for the left lacrimal; if one corrects for the posterior shift the left side of the skull underwent postmortem, the left lacrimal extends at least as far forward as its right counterpart. Closer examination reveals a similar relationship in Torrejonian specimens of *Navajosuchus* (e.g., Figs. 2D, 7C,D).

The left prefrontal is not preserved on the type of *W. brachymanus*, but the sutural surface against the nasal and lacrimal is;
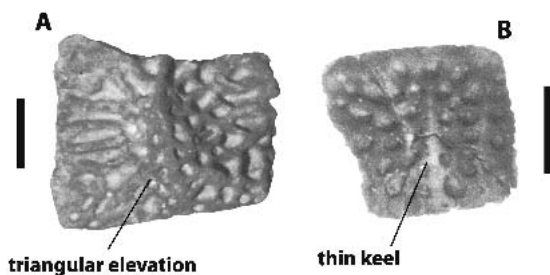
the lacrimal is missing on the right, but again the sutural surface can be seen on the margin of the maxilla (Fig. 7A,B). In both cases, the lacrimal does not extend forward of the prefrontal. The bones are nearly the same length anterior to the orbits, but the prefrontal is slightly longer.

I thus stand by my original coding of this feature and regard it as a phylogenetically informative feature and as a character distinguishing *W. brachymanus* from *A. mooki*.

Projection of the External Naris—In the analyses of Brochu (1997, 1999), *Wannaganosuchus* was coded as having an external naris projecting dorsally, while that of *A. mooki* was coded as projecting anterodorsally. Lucas and Estep (2000:187) state that they "detect no difference" between these forms.

In fact, the distinction is striking (Fig. 8). The premaxilla is wedge-shaped in lateral view in most living crocodylians, but the angle made between the planes of the dorsal and ventral surfaces is very low, and the external naris projects dorsally or very slightly anterodorsally throughout posthatching ontogeny. This is the condition found in *W. brachymanus* (Fig, 6B). But in some extinct forms, the premaxilla is strongly depressed around the lateral margin of the narial rim, and the external naris projects very strongly anterodorsally (Norell et al., 1994). This can be clearly seen in the type of *A. mooki* (Fig. 6A).

This can be a tricky character to code, as the projection of the naris in a fossil can depend both on the morphology of the undistorted premaxillae and the manner in which the snout is compressed. Simply holding a skull in lateral view and looking at the tip of the snout is not always the best way to characterize this feature, and in some specimens it cannot be reconstructed at all. In this case, both skulls have been dorsoventrally compressed but the shape of each premaxilla in lateral view is preserved.

Premaxillary Process—In most alligatoroids, the dorsal premaxillary processes—the wedges of premaxilla reaching posteriorly between the maxilla and nasal—extend no further back than the level of the second or third maxillary alveolus. This is true of *W. brachymanus* and of Eocene *Allognathosuchus*, but in *A. mooki* and *A. haupti*, they extend beyond this level and approach the level of the fourth alveolus. The same is true for *Brachychampsa*, *Stangerochampsa*, and *Chrysochampsa*, though in these forms the process is also very slender (Fig. 5). This was incorrectly coded in the 1999 matrix and has been corrected here.

Cranial Adornment—Many crocodylians bear subtle ridges on the dorsal surface of the snout. The "spectacle" seen in living caimans is a familiar example—the anteromedial surfaces of the prefrontals are sharply inset, producing a pair of U-shaped ridges that meet at the midline between the orbits. Most alligatoroids have this feature, but it was left uncoded by Brochu (1999) because although present in most living alligatorids, its expression is variable and its degree of prominence varies continuously between taxa.

Bartels (1983) characterized *Allognathosuchus* as having a smooth snout anterior to the orbits, with no spectacle present. This is true for Wasatchian and Bridgerian specimens, but *Wannaganosuchus* and *Allognathosuchus mooki* have modest spectacles. It is not easily visible in the type of *A. mooki* because of damage to that region of the skull, and this may have led Lucas and Estep (2000) to conclude that *A. mooki* has no spectacle. But other specimens (e.g., MCZ 8381) clearly show it. This characteristic serves to distinguish *W. brachymanus* from Wasatchian *Allognathosuchus*.

Summary—Several characters distinguish *W. brachymanus* from Puercan/Torrejonian "*Allognathosuchus*," including the relative lengths of the prefrontal and lacrimal, the shape of the mid-dorsal osteoderms, projection of the external naris, relative size of the incisive foramen, and length of the dorsal premaxillary process. We can further distinguish *W. brachymanus* from post-Tiffanian "*Allognathosuchus*" on the basis of the modest ros-

A

B

triangular elevation

thin keel

FIGURE 6. Dorsal midline osteoderms from (**A**) *Allognathosuchus mooki* (AMNH 6780) and (**B**) *Wannaganosuchus brachymanus* (SMM p.76.28.247). Scale equals 1 cm.
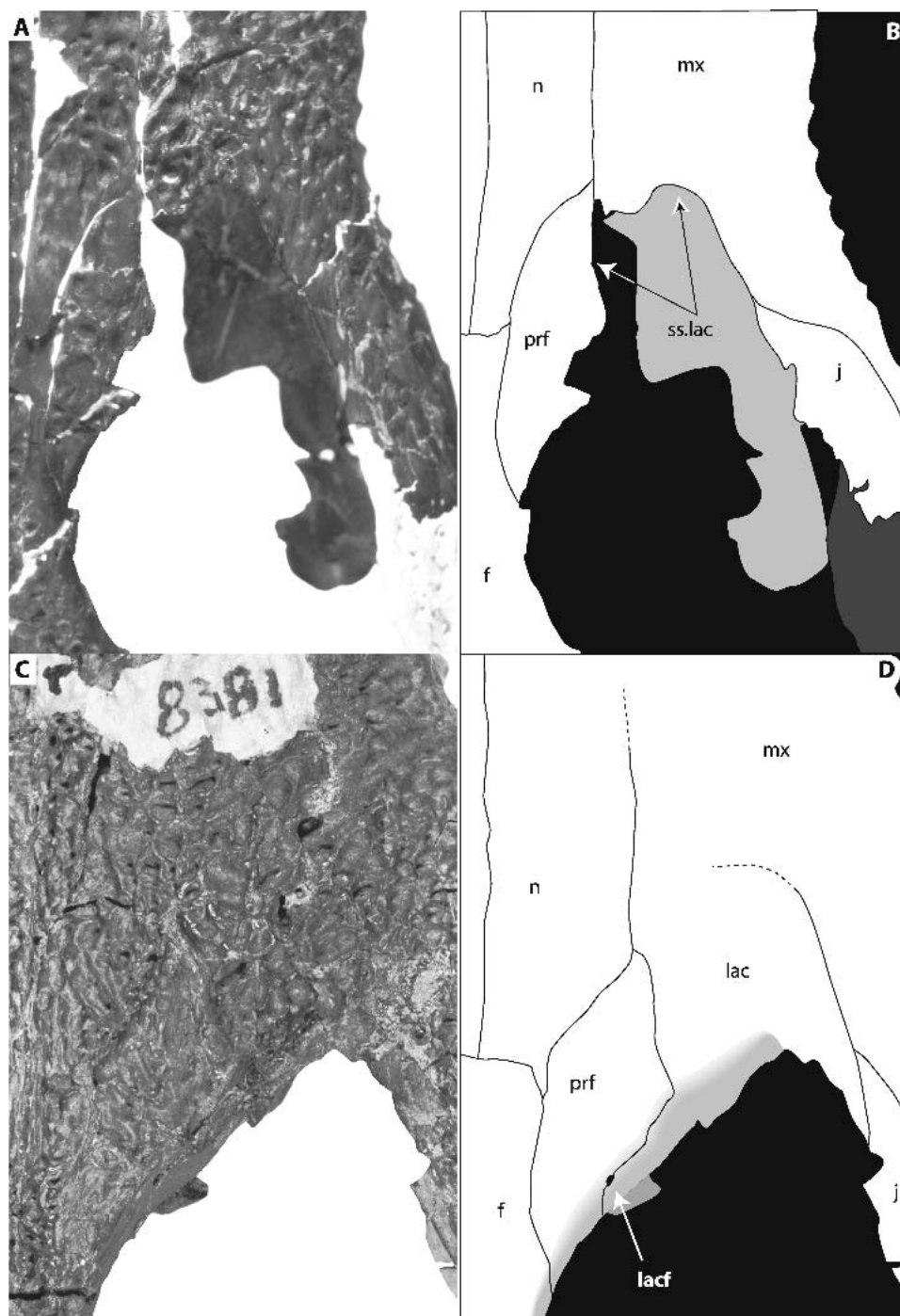
FIGURE 7.   Sutural relationships on dorsal snout surface anterior to right orbit in *Wannaganosuchus brachymanus* (SMM p.76.28.247, **A** and **B**) and *Allognathosuchus mooki* (MCZ 8381, **C** and **D**). **Abbreviations**: **f**, frontal; **j**, jugal; **lac**, lacrimal; **lacf**, lacrimal foramen; **mx**, maxilla; **n**, nasal; **prf**, prefrontal; **ss.lac**, sutural surface for lacrimal.

tral ornamentation in *W. brachymanus*. We can thus apply *W. brachymanus* as a separate terminal taxon in phylogenetic analysis.

PARSIMONY ANALYSIS

Matrix

Previous versions of the matrix used in this study were published in Brochu (1997, 1999). It originally involved 164 morpho-logical characters and 67 ingroup taxa, 34 of which were alliga-toroids. Three kinds of changes have been made—the addition of new taxa, the addition of new characters, and the recoding of previously-coded taxa. Revised codings are presented in Appen-dix 1.

Some changes were prompted by the inclusion of *Procaima-noidea utahensis* (Fig. 2L). Most notably, *P. utahensis* bears a notch on the premaxillary surface lateral to the external naris—a feature previously thought to diagnose *Alligator*. I had inad-
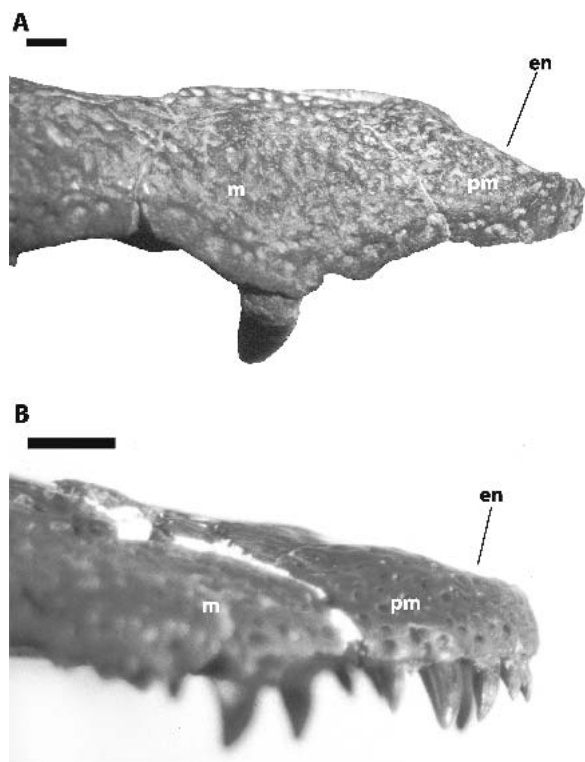
FIGURE 8. Anterior end of rostrum in lateral view; **A**, *Allognathosuchus mooki* (AMNH 6780), **B**, *Wannaganosuchus brachymanus* (SMM p.76.28.247). **Abbreviations**: en, external naris; **pm**, premaxilla; **m**, maxilla. Scale equals 1 cm.

vertently coded *P. kayi* as lacking this feature, but the premaxillae are not known in that form. Photographs I had taken of *Arambourgia gaudryi* suggested that this notch is absent (and the taxon was coded accordingly), but the plates published by Kälin (1939) show that *Arambourgia* also bears this notch.

Another newly-included taxon is *Hispanochampsa mülleri* from the Oligocene of Spain. Codings were based primarily on specimens in the Natural History Museum in London; the original description (Kälin, 1936) was also consulted, but the material I saw contradicted it in a few places. Inclusion of *H. mülleri* allows further testing of the biogeographic scenarios suggested previously (Brochu, 1999).

A third new taxon is *Albertochampsa langstoni* from the Campanian Dinosaur Park Formation of Alberta (Erickson, 1972). The type and only known specimen is a fragmentary skull, and its inclusion here allows us to test the assertion that *A. langstoni* is referable to *Allognathosuchus* (Lucas, 1992).

Lucas and Estep (2000) claimed that the surangular-dentary suture in *Allognathosuchus mooki* intersects the mandibular fenestra's margin dorsally, not anterodorsally as in most other crocodylians (and as coded in the previous matrices). A closer look at the type of *A. mooki* confirms this claim—evidently, dorsoventral compression of both mandibular rami generated cracks that misled me. The matrix has thus been recoded for this feature in *A. mooki*. I have also recoded *Ceratosuchus burdoshi*, as I am no longer convinced the suture can be seen.

Although not directly related to this particular study, the nature of the splenial symphysis in *Brachychampsa sealeyi* was recoded as unknown.

A recent study argued that *B. sealeyi* is based on an immature specimen of *B. montana* (Sullivan and Lucas, 2003). Differences between specimens of *B. sealeyi* and *B. montana* were dismissed as ontogenetic variation, individual variation, or of no taxonomic significance. But no evidence was presented that the differences lie within the known range of variation for any species, and there is no evidence that the type of *B. sealeyi* was immature at the time of death. Some of the differences between *B. sealeyi* and *B. montana* (e.g. orientation of the maxillary toothrow, even if corrections for postmortem distortion are made) lie outside the ranges of variation, ontogenetic or otherwise, for modern species beyond the earliest ontogenetic stages. Changes in toothrow orientation in modern crocodylians occur primarily in animals much smaller than any of the currently known specimens of *Brachychampsa*. *Brachychampsa sealeyi* can be distinguished from *B. montana* and is retained as an operational taxon.

A recent survey of the morphology of *Leidyosuchus canadensis* (Wu et al., 2001) indicated variation in the extent of the surangular on the retroarticular process. It was coded as not extending to the tip of the process in Brochu (1997, 1999; character 51), but Wu et al. (2001) suggested that the surangular approaches the tip in some specimens of *L. canadensis* and urged caution in coding this feature. The figure in their paper (Wu et al., 2001:fig. 5) clearly shows that the surangular does *not* reach the tip in either of the specimens, and there is no reason to recode *L. canadensis* as polymorphic in this regard.

Three new characters were added to this matrix, as discussed below:

165: Posterior maxillary alveoli round (0) or mediolaterally compressed (1). Most crocodylian alveoli are circular in outline, but they are strongly mediolaterally compressed and craniocaudally elongate in a few others, most notably the "ziphodont" pristichampsines and *Quinkana* (Langston, 1975; Willis and Mackness, 1996). Strongly compressed maxillary alveoli also occur in *Procaimanoidea*, *Arambourgia*, and *Hispanochampsa*, though they are restricted to the rear of the mouth. The teeth in these alligatoroids are not serrated.

166: Dentary symphysis extends to sixth through eighth dentary alveolus (0) or fourth or fifth alveolus (1). Actual length of the dentary symphysis can vary within living species, but the range of variation within extant species is limited to the extent of one or two alveoli—in *Alligator mississippiensis*, for example, the caudalmost extent of the symphysis can go no further than the fourth alveolus or as far as the fifth, but not outside that range. One can draw a distinction between most basal alligatoroids, in which the symphysis extends at least as far back as the sixth alveolus, and those with much shorter symphyses.

167: Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14, (1) 13 or 14 and a series behind it, or (2) 10, 11, or 12. In part, this character expresses the enlarged rear dentition of some fossil alligatorids. The general condition within Crocodylia is to have two regions of maximum alveolar diameter in the dentary—one around the fourth alveolus and another behind it. In *Alligator* and in basal alligatoroids (e.g. *Diplocynodon*, *Leidyosuchus*), the largest caudal alveoli are the thirteenth or fourteenth; in caimans, it is either the tenth, eleventh, or twelfth. The exact position of the largest alveolus varies within species, but it is never in front of the thirteenth in most taxa, and is never behind the twelfth in caimans. Behind these, alveoli grow progressively smaller. But in some blunt-snouted forms, there is a third region of maximum diameter behind the thirteenth or fourteenth alveolus (Fig. 9). This is where globular teeth erupt in those taxa bearing them—teeth erupting from the large thirteenth or fourteenth alveoli are still conical.

Analysis

This matrix was analyzed using PAUP* (ver. 4.0b8, Swofford, 2001), using a heuristic search algorithm and 100 of random addition sequence replicates. Multistate characters were treated as unordered. All alligatoroids in the previous matrix, along with
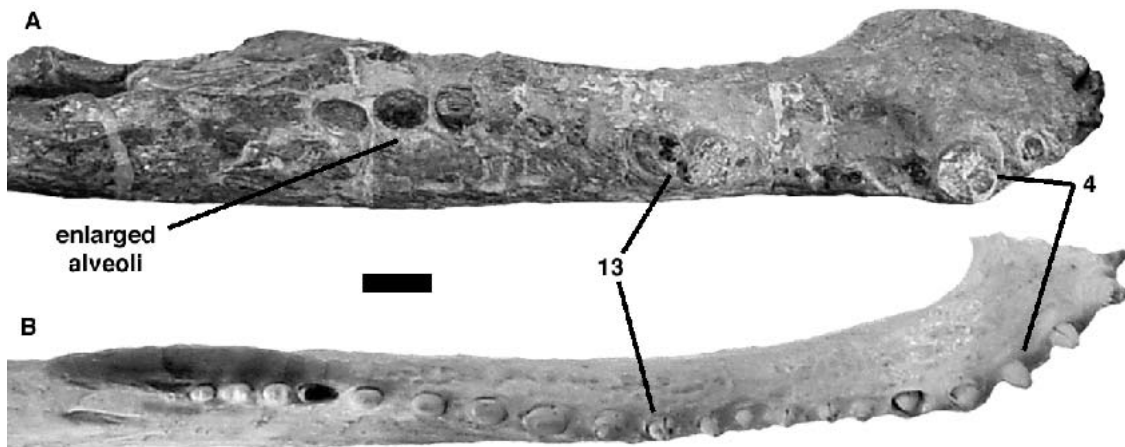
FIGURE 9.   Right dentaries of *Allognathosuchus mooki* (AMNH 6780, **A**) and *Alligator mississippiensis* (SUI uncatalogued, **B**), dorsal view. Numbers refer to alveoli. Scale equals 1 cm.

Procaimanoidea utahensis, Hispanochampsa mülleri, and *Albertochampsa langstoni* (37 ingroup taxa), were considered. These trees were rooted using *Borealosuchus sternbergii* and *Asiatosuchus germanicus* as sequential outgroups.

RESULTS

The parsimony analysis produced 297 equally optimal trees (length = 252, C.I. without autapomorphies = 0.547, R.I. = 0.800). All optimal trees were within a single parsimony island. A strict consensus of these trees is shown in Fig. 10, and a list of apomorphies is provided in Appendix II.

Overall lack of support for most nodes must be borne in mind. Few groups were supported by bootstrap analysis of 100,000 replicate data sets or are reflected in trees one step longer than optimal. Indeed, trees in which putative *Allognathosuchus* (*A. mooki, A. haupti, A. polyodon*, Willwood form) form a clade are only two steps longer, and inclusion of *W. brachymanus* in this cluster only increases length by three steps. Character support for some of the clades discussed below relies on homoplastic features, and optimizations are influenced as much by missing information as by known conditions.

The results are similar to previous analyses using this matrix in many respects—*Diplocynodon* and *Baryphracta* are sister taxa, *Brachychampsa* and *Stangerochampsa* lie outside crown-group Alligatoridae, and most North American and Eurasian Tertiary alligatoroids are more closely related to *Alligator* than they are to *Caiman. Allognathosuchus mooki, A. haupti*, and *Ceratosuchus burdoshi* are basal to all other alligatorines. *Alligator* is monophyletic, with *A. prenasalis* as the basalmost species.

There are some interesting differences. In this case, *A. mooki, A. haupti* and *C. burdoshi* form a basal clade, not a basal polytomy, at the root of Alligatorinae. A clade including *A. polyodon,* the Willwood alligatorid, and *Procaimanoidea kayi* previously formed part of a polytomy with *Arambourgia, Wannaganosuchus*, and *Alligator*; in this case, the two species of *Procaimanoidea* are closer to *Arambourgia* and *Hispanochampsa*, and *Wannaganosuchus* is closer to *Alligator*.

Support for the clade including *A. mooki, A. haupti* and *C. burdoshi* is problematic, and the group should be viewed skeptically. These taxa share rectangular mid-dorsal osteoderms (unknown for *Ceratosuchus*), but this is the ancestral condition for Alligatoroidea (Brochu, 1999). It falls out as an unambiguous synapomorphy here because mediolaterally elongate mid-dorsals are lacking in *Stangerochampsa* and alligatorines and caimanines

where the dorsal armor is known. Osteoderms are not known for *Eocaiman cavernosus*.

Ambiguous support for this cluster includes a long dorsal premaxillary process; this is also found in *Albertochampsa, Stangerochampsa*, and *Brachychampsa* (though they are more slender in these forms; Fig. 5), but caimanines and other alligatorines have shorter processes. *Allognathosuchus mooki* has an enlarged incisive foramen, but it is coded differently from that of *Stangerochampsa* or *Brachychampsa*, in which it actually intersects the maxillary-premaxillary suture, and hence acts as an ambiguous synapomorphy for the basal alligatorine cluster. The opposite character states—short premaxillary processes and small incisive foramina—formerly acted as ambiguous support for Alligatorinae (Brochu, 1999).

One of the characters unambiguously diagnosing all other alligatorines in previous analyses—a longer prefrontal than lacrimal—remains synapomorphic in this study. Because the basalmost alligatorines are now grouped together, one of the previously ambiguous characters for this node—the presence of at least eight contiguous dorsal osteoderm rows—is now an unambiguous synapomorphy.

Support for a close relationship between *Wannaganosuchus* and *Alligator* includes a single unambiguous character—presence of a medially-bowed lateral margin of the suborbital fenestra. Extant *Alligator* lack this feature, but it is found in *A. prenasalis* and *A. mcgrewi*. The lateral margins of the fenestrae are not bowed in *Procaimanoidea* or *Hispanochampsa*. Unfortunately, the fenestrae are not sufficiently preserved to allow coding of this feature in any of the putative *Allognathosuchus* considered here.

Procaimanoidea, Allognathosuchus polyodon, and the Willwood form share a dentary-surangular suture that intersects the mandibular fenestra at its dorsalmost corner. This is also true for *A. mooki*, but not for *Arambourgia* or *Hispanochampsa*. It most parsimoniously diagnoses a clade including *Allognathosuchus polyodon, Arambourgia, Procaimanoidea*, and *Hispanochampsa* in this study. The suborbital fenestrae of the Willwood form and *P. kayi* lack the posterior notch found in *Alligator*, but we do not know the condition of this character in other basal alligatorines.

Procaimanoidea shares four unambiguous synapomorphies with *Arambourgia* and *Hispanochampsa*: a deep notch lateral to the external naris on the premaxilla, mediolaterally compressed posterior maxillary alveoli, a short dentary symphysis not extending past the fifth alveolus, and the absence of a region of enlarged alveoli at the rear of the dentary. The first of these is
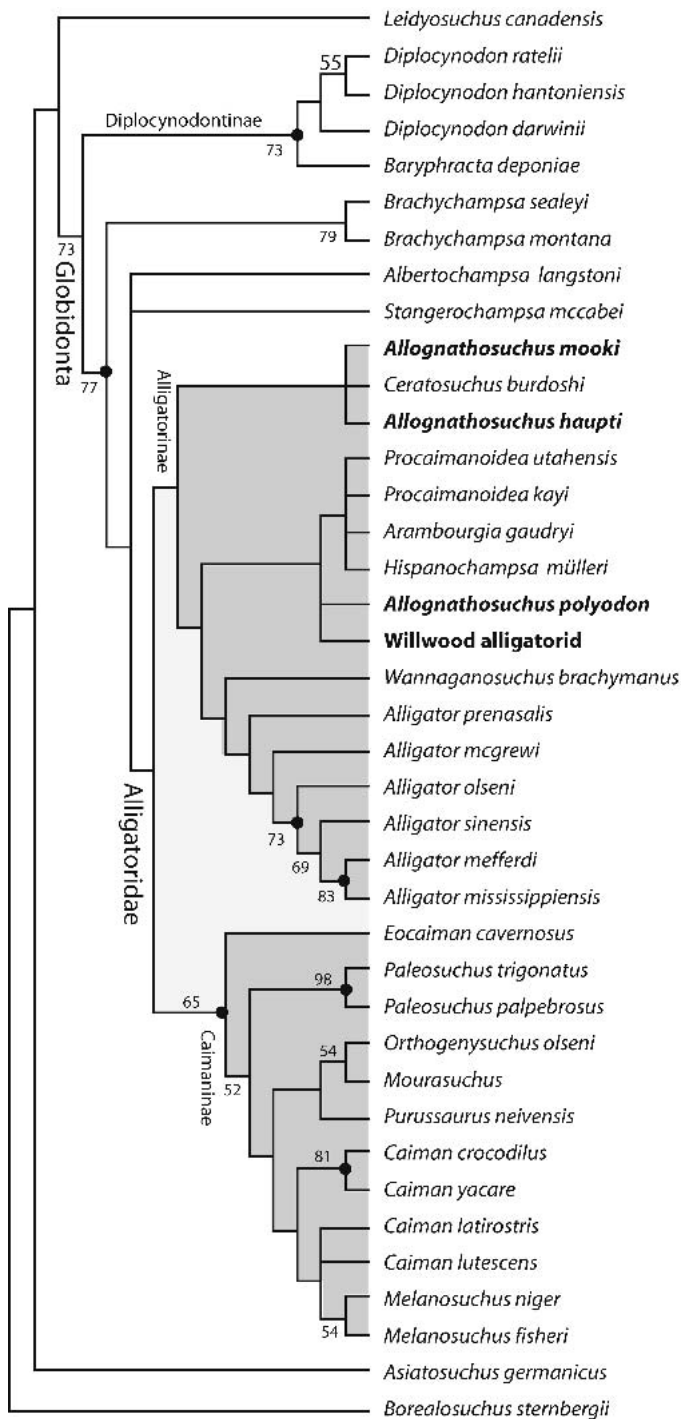
FIGURE 10. Strict consensus of 297 equally optimal trees recovered in a maximum parsimony analysis. Nodes with large dots are supported in trees one step longer than minimum, and numbers indicate bootstrap percentages (see text for discussion). Taxa in boldface are putative species of *Allognathosuchus*.

also found in *Alligator* and was previously thought to diagnose that taxon alone (Brochu, 1999). A shortened dentary symphysis also occurs in derived species of *Alligator* (e.g. *A. olseni, A. mefferdi*, extant species). The lack of a region of enlarged rear dentary alveoli is a reversal (see below), but the flattened maxillary alveoli are unique within Alligatoridae.

One character thought to characterize *Allognathosuchus*—

enlarged teeth at the back of the mouth—has a much broader distribution within Alligatoroidea according to this analysis. A region of enlarged dentary alveoli is found in *Stangerochampsa, Brachychampsa, Ceratosuchus*, and *Alligator prenasalis*, as well as all putative *Allognathosuchus*. It is most parsimoniously viewed as a synapomorphy for Globidonta, with at least three reversals: one within *Alligator*, one among caimans, and one in *Procaimanoidea + Arambourgia + Hispanochampsa*.

DISCUSSION

I remain cautious about certain aspects of these results. The close relationships between *Ceratosuchus*, "*A.*" *mooki*, and "*A.*" *haupti*; between *Allognathosuchus sensu stricto* and *Procaimanoidea*; and between *Wannaganosuchus* and *Alligator* rely on homoplastic character states, and in many cases support is weakened by the fact that relevant character states cannot be scored for closely related taxa. That *Alligator* and *Wannaganosuchus* are united on the basis of a medially-bowed lateral suborbital fenestral margin owes as much to our inability to characterize this feature in many fossil alligatorines as on the shared presence of this feature in these two taxa. But one aspect of the tree appears robust—the separation of *Alligator, Procaimanoidea, Hispanochampsa, Arambourgia, Wannaganosuchus*, and *Allognathosuchus polyodon* from a cluster of basal alligatorines including *Ceratosuchus*, "*A.*" *mooki*, and "*A.*" *haupti*.

Evolution of the Alligatorid Snout

The "specialized" morphology seen in *Allognathosuchus polyodon* appears to reflect plesiomorphy at the level of Alligatoridae. The enlarged alveoli (and presumably globular posterior teeth) and robust mandibular symphysis are all shared by the earliest alligatorids and are found outside the crown clade. Rather than representing a specialized offshoot within Alligatoridae, these animals instead appear to be a cluster of small alligatorids from which less "specialized" taxa, such as extant *Alligator*, were derived.

Indeed, reversals from the blunt-snouted condition occurred multiple times. It happened at least once in *Alligator* and among caimans. Some features are absent in *Procaimanoidea* and *Arambourgia*, but these seem to have been replaced by other derived conditions, such as mediolaterally-compressed rear maxillary dentition. In other respects, *Procaimanoidea* and *Arambourgia* resemble extant *Paleosuchus* in sharing a deep, altirostral snout, in contrast to the flatter snout seen in other alligatorids.

Historical Biogeography

European alligatorines have been assumed to represent a single dispersal event from North America (e.g., Sill, 1968; Rossmann, 2001), but phylogenetics indicates more than one. The results of Brochu (1999) could be interpreted in two ways—either two dispersal events took place from North America to Europe (one for *A. haupti* and one for *Arambourgia*), or later alligatorines (such as *A. polyodon* and *Alligator*) were part of a radiation back into North America from Europe.

The results in this study unambiguously support multiple dispersal events into Europe, but there is a complication—the unsettled relationships of *Arambourgia* and *Hispanochampsa*. The results presented here could be interpreted to suggest a single dispersal event for the two or separate dispersal events for each, depending on how the polytomy including *Arambourgia, Hispanochampsa*, and *Procaimanoidea* is resolved. Clarification of that issue will not impact the conclusion that *Arambourgia, Hispanochampsa*, and *Allognathosuchus haupti* do not represent a single radiation into Europe.

A recent analysis by Rossmann (2000) indicated the possibility

that *Allognathosuchus* dispersed to the Old World directly from South America. This argument was based on Paleocene fossils from Bolivia referred to *Allognathosuchus* (Pascual and Ortiz Jaureguizar, 1991). Since these were among the oldest *Allognathosuchus*, they might have given rise to any later *Allognathosuchus*. These fossils consist of isolated teeth and mandibular fragments (Gasparini, 1996), and their referral to *Allognathosuchus* must be viewed very skeptically. In any case, the same kind of evidence (fragmentary remains) would put *Allognathosuchus* in the Late Cretaceous of North America (e.g., Gallagher, 1993; Lillegraven and Eberle, 1999); if the Bolivian fossils are a form of *Allognathosuchus*, they are not necessarily the oldest such occurrences.

Nonmonophyly of *Allognathosuchus*

Revision of the 1999 matrix did not alter the basic conclusion regarding *Allognathosuchus*; it remains nonmonophyletic. "*Allognathosuchus*" *mooki* and "*A.*" *haupti* remain basal to other alligatorines, and later forms from the Wasatchian and Bridgerian of North America are closer to *Procaimanoidea* and *Alligator*. Other taxa previously referred to *Allognathosuchus*—*Albertochampsa langstoni* (Lucas, 1992) and *Arambourgia gaudryi* (Rauhe, 1995)—do not show any specific relationship with *Allognathosuchus polyodon*, and the former is not a crown-group alligatorid.

This conclusion was the target of sharp criticism (Lucas and Estep, 2000) based on two lines of argument—reinterpretation of character codings and an alleged failure to adhere to standard nomenclatural practice. These criticisms are discussed below.

Lucas and Estep (2000:168) stated, "...once we eliminate Brochu's errors in coding characters, all three taxa are identical in his analysis. Therefore, his claim that *Allognathosuchus* is not monophyletic is unfounded." This statement confuses taxa that are *identical* (taxa which have been coded for the same characters, and in which all states are the same) with taxa that are *redundant* (taxa in which states are identical for those characters coded in common, but in which some characters are coded for one but not the other). The difference is relevant here because not all of the states coded for one species of *Allognathosuchus* were codable in the others. The Willwood alligatorid was codable for 73.2 % of the morphological matrix in the 1997 analysis, but *A. mooki* for only 57.3% and *W. brachymanus* for 52.4%. If we accept Lucas and Estep's morphological interpretations, these three species would be redundant, but not identical.

Because redundancy and identity only refer to the intersection between taxa on a matrix, visibly distinct taxa can be redundant or identical in the context of a given analysis. The differences between them may simply not be expressed in the matrix. This is true, for example, of *Allognathosuchus polyodon* and *Procaimanoidea kayi*, which were completely redundant in the 1999 matrix, but which are clearly different animals. Lucas and Estep's argument for synonymy does not stem from a matrix, but this is a confusion that might follow from the preceding discussion.

The distinction between identical and redundant taxa again becomes relevant to their second line of reasoning, which is based on nomenclatural methodology. They state (2000:168):

"...His claim [of *Allognathosuchus* nonmonophyly] lacks a sound basis in the application of the Code of Zoological Nomenclature. Thus '*A.*' *wartheni* is not the type species of *Allognathosuchus*, so whether or not it and *Allognathosuchus mooki* form a clade is not strictly relevant to the monophyly of *Allognathosuchus*. *A. polyodon* (Mook, 1921) is the type species of the genus, so the monophyly of the genus needs to be established

by determining which of the other named species of *Allognathosuchus* forms a clade with *A. polyodon*."

The fact that *A. polyodon* was included in the 1999 analysis (which Lucas and Estep cited) renders this statement moot, but the phylogenetic status of *Allognathosuchus* can still be addressed in its absence. If taxa with the same generic name do not form a clade, then the name as used in the literature is not monophyletic. The relationship between the Willwood alligatorid and *A. mooki* is completely relevant to the question of *Allognathosuchus*' monophyly, as both are considered to be species of *Allognathosuchus* in the literature. The statement by Lucas and Estep seems to confuse phylogenetic *taxonomy* (the principle of only recognizing monophyletic groups as taxa) with phylogenetic *nomenclature* (the act of putting a phylogeny-based name on a clade; see de Quieroz, 1998, for extended discussion of the distinction). Inclusion of the type species becomes necessary if one wishes to rename any of the included taxa, but is not strictly necessary if one is only interested in whether taxa with the same genus name form a clade.

Allognathosuchus polyodon is imperfectly known and, at first, coded redundantly with both *A. wartheni* and *Procaimanoidea kayi* (Brochu, 1999). A fragmentary fossil that codes redundantly with something more complete adds nothing to a parsimony analysis (Wilkinson, 1995; Wilkinson and Benton, 1995). The information it contains is already expressed by the more complete taxon, and its inclusion can only increase the number of most parsimonious trees and the time needed for the program to run. Incomplete fossils may add critical biogeographic or stratigraphic information to a study, and their inclusion at some phase of the study may be desirable, but they will not redirect the tree—search algorithm, as they might if their character states differed in some way from other taxa in the analysis. What Lucas and Estep appear to view as a serious (and scientifically questionable) omission was a conscious act, based on concepts in the peer-reviewed literature, designed to speed up the parsimony analysis.

Validity of *Wannaganosuchus brachymanus*

Further study of the type of *W. brachymanus* reinforces the conclusion that it can be distinguished from all other known Tertiary alligatoroids. It differs from more basal alligatorines (such as "*Allognathosuchus*" *mooki*) in the presence of square mid-dorsal osteoderms and a longer prefrontal than lacrimal; and other character states with less phylogenetic signal (such as the orientation of the external naris) also serve to distinguish them. It differs from other *Allognathosuchus* (including fossils from the Clarkforkian and Wasatchian) in the presence of a modest "spectacle" between the orbits.

The characters distinguishing *W. brachymanus* from other alligatorines are subtle, as are those separating most basal alligatorines. One could argue that these are insignificant or the result of some sort of intraspecific variation. Character "significance" is a subjective assessment with little role in modern systematics, but variation is a real issue. The approach taken here regards the stated range of variation for a given species as a falsifiable hypothesis. It can be falsified by finding states lying outside the stated range. Subtlety is not evidence for variability; the onus is on those who believe these characters to represent some sort of intraspecific variation to demonstrate it. Otherwise, we are left with scientifically useless circular assertions—we know two erstwhile species are conspecific because the diagnostic characters separating them are ontogenetic variants, but we only know the character states to be ontogenetically variable because we regard specimens showing them to be conspecific.

The claim made here is that *W. brachymanus* is a valid species. Given the degree of uncertainty in that portion of the tree,

we still cannot rule out the possibility that future work will tie *W. brachymanus* with *Allognathosuchus*. Should this happen, we could regard *Wannaganosuchus* as a junior synonym of *Allognathosuchus*. But for the time being, there is no solid evidence for this conclusion.

Taxonomic Recommendations

Current evidence favors a nonmonophyletic "*Allognathosuchus*," however weakly. Whether generic names (praenomina) should refer to clades is currently a matter of debate (Cantino, et al., 1999). Assuming we wish to continue using *Allognathosuchus* as a taxon name, Fig. 10 suggests two phylogenetic solutions. Reducing its membership to a specific clade including *Allognathosuchus polyodon* and *Allognathosuchus wartheni* would require applying different generic names to *Allognathosuchus haupti* and *Allognathosuchus mooki*, and as discussed previously (Brochu, 1999), alternative names are already in place in the literature—*Hassiacosuchus* for *A. haupti* and *Navajosuchus* for *A. mooki*. Expanding *Allognathosuchus*' membership, perhaps by defining *Allognathosuchus* as the last common ancestor of *A. polyodon* and *A. mooki* and all of its descendents, would require us to give all known alligatorines the same generic name, as all are descended from the last common ancestor of *A. polyodon* and *A. mooki*.

Both approaches have strengths. Both would improve nomenclatural stability, as most species would have the same generic name under one solution and most would have their own name under the other. Changes in phylogenetic hypothesis would be unlikely to require wholesale nomenclatural changes. These would not *fix* stability, as would some of the solutions proposed by Cantino et al. (1999); for example, shifting *Alligator mcgrewi* to a position closer to *Allognathosuchus polyodon* would mean a name change to *Allognathosuchus mcgrewi*. But we would have more stability than currently exists.

The restricted approach has an additional benefit, as it maximizes the precision of each praenomen's meaning. Whereas *Allognathosuchus* refers to a wide array of extinct alligatorines in the current system, it would refer to a more restricted assemblage in the limited sense. A phylogenetically-defined *Allognathosuchus* would refer to a very specific clade and would impart a universal meaning to the name, and if that name circumscribes a small number of species, it would convey very precise morphological, stratigraphic, and biogeographic information. A broader definition of *Allognathosuchus* would, conversely, convey much broader morphological or distributional information. It would imply, for example, that two different dispersal events from North America to Europe occurred within *Allognathosuchus*.

The expanded meaning of *Allognathosuchus* would be problematic in the Linnean system, as *Alligator* Daudin 1809 has priority over *Allognathosuchus* Mook 1921. In the phylogeny suggested by Fig. 10, *Alligator* is a descendent of the last common ancestor of *A. polyodon* and *A. mooki*. The correct generic name in the Linnean system for all of these animals would be *Alligator*. The Puercan alligatorine from New Mexico thus becomes *Alligator mooki*.

Some proposed translations of species into the phylogenetic system (Cantino et al., 1999) would fix the generic and specific names for a binomial, regardless of relationship. "Genera" would thus not be taxa in and of themselves, and *Allognathosuchus mooki* would remain *Allognathosuchus mooki* regardless of whether it is closer to *A. polyodon*, *Ceratosuchus burdoshi*, or *Homo sapiens*. These approaches would certainly maximize stability, as no praenomen would ever change; but it would sharply diminish the informative value of the praenomen.

I recommend applying different praenomina to those taxa clearly unrelated to the type species. This improves stability and clarifies the meaning of *Allognathosuchus*. We can apply the name *Navajosuchus* to the Puercan-Torrejonian form from New Mexico and *Hassiacosuchus* to the Messel alligatorid—hence, *Navajosuchus mooki* and *Hassiacosuchus haupti*. Though future analyses might draw *W. brachymanus* closer to *Allognathosuchus sensu stricto*, the present analysis does not support this conclusion, and I recommend preservation of *Wannaganosuchus* until firm evidence places it within a clade called *Allognathosuchus*.

It is difficult to distinguish USNM 4112 (the holotype of *Allognathosuchus polyodon*) from most Paleogene alligatorids. If the type species of *Allognathosuchus* is undiagnosable, then the name *Allognathosuchus* itself is undiagnosable. Making *Allognathosuchus polyodon* a *nomen dubium* would solve the problem of *Allognathosuchus*' content once and for all. It thus has a certain appeal. But given the importance the name *Allognathosuchus* has in the paleontological literature, an approach that preserves the name with a restricted content is preferable. It might be desirable, for example, to establish AMNH 6049 as a neotype for *Allognathosuchus polyodon* (Cope, 1873). With this specimen, we can distinguish *A. polyodon* from *Hassiacosuchus* and *Navajosuchus* on the basis of a longer prefrontal than lacrimal; from *Wannaganosuchus* on the basis of a smooth snout lacking any trace of a "spectacle;" from *Alligator* on the absence of a notch lateral to the external naris and internarial bar; and from *Procaimanoidea*, *Arambourgia*, and *Hispanochampsa* on the presence of enlarged, globular posterior dentition.

We still face the problem of the Wasatchian and Clarkforkian alligatorids, which may or may not represent a single species, and which may or may not pertain phylogenetically to *Allognathosuchus*. Detailed descriptive work is required to understand these fossils, and this should involve the study of both discrete and continuous characters.

Another problem, from a phylogenetic view, concerns the Eocene European alligatorids not considered here. Kuhn (1938) described two species from the Geiseltal locality in Germany—*Caimanosuchus brevirostris* and *Eocenosuchus weigelti*—that are very similar to each other. Rauhe (1995) considered them to be a single species of *Allognathosuchus* (*A. brevirostris*). The relationship between the lacrimal and prefrontal in this form is identical to that in *Hassiacosuchus haupti*. It would be most prudent to refer this species to *Caimanosuchus* until it can be analyzed phylogenetically. Additional alligatoroids similar to *Brachychampsa* are known from the Late Cretaceous of Spain (Buscalioni et al., 1997) and merit further attention.

Finally, I recommend a careful approach toward *Allognathosuchus*. The fragmentary remains identified as *Allognathosuchus* in the literature have often been referred to it on the basis of plesiomorphic character states. It would be more prudent to simply refer them to "Alligatoridae incertae sedis" until future work is completed on Early Tertiary alligatorids from North America and Eurasia.

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APPENDICES 1 AND 2

Supplemental data available from SVP websiste: http://www.vertpaleo.org/jvp/JVPcontents.html.

NOTE ADDED IN PROOF

After this paper was revised, a more detailed discussion of *Chrysochampsa* was published by Lucas and Sullivan (2004). Although not referring *C. mlynarskii* specifically to *A. mooki,* they based a referral to *Allognathosuchus* in part on a dismissal of differences listed by Estes (1988) and on the shared snout breadth, heterodont dentition, splenial symphysis, and the elevated toothrow behind the 13th dentary alveolus. At a coarse level, these features apply to all basal alligatorines; in any case, unlike anything else called *Allognathosuchus, Chrysochampsa* does not have an extensive splenial symphysis.

Lucas, S. G., and R. M. Sullivan. 2004. The taxonomic status of *Chrysochampsa,* an Eocene crocodylian from North Dakota, USA and the paleobiogeography of *Allognathosuchus.* Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 2004:461–472.