

CRANIAL ANATOMY OF *ENNATOSAURUS TECTON* (SYNAPSIDA: CASEIDAE) FROM THE MIDDLE PERMIAN OF RUSSIA AND THE EVOLUTIONARY RELATIONSHIPS OF CASEIDAE

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ABSTRACT—Detailed description of the Middle Permian Russian caseid *Ennatosaurus tecton* shows that three autapomorphies distinguish it from other caseids: a broad anterior ramus of the jugal, a large contribution of the frontal to the dorsal orbital margin, and a relatively narrow parasphenoid body. Phylogenetic analysis of Caseidae yields a single most parsimonious tree and its topology posits *Ennatosaurus tecton* as the sister taxon to the clade of the North American caseids *Angelosaurus dolani* and *Cotylorhynchus romeri*. Phylogenetic analysis supports the position of *Oromycter dolesorum* from the Lower Permian Richards Spur locality as the most basal member of Caseidae. In addition, the genus *Casea* is resolved as paraphyletic, whereby *C. rutena* forms the sister taxon to the clade containing *E. tecton*, *C. romeri*, and *A. dolani*. The current topology reveals that the pattern of dental complexity in terms of the number of apical cuspules is homoplasious, cautioning against its use as a unidirectional phylogenetic character.

INTRODUCTION

Caseidae are a monophyletic clade of basal synsapsids characterized by a disproportionately small cranium with a procumbent snout that overhangs the tooth row. Members of Caseidae are superficially conservative in morphology, differing most significantly from each other in size, which ranges from just under one meter to greater than three meters in total body length. Caseids are considered important components of some of the earliest terrestrial ecosystems in vertebrate history. Their hypothesized herbivorous lifestyle places caseids among the earliest terrestrial tetrapods to occupy the role of primary consumer (Olson, 1962) and they are, therefore, of particular interest to understanding early amniote-dominated ecosystems. Here we reassess the cranial anatomy of the youngest caseid, *Ennatosaurus tecton*, and perform the first cladistic analysis of the group.

TAXONOMIC BACKGROUND

In his review of the family, Olson (1968) considered caseids to be a diverse group of basal synsapsids with eight recognized genera. These included the well-known North American genera *Casea*, *Cotylorhynchus*, *Angelosaurus*, and the Russian genus *Ennatosaurus*, as well as the poorly known forms *Caseopsis*, *Caseoides*, and *Phreatophrasma* (Williston, 1910a; Stovall, 1937; Olson and Beerbower, 1953; Efremov, 1954, 1956; Olson, 1962). The eighth genus once assigned to Caseidae, *Trichasaurus*, was recognized to be problematic and of equivocal taxonomic affinities by Olson (1968). In that paper Olson (1968) excluded *Trichasaurus* from Caseidae and suggested a more appropriate assignment was to Edaphosauridae.

The other Russian caseid, *Phreatophrasma aenigmaticum*, as its name implies, was also recognized early on to be problematic.

Phreatophrasma aenigmaticum is known only from a single isolated femur, which possesses both caseid and edaphosaurid features (Olson, 1962; 1968). It remained tentatively assigned to Caseidae by both Olson (1968) and later Reisz (1986), perhaps in anticipation that the discovery of more material would shed light on its true affinities. Unfortunately, this has not been the case and *P. aenigmaticum* remains poorly understood. In the most recent survey of Russian tetrapods Ivakhnenko et al. (1997) listed *P. aenigmaticum* as belonging to an indeterminate family, excluding it from Caseidae. This most recent treatment of *P. aenigmaticum* will be followed here.

One or more species have been described for each of the eight caseid genera noted above. However, the validity of many of these species, and even entire genera, has been called into question (see Reisz, 1986). Taxonomic changes will be assisted with the discovery of new specimens and the preparation of the numerous specimens already in museum collections, enabling the range of variation and diversity to be understood more clearly.

Unfortunately, caseid discoveries are historically rare. Only two new taxa have been formally described since the early work of Olson (1962, 1968) and one other specimen from the Bromacker Quarry in Germany is in the process of description (D. Berman, pers. comm.). The first of the newly described taxa was found near the town of Rodez in the Aveyron Province, France. This fossil was assigned to a new species of *Casea*, *C. rutena*, based on the possession of several primitive features it shares with its North American ally, *C. broilii*, such as the very small and seemingly unspecialized cranium, ubiquitously distributed palatal teeth, and a high phalangeal formula (Sigogneau-Russell and Russell, 1974).

The second recently described taxon is represented by highly fragmentary remains from the Dolese Brothers limestone quarry, better known as the Richards Spur locality, in Oklahoma. A new genus was erected for the remains, *Oromycter* (Reisz, 2005), and the species was named after the quarry operators and owners of the land on which it was found, *O. dolesorum* (Reisz, 2005). This specimen also possessed a number of primitive fea-

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tures. The presence of several additional primitive features, which even *Casea broilii* did not possess, led to the suggestion that *O. dolesorum* occupied the most basal position in Caseidae (Reisz, 2005), possibly ousting *C. broilii* from its long-held position (Olson, 1954; Reisz, 1986, 2005).

The few North American localities from which caseids have been recovered occupy a geographically restricted part of the Permian deposits of Texas and Oklahoma. Similarly, the two definitive European taxa, *Ennatosaurus tecton* and *Casea rutena*, are known only from three closely residing localities in Russia and a single locality in France, respectively. Often, only a single caseid taxon represented by few specimens is recovered at each locality, making caseid fossils relative rare in comparison to contemporaneous taxa (Olson, 1956, 1968). The relative rarity of caseid fossils has been suggested to be the product of a preservation bias against them because of their preferred habitat (Olson, 1962, 1968). Caseids are found in deposits that are thought to represent environments distinct from the much more typically preserved lowland, deltaic environments as indicated by the sedimentology and associated fauna. Instead, caseids are found in deposits thought to represent a drier, more upland environment with ephemeral ponds and stream systems (Olson, 1962; Sullivan and Reisz, 1999; Eberth et al., 2000; Reisz, 2005; D. Berman, pers. comm.).

Caseids are one of the longest-lived lineages of pelycosaur-grade synapsids and yet specimens are still few in numbers. Virtually nothing is known of the origin and early history of the group. The hypothesized sister taxon relationship between Caseidae and Eothyrididae (Reisz, 1986) places the latest possible divergence time at or near the Permo-Carboniferous boundary (~300 Ma). Since the earliest known caseids, *Oromycter dolesorum* and *Casea broilii*, come from upper Lower Permian horizons (Williston, 1910a; Reisz, 2005), a lengthy ghost lineage (~10 Ma) spanning much of the Early Permian must be invoked.

From this first appearance in the fossil record, caseids are found in the succeeding three formations in Texas, the Choza, San Angelo, and Flowerpot, and they are also present in the Hennessey Formation of Oklahoma, which is hypothesized to be contemporaneous with the Vale and Choza (Olson, 1962, 1968). These caseid-bearing formations appear to terminate at the upper boundary of the Early Permian (Lucas, 2004). The Russian form, *Ennatosaurus tecton*, occurs substantially later than the last known North American caseid. The oldest terrestrial Permian beds in Russia are of early Middle Permian age (Lucas, 2004), and the localities hosting *E. tecton* are late Middle Permian (V. Lozovsky, pers. comm.). As the youngest member of Caseidae, *E. tecton* is a vital taxon for our understanding of the evolutionary history of the group and their eventual demise.

Since its discovery, *Ennatosaurus tecton* has eluded detailed examination because of a rather unique set of circumstances (Olson, 1968). Dr. B. V'yushkov planned to conduct the first taxonomic description and diagnosis of *Ennatosaurus tecton*. In anticipation of this forthcoming work, Efremov (1956) dealt only briefly with *E. tecton* in his publication noting the presence of American faunal elements in the Permian deposits of Russia. Unfortunately, the death of Dr. B. V'yushkov meant that the thorough description of *E. tecton* was not completed. A translated portion of Efremov's (1956) brief description and diagnosis is provided in Olson (1962). It consists in large part of distinguishing features of the marginal dentition, whereby fewer and larger teeth with a more complex apical cuspule pattern characterize *E. tecton* in comparison to those of the North American forms. In addition, Efremov (1956) noted *E. tecton* as having enormous external nares, strong tooth-bearing pterygoids, and a large pineal foramen. Olson (1962), in adding to this diagnosis, further described the unique dentition of *E. tecton* as having the two large conical, non-serrated anterior premaxillary teeth and only eight maxillary teeth (ten on each side of the lower jaw).

Olson (1962) also diagnoses the absence of foramina below the orbitonarial bar as a distinctive feature of *E. tecton*. Olson's (1962) early descriptions were elaborated slightly in a later, more comprehensive study of Caseidae (Olson, 1968). However, the addition of autapomorphies, besides dental characters, was limited and the description and diagnosis remained inadequate. More recently, Ivakhnenko (1990) re-illustrated the skull of *E. tecton*, stating that earlier studies on the taxon lacked satisfactory illustrations. Unfortunately, Ivakhnenko's (1990) reconstruction suffered several inaccuracies, which are detailed below in the description. This current work aims to provide a detailed diagnosis for *E. tecton* based on a thorough description and the first technical reconstruction of the taxon.

Institutional Abbreviations—**FMNH**, Field Museum of Natural History, Chicago; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **OMNH**, Sam Noble Museum of Natural History, University of Oklahoma, Norman; **PIN**, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

SYSTEMATIC PALEONTOLOGY

SYNAPSIDA Osborn, 1903

CASEASURIA Williston, 1912

CASEIDAE Williston, 1912

ENNATOSAURUS TECTON Efremov, 1956

Figs. 1–5

Holotype—PIN 1580/17, nearly complete skull and associated lower jaw.

Type Locality and Horizon—The Moroznitsa locality (1580/n), near the towns of Pinega and Karpoga, on the Pinega River, northwestern Russia, whose strata are assigned to the earliest early Tatarian age (late Guadalupian) of the Middle Permian (V. Lozovsky, pers. comm.).

Referred Material—Four additional skulls and associated lower jaws of varying completeness from the type locality are referred to *Ennatosaurus tecton*: specimens PIN 1580/14, 19, 24, and 122. One additional skull and associated lower jaw has been recovered from the Nyisagora locality (4543/n), on the Mezen River, near the junction with the Vashka River. Locality 4543 occurs within the earliest early Tatarian (late Guadalupian) of Russia (V. Lozovsky, pers. comm.). Additional, uncatalogued materials from this locality include a fragment of the cheek region (PIN 4543/uncatalogued 1) and a fragment of dentary (PIN 4543/uncatalogued 2).

Revised Diagnosis—Autapomorphic in its possession of a thick anterior ramus of the jugal, large contribution of frontal to the dorsal orbital rim (>1/2 dorsal rim length), and a narrow parasphenoid body shape. Distinguished from other caseids by possession of ten upper jaw teeth: two large, conical premaxillary teeth, the remaining marginal teeth spatulate and bearing a complex apical serration pattern consisting of five to seven longitudinally arranged cuspules.

Remarks—*Ennatosaurus tecton* material (PIN 4653/2, formerly 4643) has also been reported from a third locality, the Karaschelje locality (4643/n; Ivakhnenko et al., 1997). The material consists of a tooth-bearing element. The assignment of this to Caseidae is questionable, as the dentition strongly resembles that in pareiasaurian reptiles (RR, pers. obs.).

DESCRIPTION & COMPARISONS

Skull

The current description and skull reconstruction for *Ennatosaurus tecton* (Fig. 1), including all measurements, were based on specimen PIN 4543/1 (Figs. 2–5) unless otherwise indicated. Photographs of other specimens of *E. tecton* were employed to pro-

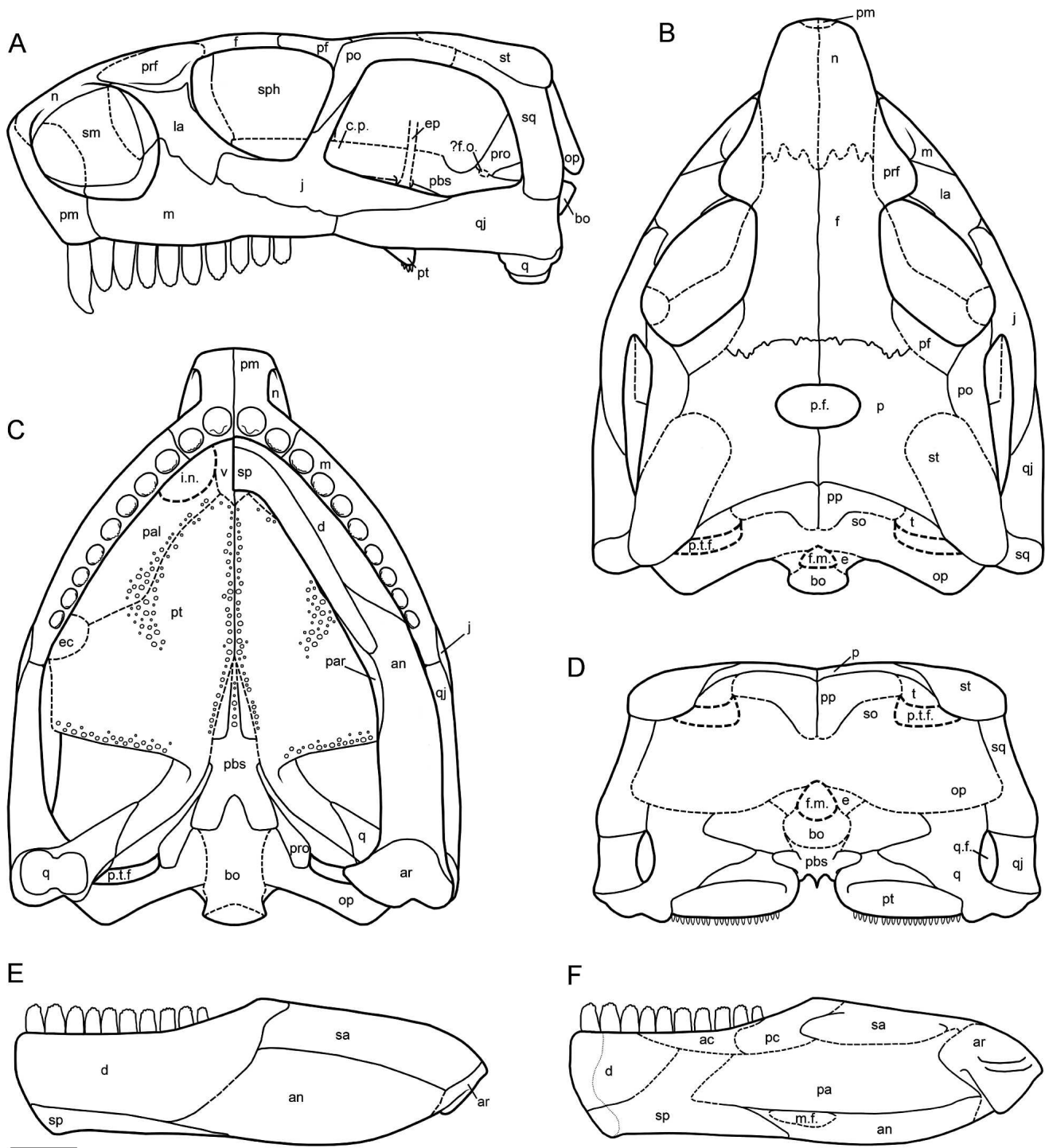


FIGURE 1. Reconstruction of the skull (A–D) and lower jaw (E, F) of *Ennatosaurus tecton* PIN 4543/1. The skull in: **A**, lateral; **B**, dorsal; **C**, ventral; **D**, occipital views. The lower jaw in: **E**, lateral and, **F**, medial views. Scale bar equals 2 cm. **Anatomical abbreviations:** **ac**, anterior coronoid; **an**, angular; **ar**, articular; **c.p.**, cultriform process; **d**, dentary; **ect**, ectopterygoid; **ep**, epipterygoid; **f**, frontal; **f.m.**, foramen magnum; **f.o.**, fenestra ovalis; **i.n.**, internal naris; **j**, jugal; **la**, lacrimal; **m**, maxilla; **m.f.**, Meckelian foramen; **n**, nasal; **op**, opisthotic; **p**, parietal; **pal**, palatine; **par**, prearticular; **pbs**, parabasisphenoid; **pc**, posterior coronoid; **p.f.**, parietal foramen; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pp**, postparietal; **prf**, prefrontal; **pro**, prootic; **pt**, pterygoid; **p.t.f.**, posttemporal fenestra; **q**, quadrate; **q.f.**, quadrate foramen; **qj**, quadratojugal; **sa**, surangular; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **sph**, sphenethmoid; **sq**, squamosal; **st**, supratemporal; **t**, tabular; **v**, vomer.

vide qualitative information regarding the overall shape of certain features of the skull, as well as information regarding the range of variation of certain features.

PIN 4543/1 (Figs. 2–5) consists of a moderately well-preserved

skull and articulated lower jaw. The specimen is mediolaterally crushed and sheared, such that the skull roof is displaced to the left of the palate, and the cheeks and lower jaw are displaced to the right. The ventral margin of the left side of the skull is further

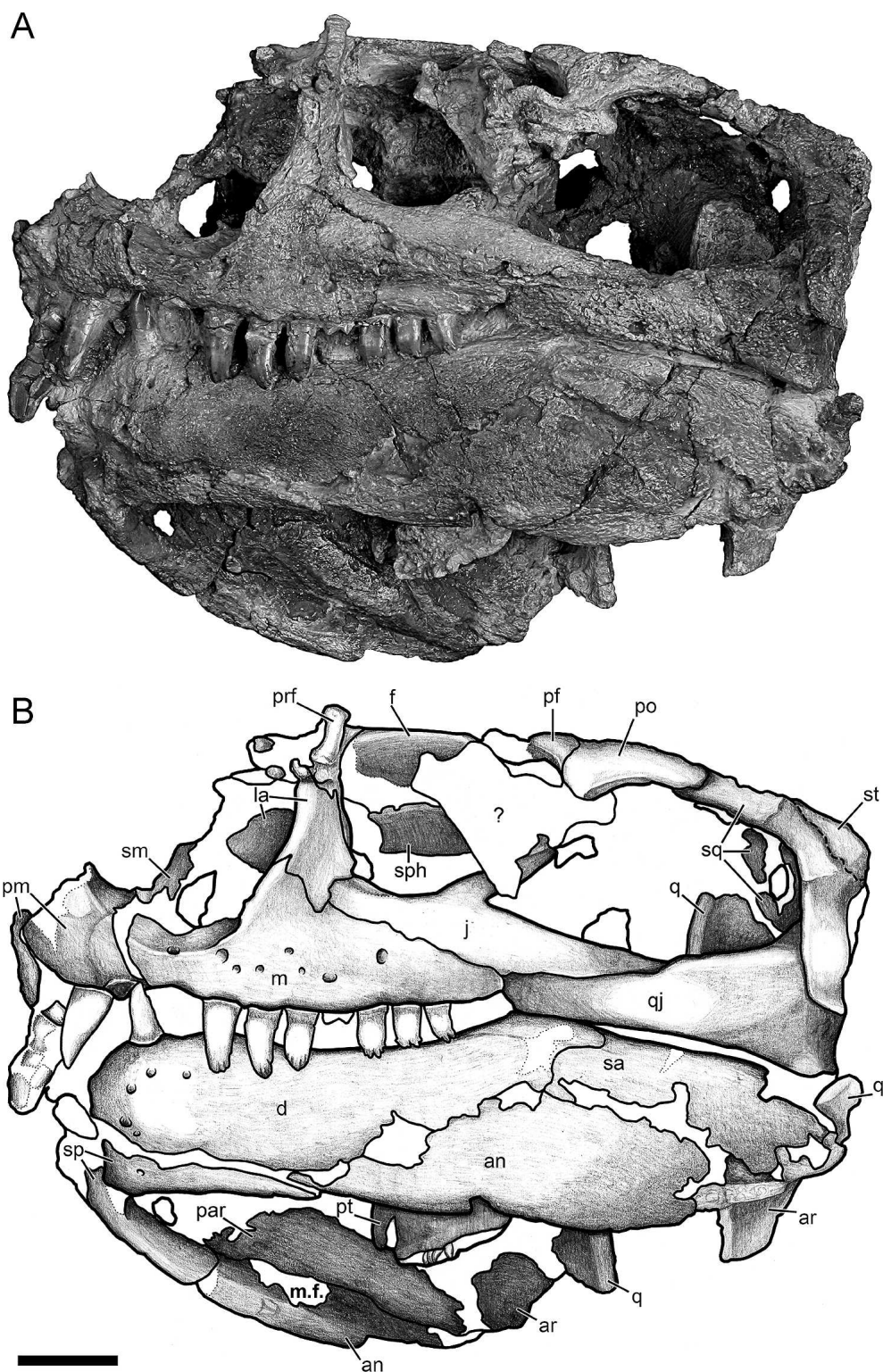


FIGURE 2. *Ennatosaurus tecton* (PIN 4543/1) in lateral view. **A**, photograph; **B**, line drawing. Abbreviations given in Figure 1. Scale bar equals 2 cm.

sheared anteriorly. The right side of the skull is substantially more damaged than the left side. The skull roof is incomplete anteriorly and heavily damaged posteriorly. The occipital plate elements are for the most part intact, as is the right side of most braincase elements. The basioccipital-exoccipital complex is

missing completely. In dorsal aspect, portions of both the right and left side of the palate are visible; however, it is heavily damaged and partially obscured by matrix. In ventral view only the posterior two thirds of the palate are visible and are also heavily damaged.

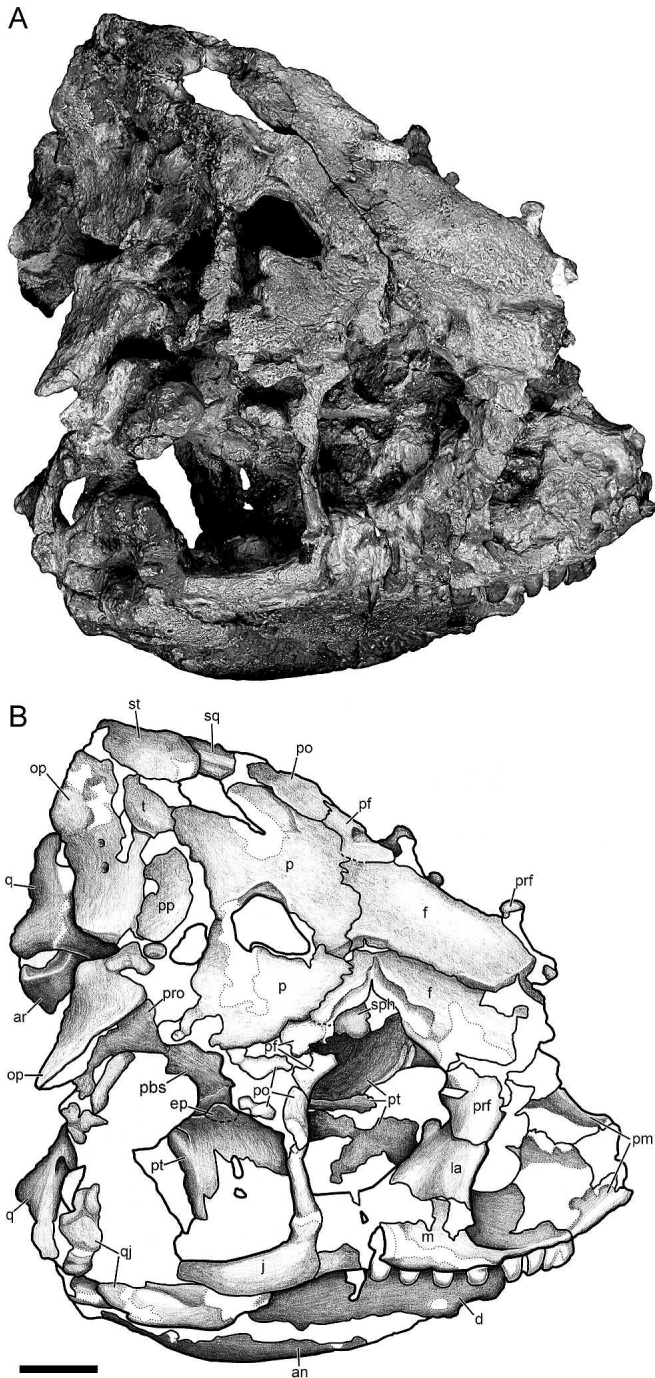


FIGURE 3. *Ennatosaurus tecton* (PIN 4543/1) in dorsal view. **A**, photograph; **B**, line drawing. Abbreviations given in Figure 1. Scale bar equals 2 cm.

The skull morphology of *Ennatosaurus tecton* conforms to that seen in other caseids in a variety of characteristics. The skull is anteroposteriorly short and also broad relative to its length. It is also shallow dorsoventrally. *Ennatosaurus tecton* possesses the typical procumbent snout of caseosaurians, and this feature appears to be particularly well developed. *Ennatosaurus tecton* also has large external nares and lateral temporal fenestrae when compared to other caseids. The enlargement of the nares and temporal fenestrae appears to occur at the expense of the orbital and postorbital bars, as these are substantially narrower

than in other caseids. The antorbital region is elongate in comparison to other caseids, such as *Casea rutena* and *Casea broilii*, although these proportional differences likely reflect allometries typically observed when comparing vertebrate skulls of such substantially different sizes. The external surface of the skull is sculptured, as is the case in all caseids. The sculpturing of *E. tecton* is much finer and subtler on the skull roof than that observed in other caseids, such as *Cotylorhynchus romeri* and *Casea rutena*.

In lateral view (Figs. 1A) the skull table is gently convex above the orbit. The skull roof is deeper in the posterior portions because of a slight doming of the parietals and the posteroventrally angled ventral cheek margin. The posterior margin of the skull is slightly inclined anterodorsally, and the occiput follows this inclination, projecting slightly beyond the posterior margin of the skull. In dorsal view (Figs. 1B) the outline of the skull roof is spade-shaped. The skull table is narrow anteriorly with the exception of a brief expansion at the orbitonarial bar formed by the prefrontal. The skull table broadens substantially in the posterior portion of the orbit and then less so beyond the postorbital bar. The cheek region is wider than the skull table.

The palate is broad and plate-like with dentition limited to three discrete fields (Figs. 1C). A narrow interpterygoid vacuity divides the posterior portions of the palate at the midline. The basal tubera of the parasphenoid are narrow in comparison to other caseids, and the element has a long, blade-like cultriform process bearing teeth. The occiput is short and broad with plate-like morphology (Fig. 1D). The plate is composed largely of the opisthotic, because the supraoccipital is small and laterally restricted between the posttemporal foramina.

The lower jaw (Figs. 1E, F) is especially deep posterior to the coronoid eminence when compared to other caseids and tapers slightly to a consistent depth at the tooth-bearing region. The jaw is dominated by a large dentary, which is the condition typical for caseids. A strong medially directed process off the articular is present at the level of the articular facets for the quadrate.

Skull Roof—The premaxilla is a small element that occupies the anteriormost portion of the skull roof (Fig. 2). The premaxilla in *Ennatosaurus tecton* consists of a dorsally extending ramus forming the anterior margin of the external naris, a posteriorly extending tooth bearing ramus supporting two large, apically curved, conical teeth, and a short palatal ramus. In lateral view the anterior margin of the premaxilla slopes posteroventrally, resulting in a strongly procumbent snout. The ventral margin is slightly convex in *E. tecton*, as in *Cotylorhynchus romeri* and *Casea rutena*. Both premaxillae in PIN 4543/1 are incomplete dorsally such that the location of the suture with the nasal cannot be determined. The anterior margin of the skull is, however, completely preserved in PIN 1580/17, and the premaxilla-nasal contact occurs at the anterodorsal apex of the snout. The dorsal ramus of each premaxilla contributes to a narrow internarial bar, which is narrower than that in *Casea rutena*, but similar in width to that in *Cotylorhynchus romeri*. The tooth-bearing ramus is short, terminating under the anterior half of the external naris. A shelf of bone extends medially from the narial border, creating a narrow floor within the narial chamber, and thus emarginates the external naris. The palatal ramus of the premaxilla is not observable in any of the specimens, but likely would have formed a portion of the anterior border of the internal naris and medially would have sutured with the vomer as it does in the other caseids. The internal naris is not preserved in PIN 4543/1 or visible in the other specimens.

The maxilla is roughly triangular in lateral view in *Ennatosaurus tecton* (Fig. 2). The height of the postnarial process of the maxilla, which is comparable to that in *Cotylorhynchus romeri* in reaching to just beyond mid-height level of the external naris, but differs from that in *Casea rutena* in being substantially shorter. Posteriorly the maxilla tapers to a narrow contact with the

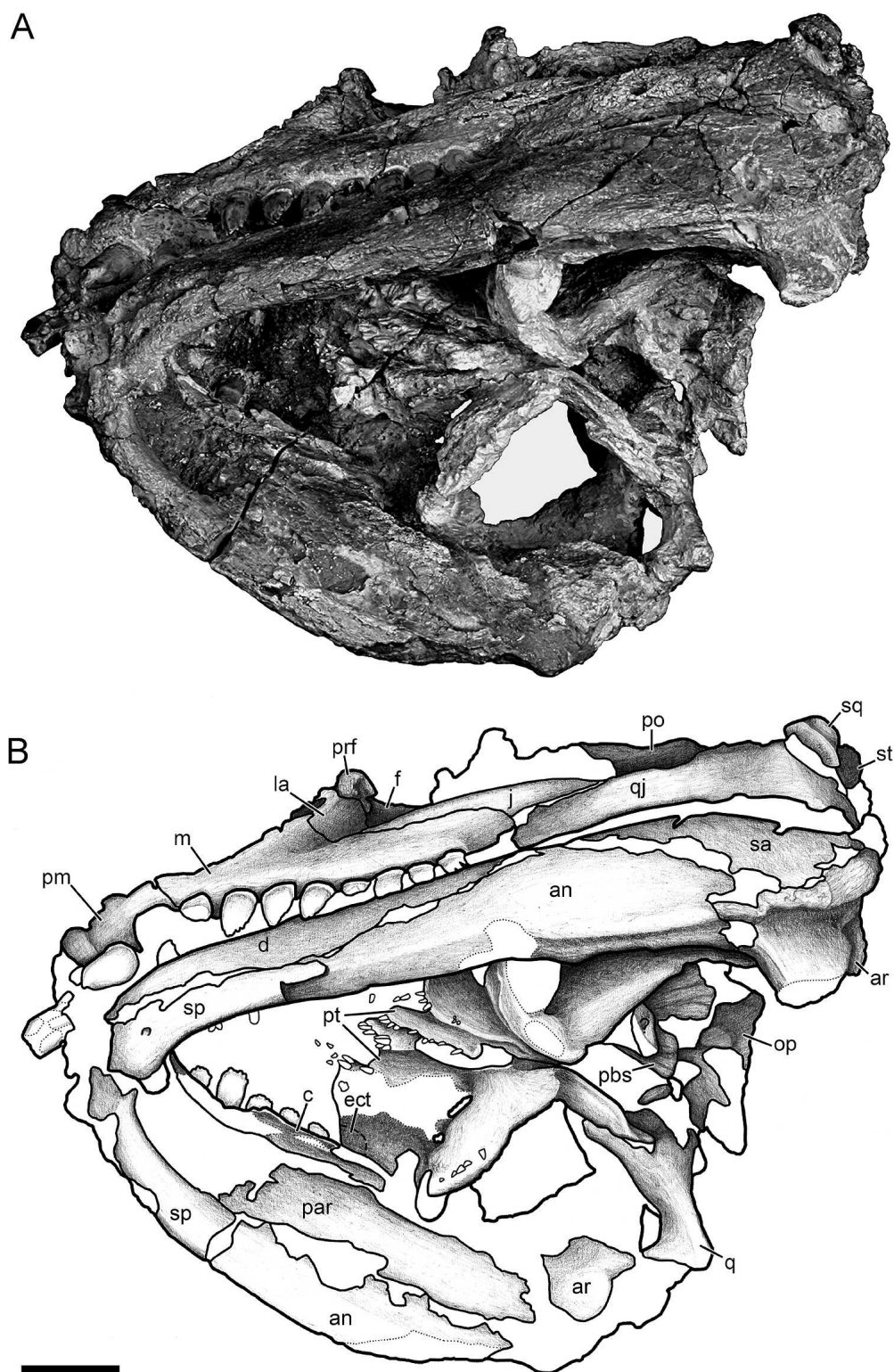


FIGURE 4. *Ennatosaurus tecton* (PIN 4543/1) in ventral view. **A**, photograph; **B**, line drawing. Abbreviations given in Figure 1. Scale bar equals 2 cm.

quadratojugal just posterior to the level of the postorbital bar. The slightly convex ventral margin reaches its greatest ventral extent about the level of the third tooth, below the orbital bar. As observed in all caseids, the lateral surface of the maxilla is perforated by numerous foramina, and it is completely ex-

cluded from the orbit by a substantial lacrimal-jugal contact. A medial extension of the maxilla contributes to the posterior portion of the floor of the narial emargination. An isolated midventral skull fragment (PIN 4543/uncatalogued 1; Fig. 6) reveals in medial view that the jugal has an extensive contact with the

A



B

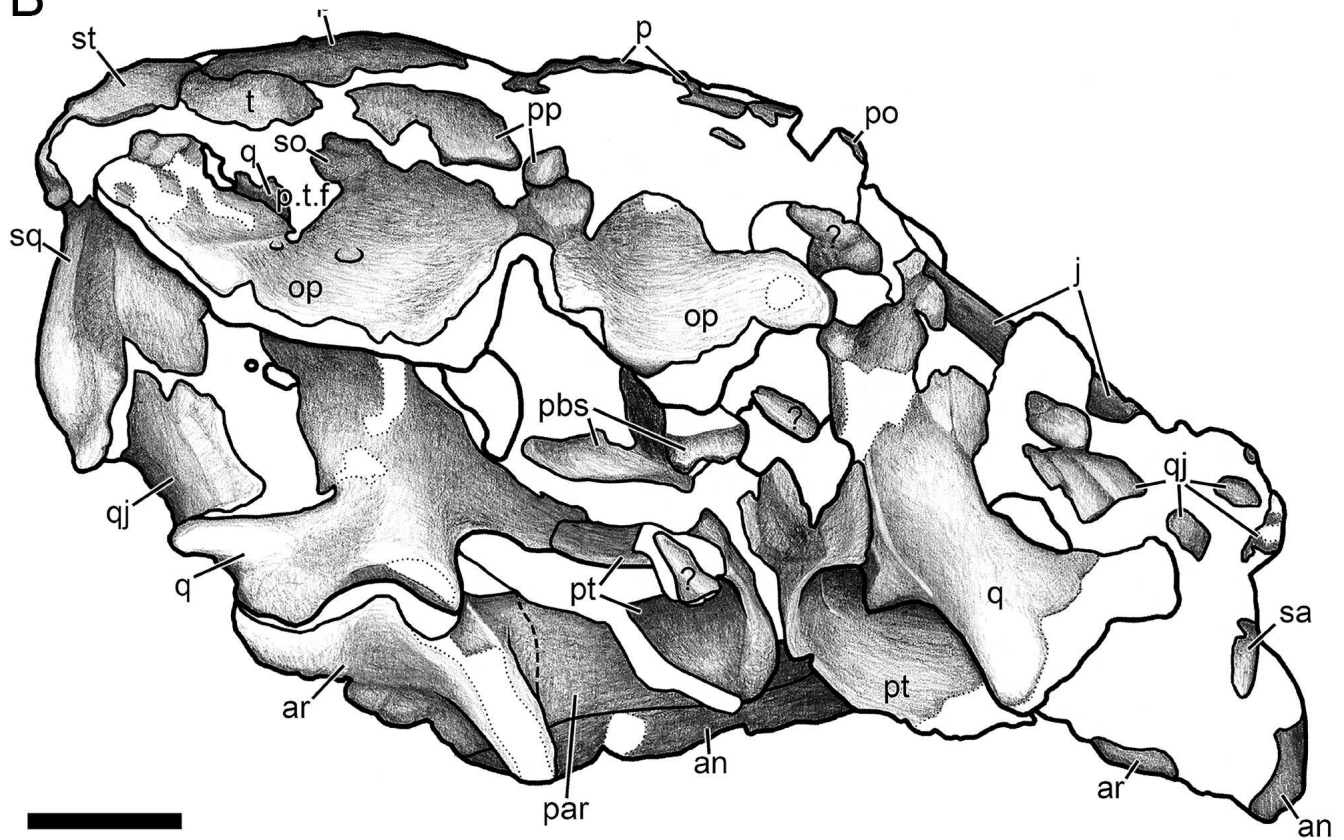


FIGURE 5. *Ennatosaurus tecton* (PIN 4543/1) in occipital view. **A**, photograph; **B**, line drawing. Abbreviations given in Figure 1. Scale bar equals 2 cm.

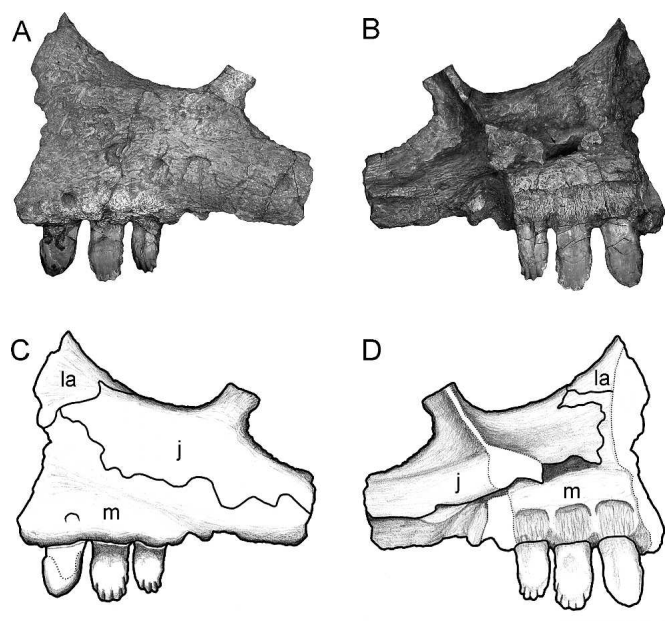


FIGURE 6. Photographs and drawings of an isolated fragment of the left cheek region from *Ennatosaurus tecton* (PIN 4543/uncatalogued 1). **A**, lateral and **B**, medial view. **Anatomical abbreviations:** j, jugal; la, lacrimal; m, maxilla. Scale bar equals 1 cm.

dorsal surface of the alveolar shelf at the level of the postorbital bar.

The alveolar shelf supports eight teeth. This number of teeth in *Ennatosaurus* is substantially less than that of other caseids, such as *Cotylorhynchus romeri* and *Casea rutena* that have 15 and 11, respectively. The maxillary teeth decrease serially in size posteriorly as well as becoming less circular and more labiolingually flattened in cross-section. The teeth have subcircular bases with a slightly expanded shoulder near the base on the lingual surface (Fig. 7). Apically the lingual surface of the tooth becomes flattened and the crown is recurved lingually, resulting in a spatulate appearance. The crown margins possess five to seven longitudinally arranged cusps, with the anterior teeth exhibiting greater wear or being less clearly defined.

The septomaxilla is represented by only fragments of smooth, thin bone visible in lateral view near the premaxilla-maxilla suture in PIN 4543/1 (Fig. 2), but are complete in PIN 1580/14 and PIN 1580/17. In these latter specimens the ventral margin of the septomaxilla contacts the medial shelf of the maxilla, but compression of the skull roof has obscured the dorsal margin of the septomaxilla and its contact with the nasal. Ivakhnenko (1990) reconstructed the lacrimal as contacting the posterior margin of the septomaxilla, but unfortunately, this cannot be confirmed in PIN 4543/1.

The left lacrimal is nearly complete in PIN 4543/1 (Fig. 2). The lacrimal occupies the central portion of the orbitonarial bar, bounded dorsally by the prefrontal and ventrally by the maxilla and jugal. The thin posterior process that overlaps the jugal and forms the anterior margin of the orbit is missing, but the articulating facet within the jugal is present. The anterodorsal portion of the lacrimal is also incomplete in PIN 4543/1, but likely had a splint-like extension anteriorly deep to the prefrontal that formed the posterodorsal corner of the external naris. The anterior region of the lacrimal thickens medially to create a posterior narial wall that widens ventrally to become smoothly continuous with that of the maxilla. The anterior portion of the ventral margin of the lacrimal is highly irregular and directed

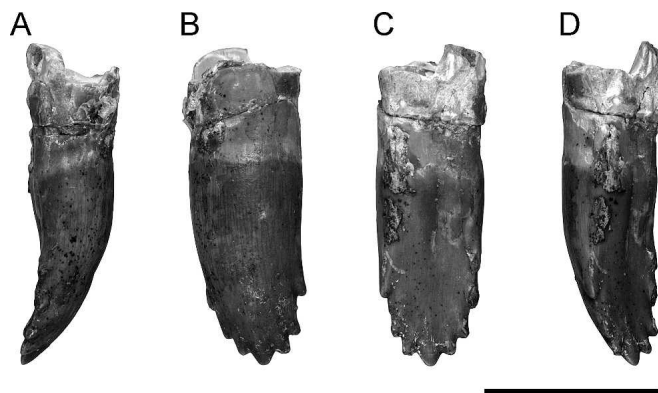


FIGURE 7. Isolated left maxillary tooth 2 from *Ennatosaurus tecton* PIN4543/1. **A**, mesial; **B**, labial; **C**, lingual; and **D**, distolingual oblique views. Scale bar equals 1 cm.

posteroventrally. The posterior half of the ventral margin of the lacrimal is also irregular, producing a posteroventrally directed triangular process that wedges a short distance between the maxilla and jugal (Fig. 2). A small lacrimal foramen is present on its orbital margin.

The nasal forms almost the entire dorsal margin of the external naris. In PIN 1580/14 and PIN 1580/17 the nasals are complete and are short, paired bones that extend from roughly the level of the mid-length of the prefrontal to the tip of the snout. The nasals of *Ennatosaurus tecton* are roughly rectangular in outline, which is similar to the morphology observed in *Cotylorhynchus romeri*, but differ from that in *Casea rutena*, where the nasals appear to expand in width anteriorly (Sigogneau-Russell and Russell, 1974). The dorsal surface of the nasal in *E. tecton* (Fig. 5B) does not appear to extend onto the lateral surfaces of the skull as in *Cotylorhynchus romeri* and *Casea rutena*, but rather is restricted to the skull table. The nasals do, however, project smooth bone ventrally to contribute to the emargination of the narial chamber.

The prefrontal caps the orbitonarial bar and is composed of a dorsal skull table portion and a ventrally extending lateral ramus (Fig. 2). Both prefrontals are severely damaged and incomplete in PIN 4543/1, but the left one preserves the ventral portion of this bone, whereas in PIN 1580/17 the dorsal portion of both are well enough preserved to allow description. The skull table portion of the prefrontal extends approximately equally in both the anterior and posterior directions beyond the orbitonarial bar (Fig. 3). This is in contrast to *Casea rutena*, where there is very little anterior extension beyond the orbitonarial bar (Sigogneau-Russell and Russell, 1974). The anterior and posterior extensions are also nearly equal in *Cotylorhynchus romeri*, but differ in that the extensions are much longer (Laurin and Reisz, 1995). The medial margin of the prefrontal borders both the nasal and the frontal in roughly equal proportions. The lateral surface of the prefrontal is sculptured like the rest of the skull roof, whereas that contributing to the anterior orbital wall is smooth. A ventral orbital process of the prefrontal that is not visible in lateral view extends a short distance on the anterior orbital wall, as in *C. romeri*. The prefrontal appears to be excluded from the external naris in *Ennatosaurus tecton* by a nasal-lacrimal contact, as in both *C. romeri* and *Casea rutena*, but cannot be described with certainty.

The subrectangular frontal (Figs. 2 and 3) is highly autapomorphic in *Ennatosaurus tecton* by virtue of its large contribution to the dorsal border of the orbit. The frontal occupies approximately 50% of the dorsal margin of the orbit. This is in contrast to the frontal being nearly completely excluded (less than 10% of

the margin of the orbit) from the dorsal margin of the orbit in both *Cotylorhynchus romeri* and *Casea rutena*, which exhibit the plesiomorphic condition for basal synspsids (Fig. 1B; Reisz, 1986).

The frontals become slightly constricted at the level of the contribution to the dorsal orbital rim (Fig. 3). The lateral margin of the antorbital portion of the frontal contacts the prefrontal over the orbitonarial bar. The transverse frontal-nasal suture is deeply interdigitated, whereas the slightly wider, transverse frontal-parietal suture is less complicated. The frontals thicken toward their midline contact, where in PIN 4543/1, the ventral surface is contacted closely adjacent to the midline by the sphenethmoid.

The parietal is a broad element in *Ennatosaurus tecton* that forms the bulk of the posterior skull table, and has a highly conservative morphology among caseids. The joined parietals together are subrectangular with a slightly convex anterior margin (Fig. 3). In *E. tecton* the lateral margin of the parietal is overlapped by the large supratemporal, resulting in a small, posterolateral, wing-like exposure of the parietal. A similar configuration appears to be present in both *Cotylorhynchus romeri* and *Casea rutena*. The parietal-frontal contact is serrated at its anterior margin and difficult-to-discern sutures with the postfrontal and postorbital are present along its lateral margin. In PIN 1580/14, the posterior margin of the parietal contacts the postparietal medially and the tabular laterally. The supraoccipital appears to contact the posterior margin of the parietal deep to the postparietal and tabular.

The position of the pineal foramen along the interparietal suture is difficult to determine in PIN 4543/1 because of its incomplete posterior margin (Fig. 3). In other specimens of *Ennatosaurus* it has been figured midway along the medial margin of the parietal (Olson, 1968; Ivakhnenko, 1990). This is in contrast to the more anteriorly located pineal foramen in both *Cotylorhynchus romeri* and *Casea rutena*.

A partial left postparietal is preserved in PIN 4543/1 (Fig. 4), but the element is more completely preserved in PIN 1580/14, PIN 1580/17, and PIN 1580/24, where it is a distinct, paired element, rather than fused into an interparietal, as has been interpreted in *Casea rutena* (Sigogneau-Russell and Russell, 1974). Together the postparietals are roughly V-shaped in posterior view and are incorporated into the occiput. In *Ennatosaurus tecton* and *C. rutena* the lateral ramus of the postparietal is short and deep in comparison to the long and slender ramus of *Cotylorhynchus romeri*. The postparietal is very smooth except for fine longitudinal striations in contrast to the rough surface of the supraoccipital. The ventral border of the postparietal is damaged in PIN 4543/1 and the nature of its suture with the supraoccipital cannot be observed. The postparietal is also incomplete laterally, but likely extends to the level of the medial margin of the posttemporal foramen, as in both *Casea rutena* and *Cotylorhynchus romeri*. The postparietal is presumed to contact the tabular laterally, as in most basal synspsids (Reisz, 1986). Olson's (1968) reconstruction depicted the postparietal as failing to contact the tabular, a condition not supported here.

The supratemporal is a large anteromedially oriented element in caseids, occupying the posterolateral corner of the skull roof. The left supratemporal in PIN 4543/1 preserves only most of the posterior portion of the element (Fig. 3). Once interpreted as the squamosal (Ivakhnenko, 1990), the supratemporal is a rugose element posteriorly and is tightly sutured to the dorsal surface of the squamosal. The incomplete anterior and medial portions limit observation of the full extent of the supratemporal in PIN 4543/1. In *Cotylorhynchus romeri* and *Casea rutena* the supratemporal has a long anteroposterior extension that reaches a level above the anterior half of the temporal fenestra. In PIN 1580/17 the supratemporal appears to be also elongated, over-

lapping the parietal, as it also does in the other two caseids. The supratemporal overlaps the posterior portion of the postorbital and the entire dorsal surface of the squamosal. It also contacts the tabular along its posteromedial margin.

A small fragment of bone located lateral to the left postparietal is interpreted as the tabular in PIN 4543/1 (Figs. 3 and 4), but the right tabular is absent. Our interpretation of the tabular differs from that of Olson (1968) who described it as a slender bone located mainly on the skull table between the parietal and supratemporal. The bone Olson (1968) identified as the tabular is likely the medial portion of the supratemporal. The tabular is a small, smoothly surfaced bone, which in *E. tecton* is an occipital element bounded anteriorly by the parietal, the supratemporal anterolaterally, the posttemporal foramen ventrally, and the postparietal medially. In addition, it is underlain by the supraoccipital. The occipital flange of the squamosal underlies the preserved portion of the tabular and may actually contact it deep to the supratemporal.

A postfrontal was not included in the most recent reconstruction of *Ennatosaurus tecton* (Ivakhnenko, 1990) despite earlier descriptions of its presence (Olson, 1968). In PIN 4543/1 it is a small, narrow bone occupying the posterodorsal corner of the orbit (Fig. 2), and like the prefrontal, is almost entirely restricted to the dorsal skull table except for a ventrally extending process that contributes to the postorbital bar. The skull table portion narrows anteriorly as it contacts the frontal and parietal along its medial margin and the postorbital laterally (Fig. 3). The postorbital overlaps all but a small portion of the ventral orbital process, as indicated by a large sutural scar in the right postfrontal in PIN 4543/1. The postfrontal contribution to the dorsal margin of the orbit is much reduced compared to that in *Cotylorhynchus romeri* and *Casea rutena* because of the much greater contribution of the frontal to this region.

Both postorbitals are incompletely preserved in PIN 4543/1. The left is the most complete, missing the anterior portion of its medial component that narrowly overlapped the postfrontal and also the tip of its ventrally extending process. The postorbital borders the lateral margin of the skull table while forming the anterior half of the dorsal margin of the temporal fenestra and contributes substantially to the upper half of the postorbital bar (Figs. 2 and 3). The dorsomedial margin of the posterior component of the postorbital contacts the lateral margin of the parietal and supratemporal before ending in a narrow transverse contact with the squamosal and it is bounded posteriorly by the supratemporal.

The jugal is best exemplified by the nearly complete left one in PIN 4543/1. The jugal is a triradiate element that occupies the cheek region below the orbit and temporal fenestra, as well as contributes to the postorbital bar (Fig. 2). The anterior, suborbital process in *Ennatosaurus tecton* is autapomorphic among caseids in that it is much deeper and extends much farther anteriorly, creating an extensive sutural contact with the lacrimal. In both *Cotylorhynchus romeri* and *Casea rutena* the anterior ramus is extremely slender and terminates in a narrow vertical contact with the lacrimal. The dorsal postorbital ramus is very slender in *E. tecton*, half the width of that in *C. rutena*, and also slightly narrower than that in *Cotylorhynchus romeri*. As in *C. romeri*, this ramus forms the ventral half of the postorbital bar, tapering in a posterodorsal oblique suture with the postorbital. The posterior ramus of the jugal borders the ventral margin of the very large temporal fenestra for over half its length. The ventral margin has a sinuous suture with the maxilla. The jugal is excluded from the ventral margin of the skull by a maxilla-quadratojugal contact, as in other caseids. As is also typical for caseids, there is no contact between the jugal and squamosal.

In lateral view the squamosal has an outline of an inverted L, forming the posterior-most margin of the skull roof, as well as

contributing to the posterior wall of the adductor chamber (Figs. 2 and 4). The squamosal is comprised of a short anterior ramus and a long ventral ramus. The anterior ramus of the squamosal contributes to the dorsal border of the temporal fenestra and contacts the postorbital anteriorly. The anterior process is very slender in *Ennatosaurus tecton*, similar to that in *Casea rutena* but different from that in *Cotylorhynchus romeri* (OMNH 04329). The rugose posterior portion of the supratemporal covers the entire dorsal surface of the squamosal. The ventral process of the squamosal, termed the 'paraquadratum' by Ivakhnenko (1990), supports a large, medially directed flange on its posterior margin that closes the adductor chamber posteriorly. This occipital flange of the squamosal occurs dorsal to the posterior portion of the quadratojugal and contacts the ascending process of the quadrate along its medial edge and above the level of the quadrate foramen. The ventral process in *E. tecton* is very slender in lateral view and comparable in width to that in *C. rutena* (Sigogneau-Russell and Russell, 1974). The distal end of the ventral process overlaps the posterodorsal portion of the quadratojugal and terminates at a relatively open sutural contact.

The quadratojugal is a wedge-shaped element in *Ennatosaurus tecton* that widens vertically posteriorly, producing a gradual deepening of the cheek below the level of the maxillary dentition (Fig. 2). In both *Cotylorhynchus romeri* and *Casea rutena*, the ventral margin of the quadratojugal is also posteroventrally angled as in *E. tecton*; however, it is much more slender, maintaining nearly uniform vertical height throughout its length. The quadratojugal extends anteriorly to a level nearly equal to the temporal fenestra, though the jugal restricts its contribution to the posterior third of the margin of the fenestra. A medial flange of the quadratojugal smoothly curves onto the posterior surface of the skull to contribute to the posterior wall of the adductor chamber and form the lateral margin of the quadrate foramen. The medial flange is smooth and contacts the posterior surface of the quadrate just dorsal to the large condyles. Above this, the quadratojugal forms the lateral margin of the quadrate foramen.

Palatoquadrate Complex—In PIN 4543/1 the vomers are obscured from a ventral view of the palate by the tightly attached lower jaw. They are also further obscured by the procumbent nature of the snout. Olson (1968) reconstructed the vomers following the typical basal synapsid morphology (e.g., Romer and Price, 1940), as narrow elements, contacting one and other along the midline, and wedged between the internal nares. Posterior to its narrow contribution to the internal naris the vomer is bounded by the palatine laterally and pterygoid posteriorly. Olson (1968) also reconstructed palatal dentition of the vomers as consisting of a single row on each, a situation that cannot be confirmed here.

The majority of the right palatine is broken in PIN 4543/1, and both matrix and the skull table obscure most of the left one. The palatine is a thin plate of bone that forms the lateral and anterior portions of the palate (Fig. 5). In *Cotylorhynchus romeri*, the anterior margin of the palatine borders the posterior margin of the internal naris. This contribution of the palatine to the internal naris is not discernable in PIN 4543/1, but is presumed to exist because of the consistency of this feature among basal synapsids (Romer and Price, 1940; Reisz, 1986). The lateral margin contacts the maxilla in the most extensive contact with the skull roof of all the palatal bones. The medial contact of the palatine with the pterygoid is difficult to make out in PIN 4543/1. In Olson's (1968) reconstruction the placement of this suture is such that the pterygoid is greatly expanded and the palatine forms a narrow, rectangular strip. A similar morphology is reconstructed here.

Although palatal dentition is preserved on the palatine in PIN 4543/1, the distribution cannot be discerned because of the pres-

ence of matrix. The pattern has been interpreted in both *Ennatosaurus tecton* and *Cotylorhynchus romeri* as a narrow elongate cluster of teeth that extends a short distance on the pterygoid before continuing nearly the entire anterior length of the palatine-ptyerygoid contact (Olson, 1968; Laurin and Reisz, 1995).

Despite experiencing a high level of shearing and distortion, the pterygoids are mostly intact in PIN 4543/1. The pterygoid is a thin but extensive element that occupies the posterior and lateral border of the palate (Fig. 5). *Casea rutena* exhibits a large interpterygoid vacuity, but based on observations of PIN 4543/1 and PIN 1580/14, the morphology of the pterygoid in *Ennatosaurus* is considered to be more similar to that of *Cotylorhynchus romeri* (OMNH 04329), where it encloses a very small vacuity that surrounds the cultriform process of the braincase.

The pterygoid can be described in terms of the palatal, transverse, and quadrate processes (Figs. 4 and 5). The convex lateral margin of the palatal process of the pterygoid contacts the ectopterygoid and palatine as it converges anteriorly on the midline, ending in a narrow contact with the palatal process of the premaxilla. The palatal process possesses two dental fields: one along its midline margin and the other directed anterolaterally. The palatal teeth on the pterygoid do not appear to be as massive as those in *Angelosaurus dolani* (Olson, 1968, Fig. 7D) or *Cotylorhynchus romeri* (OMNH 04329).

The transverse flange is heavily crushed and folded upon itself in PIN 4543/1. It forms the posterior portion of the palate and its posterior margin is strongly deflected ventrally, projecting below the level of the ventral margin of the skull. Olson (1968) and Ivakhnenko (1990) reconstructed the posterior margin of the transverse flange as being directed slightly anterolaterally. The transverse flange bears roughly a single irregular row of well-developed teeth along its posterior margin. Evidence of additional much smaller teeth on the body of the transverse flange is present; however, these teeth appear to have been prepared away or incompletely preserved.

The quadrate process of the pterygoid is a thin plate of bone that extends posterodorsally from the transverse flange to meet the pterygoid flange of the quadrate. The quadrate process of the pterygoid overlaps the quadrate medially. At the anterior-most margin of the quadrate process, the ventral portion of the small, plate-like epipterygoid overlies this process.

Only fragments of the right ectopterygoid are visible in PIN 4543/1 (Fig. 4), with matrix and bone obscuring the left. Olson (1968) reconstructed the ectopterygoid in *Ennatosaurus tecton* in a very similar location and morphology to that which was reconstructed in *Cotylorhynchus romeri* (Laurin and Reisz, 1995). It is roughly hemispherical in outline in dorsal view, bounded anteriorly and medially by the palatine and pterygoid, respectively. Its lateral surface is firmly sutured to the jugal. Olson (1968) described the presence of palatal teeth on the ectopterygoid, but this cannot be confirmed here.

The quadrate consists of an ascending plate, a thin, plate-like pterygoid process, and large ventral condyles for articulation with the lower jaw (Figs. 4 and 5). Ventrally, the triangular ascending plate of the quadrate forms the medial margin of the quadrate foramen and contacts the occipital flange of the squamosal, to close the adductor chamber. In posterior view the condylar surface is slightly angled ventromedially. The shapes of the condyles are uncertain, but are presumed to be similar to those in other caseids, such as *Cotylorhynchus romeri*, where they are ovoid. This morphology is mirrored in the shape of the mandibular glenoid. The condyles terminate below the level of the marginal dentition, which is a typical feature of caseids and herbivorous animals in general (Kemp, 1982).

The epipterygoid is a small element located dorsally at the anteriormost corner of the quadrate process of the pterygoid

along its medial margin (not visible). The presence of an epipterygoid has only been confirmed in two caseids, *Casea broilii* and *Ennatosaurus tecton* (Olson 1968), although it was undoubtedly present throughout the group. In PIN 4543/1, the ventral portion of the right epipterygoid is preserved, corroborating Olson's (1968) earlier observations of its presence. The epipterygoid is composed of a ventral body in the plane of the palate, overlapping the pterygoid, and a thin vertical process that extends toward the underside of the parietal. The ventral body of the epipterygoid accepts the basiptyergoid process of the basisphenoid. The nature of this articulation cannot be observed in PIN 4543/1. The vertical portion of the epipterygoid is missing in PIN 4543/1, but would have been a slender rod-like process, as indicated by the fractured surface on the ventral portion of the element.

Braincase—The sphenethmoid is a vertical structure extending ventrally from the skull table into the interorbital space. The presence of a sphenethmoid has only been confirmed in *Casea broilii* and *Ennatosaurus tecton* among caseids (Olson, 1968). A partial sphenethmoid is present in PIN 4543/1, extending from the frontal ventrally toward the cultriform process.

Only the basal tubera and a fragment of the cultriform process of the parasphenoid are preserved in PIN 4543/1 (Figs. 2, 3). In comparison with other caseids the parasphenoid is autapomorphic for *Ennatosaurus tecton* in its relatively narrow width of the basal tubera in comparison to other caseids (Fig. 5C). The parasphenoid also possesses a deep cultriform process extending to approximately the longitudinal midpoint of the orbit. The dorsal margin of the parabasisphenoid has a deep excavation interpreted here as the sella turcica. Posterodorsally, the basisphenoid contacts the prootic. A fracture is present in PIN 4543/1 and might coincide with the suture between these two bones. If the suture does in fact run through the fractured region, then the prootic, rather than basisphenoid, appears to contribute to the posterior vertical wall of the sella turcica. This would be similar to the condition observed in some of the more derived basal synapsids (Reisz, 1986). A small opening, possibly representing the fenestra ovalis occurs along this suture. Its location matches closely the description given by Romer and Price (1940) whereby the basisphenoid forms the ventral and posterior margins of the fenestra. There is no stapes preserved in PIN 4543/1 to add support to this interpretation.

The prootic forms the anterior portion of the lateral wall of the braincase. Both prootics are present in PIN 4543/1, though only the right one is in articulation (Fig. 3). Here, the prootic is an anteroventrally inclined bone, extending from the beneath the dorsal margin of the supraoccipital just medial to the posttemporal foramen. It continues anteriorly a short distance until it makes contact with the basisphenoid. Olson (1968) illustrated an unusually long process that he termed the 'prootic process,' extending from the prootic to the basisphenoid in *Angelosaurus romeri*. *Ennatosaurus tecton* lacks such a hypertrophied process. The suture with the basisphenoid appears to be obscured by a fracture running through the area. Olson (1968) described a groove on the prootic leading anteriorly from the posttemporal foramen in caseids. No such groove was observed in this region in PIN 4543/1, or in *Cotylorhynchus romeri* (OMNH 04329).

The supraoccipital forms the dorsal portion of the occipital plate, where it is ventrally fused to the opisthotic (Fig. 5). The supraoccipital is heavily damaged in PIN 4543/1, but appears as a relatively small and laterally restricted bone when compared to those of other basal synapsids (Romer and Price, 1940; Reisz, 1986). The main body of the bone forms the medial margin of the posttemporal foramen. As is the case for all caseids, and basal synapsids in general, the distinction between the supraoccipital and the opisthotic is nearly impossible to identify. The surface of the supraoccipital area is marked by dorsolateral striations,

whereas striations on the area of the opisthotic are oriented ventrolaterally. A faint border of separation between these two may demark the boundaries of these two bones. This border occurs approximately at the level of the ventral margin of the posttemporal foramen, resulting in a dorsoventrally short supraoccipital in *Ennatosaurus tecton*. The lateral process of the supraoccipital appears to contact the ventral surfaces of the parietal and tabular.

The opisthotic occupies the ventral portion of the occipital plate, forming broad, rectangular paroccipital processes (Fig. 5). The medial portion of the opisthotics are disturbed by a deep cleft in PIN 4543/1, likely formed when the basioccipital-exoccipital complex broke away from the braincase. The paroccipital process is broad and forms the ventral border of the posttemporal foramen. As in *Cotylorhynchus romeri*, the paroccipital process in PIN 1580/14 flares dorsoventrally as it approaches the squamosal. The opisthotic appears not to have contacted the squamosal, as suggested by Olson (1968). Rather, it appears as though the entire occiput, comprising the supraoccipital, opisthotic, exoccipital, and basioccipital, was offset posteriorly from the transverse plane extending beyond the posterior margin of the squamosal and quadrate.

The basioccipital is a median element that is ventral to the opisthotic and forms the posterior floor of the braincase. The basioccipital is missing in PIN 4543/1, which is unexpected given the typically strongly sutured union between the basioccipital and basisphenoid (Olson, 1968). The basioccipital is preserved in PIN 1580/14, though details are difficult to discern from the available photographs. It appears as though the basioccipital forms the ventral border of the foramen magnum in PIN 1580/14. This contrasts with the condition reconstructed for *Cotylorhynchus romeri* in which the exoccipitals exclude the basioccipital from the margin of the foramen magnum (Laurin and Reisz, 1995). In PIN 1580/14 the exoccipitals are sutured to the dorsal surface of the basioccipital. This is similar to the condition interpreted for *Ennatosaurus tecton* by Olson (1968) and also *Casea rutena* (Sigogneau-Russell and Russell, 1974). The occipital condyle appears to be roughly crescent-shaped in posterior view. A sharply ventrally deflected articular surface of the occipital condyle is characteristic for caseids (Olson, 1968).

The exoccipitals are not present in PIN 4543/1, but can be seen in PIN 1580/14 where they contact the basioccipital ventrally and the medial margin of the posterior surface of the opisthotic dorsally. Together the exoccipitals form the lateral and portions of the dorsal margin of the foramen magnum. In *Ennatosaurus tecton* the dorsal portion of the exoccipital flares laterally into a wing-like shape and almost meets its mate at the dorsal midline of the foramen magnum. A similar condition has been suggested for *Cotylorhynchus romeri*, but not for *Casea rutena*.

Lower Jaw—The dentary is a massive tooth-bearing element that occupies approximately 60% of the length of the lateral surface of the lower jaw (Fig. 2). In lateral view the dentary is similar in morphology to that in *Cotylorhynchus romeri* and *Casea rutena* in being roughly rectangular anteriorly and gradually tapered posterodorsally, terminating at the dorsal margin of the lower jaw. The dentary forms all but a small ventral portion of the mandibular symphysis. The ventral margin of the dentary is narrowly excluded from the ventral margin of the mandible by a splint-like exposure of the splenial that tapers posteriorly. In *Cotylorhynchus romeri* (Laurin and Reisz, 1995) the surangular overlaps the posteriormost tip of the dentary, excluding it from the dorsal margin of the lower jaw. This is not seen in *E. tecton* or *Casea rutena*.

In medial view the dentary is overlain by the splenial anteriorly, as well as by the prearticular centrally and the coronoid(s) dorsally (Fig. 4). The internal surface of the alveolar margin is slightly swollen in the form of a maxillary shelf to accommodate

the marginal dentition. The dentary typically forms the roof and lateral wall of the Meckelian canal (Romer and Price, 1940; Romer, 1956), and would presumably do the same in *Ennatosaurus tecton*.

Olson (1962) reported ten teeth in each mandible of the lower jaw of *Ennatosaurus tecton*. The lingual surfaces of five teeth can be observed in PIN 4543/1, as well as in an isolated fragment of dentary (PIN 4543/uncatalogued 2; Fig. 8), and show the same broadly spatulate morphology as the maxillary teeth. The cusps are very well developed and range in number between five and seven. As in the upper dentition, the dentary teeth also decrease serially in size posteriorly, possess an expanded shoulder on the lingual surface, and have lingually curved crowns.

The splenial forms the ventral margin of the anterior half of the lower jaw (Fig. 2). Anteriorly the splenial is deep, roughly double the depth of the posterior portions in lateral view, and forms the ventral portion of the mandibular symphysis. In lateral view the splenial is long and slender, and gradually narrows posteriorly along the ventral margin of the lower jaw from the symphysis to a level just anterior to the low coronoid eminence. In medial view, it is much wider but is incomplete dorsally in PIN 4543/1 (Fig. 4). It forms the ventral third of the symphysis and then divides a short distance posteriorly into two moderately broad processes: one extending along the ventral margin of the lower jaw, contacting the ventral margin of the prearticular before ending in an overlapping posteroventral oblique suture with the angular; the second process extends posterodorsally between the exposure of the dentary and prearticular before contacting the ventral margin of the coronoid(s). It is typical of early amniotes for the splenial to contact the coronoid(s) (Romer, 1956), and was described in *Ennatosaurus tecton* by Olson (1962) and in other caseids, such as *Cotylorhynchus romeri* (Laurin and Reisz, 1995), but unfortunately cannot be confirmed in PIN 4543/1. The reconstruction here of the relationship between the splenial and prearticular in *E. tecton* follows that illustrated by Olson (1968). This is also interpreted to be the pattern in *C. romeri* (Laurin and Reisz, 1995).

The number of coronoids present in *Ennatosaurus tecton* PIN 4543/1 is difficult to determine because of damage to the region. Primitively, multiple coronoids are present in amniotes (Romer, 1956). Olson (1968) reconstructed the lower jaw of *E. tecton* with two coronoids, which conflicted with earlier interpretations of only a single coronoid present in caseids (Romer and Price, 1940). Olson (1968) noted that *Casea broilii* likely had two coronoids, which contradicts Williston's (1913:fig. 2) earlier illustration of only a single coronoid for this species.

Sigogneau-Russell and Russell (1974) reported the possible presence of the base of a second or posterior coronoid in *Casea rutena* (MNHN MCL-2), but this is also difficult to determine with certainty. *Cotylorhynchus romeri* possesses only a single, large anterior coronoid (Romer and Price, 1940; Laurin and Reisz, 1995). The reconstruction of *E. tecton* presented here follows Olson (1968) in illustrating two coronoids, as there is no evidence to the contrary.

In PIN 4543/1 isolated denticle-like structures preserved in the region of the posterior coronoid that may have been attached to this element were subsequently prepared away, but remnants of their bases remain in place. The presence of coronoid dentition is a primitive feature in amniotes (Romer, 1956) and among the caseids has been reported in the basal form *Casea broilii* (Williston, 1910b; Romer and Price, 1940).

The lateral exposure of the surangular is restricted to the posterior portion of the lower jaw (Fig. 2). This element appears to be smaller than that in either *Cotylorhynchus romeri* or *Casea rutena*. It is narrowly rectangular, extending between the articular and the low coronoid eminence formed by the dentary while maintaining a ventral contact with the angular. The surangular in PIN 4543/1 is poorly exposed in medial view. It contacts the coronoid anterodorsally and likely formed the lateral wall of the Meckelian canal, as is typical in basal amniotes (Romer and Price, 1940; Romer, 1956). Primitively the surangular extends posteriorly to wrap around to the end of the mandible to completely sheath the lateral surface of the articular (Romer, 1956). The overlapping of the articular by the surangular is apparent in *E. tecton*; however, it does not continue onto its posterior surface, thus allowing the articular to be observed in lateral view (Fig. 2).

The angular is the second largest element of the lower jaw. Ivakhnenko (1990) reconstructed the angular as larger than the dentary, which is not supported by PIN 4543/1, where the angular occupies the greater portion of the lateral surface of the lower jaw (Fig. 2). Anteriorly the angular is overlapped slightly by the dentary whereas its entire dorsal margin contacts the surangular. The angular tapers in depth both anteriorly because of the tapering of the dentary and posteriorly to its termination at the posterior margin of the lower jaw. The angular, along with the surangular, overlaps all but a narrow, rugose-surfaced, posterior margin of the articular. Although the angular in PIN 4543/1 is slightly incomplete at its posteriormost margin, a sutural scar delineates clearly its extent.

In medial view (Fig. 4) the angular forms the floor and lateral wall of the adductor fossa (Romer, 1956). A small elongate oval Meckelian foramen is bounded by the angular ventrally and the prearticular dorsally. The prearticular overlaps the middle portion of the angular as it forms the medial wall of the Meckelian canal (Romer, 1956). As in *Cotylorhynchus*, the ventral margin of the angular is a thin keel in PIN 4543/1 that serves as an attachment site for the anterior and posterior pterygoideus muscles (Kemp, 1982).

Although the margin of the prearticular in PIN 4543/1 is damaged, it obviously has the form of a long, thin, dorsoventrally slender plate of bone on the medial surface of the lower jaw (Fig. 4). Olson (1968) depicted the prearticular in *Ennatosaurus tecton* as bounded by the coronoid dorsally, the splenial anteriorly, and the angular ventrally. Posteriorly, the prearticular typically overlaps the medial surface of the articular (Romer, 1956), though the extent of the overlap cannot be determined in PIN 4543/1.

The articular is a small, complex bone that bears the articulating surface to receive the quadrate condyles (Fig. 4). The small laterally exposed surface of the articular is highly rugose. The articular is sandwiched between the surangular and angular laterally, the prearticular medially, and the articular surface possesses two subparallel anteroposteriorly oriented depressions.

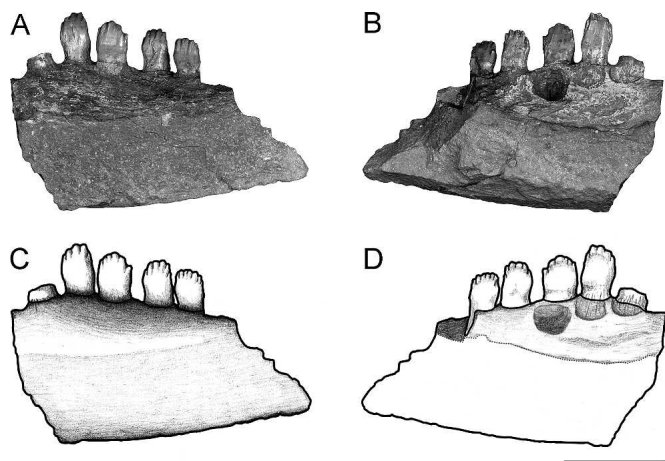


FIGURE 8. Photographs and drawings of an isolated fragment of the left dentary from *Ennatosaurus tecton* (PIN 4543/uncatalogued 2). **A**, lateral and **B**, medial view. Scale bar equals 1 cm.

The plane of the articular surface slopes medioventrally, as in *Cotylorhynchus romeri* and probably in *Casea rutena*. The articular surface occupies a level below that of the dentition, a convergently acquired feature common to many herbivorous animals (Davis, 1964; Throckmorton, 1976; Greaves, 1995; Lee et al., 1997). A broad medially directed process in PIN 4543/1 supports the articular surface ventrally. Ivakhnenko (1990) included a retroarticular process in his reconstruction of *Ennatosaurus tecton*, but this is likely a misinterpretation of the large medial process.

PHYLOGENETIC ANALYSIS

Our phylogenetic analysis of Caseidae was performed on six taxa from five of the eight described genera in the group. The three most speciose of the North American caseid genera are *Casea*, *Cotylorhynchus*, and *Angelosaurus*. In all three genera the characters used to distinguish new species from earlier described congeners were based on differences in size and proportions of various elements (Olson, 1954, 1962; Olson and Beerbower, 1953; Olson and Barghusen, 1962). In the absence of a well-documented ontogenetic series for these taxa, it is not possible to determine whether the more recently described species are distinct taxa. They were therefore excluded from the current analysis and await re-evaluation. The taxa excluded are *Casea nicholsi*, *Casea halselli*, *Cotylorhynchus bransoni*, *Cotylorhynchus hancocki*, *Angelosaurus greeni*, and *Angelosaurus romeri*. The highly fragmentary postcranial remains of the single species of *Caseiodes*, *C. sanangeloensis*, were noted to be very similar to those of *Casea*, again differing only in relative proportions of certain elements (Olson and Beerbower, 1953). Similarly, *Caseopsis agilis* was described as a lightly built caseid differing only from other caseids of similar size in the relative proportions of the limbs and a tall iliac blade (Olson, 1962). Until further study, none of these taxa can be confidently presumed as valid based on their current diagnoses and were therefore, also excluded from the current analysis. The ingroup taxa used were *Casea broilli*, *Casea rutena*, *Ennatosaurus tecton*, *Cotylorhynchus romeri*, *Angelosaurus dolani*, and *Oromycter dolesorum*.

Two diadectomorphs, *Diadectes* and *Limnoscelis*, and Reptilia were used as the outgroup taxa in the current analysis. Several representative basal reptile taxa were examined to establish the character polarity for the node. The outgroups were rooted at a basal polytomy in PAUP*4.0b10 (Swofford, 2002). Two varanopid taxa, *Mycterosaurus* and *Varanops*, were included as well, but not designated as outgroups in PAUP.

A character list (Appendix 1) consisting of 73 cranial and 33 postcranial characters was used in this analysis. The character-taxon matrix (Appendix 2) was analyzed in PAUP* 4.0b10 (Swofford, 2002), using the branch and bound algorithm. All characters were unordered. A single most-parsimonious tree with a length of 182 steps was obtained (Fig. 9). The tree has a Consistency Index (CI) of 0.71, a Homoplasy Index (HI) of 0.29, a Retention Index (RI) of 0.76, and a Rescaled Consistency Index (RC) of 0.54. Bootstrap (1000 replicates using the Branch and Bound algorithm) and Bremer decay analyses were performed on the matrix to assess the robustness of the tree.

DISCUSSION

Caseid Phylogeny and Character Analysis

The current phylogenetic hypothesis (Fig. 9) is well supported as indicated by high bootstrap values (most greater than 90%) and Bremer decay indices (most above 3). The following is a discussion of the unambiguous, shared cranial characters for each of the major caseasaurian and caseid nodes. The number listed here corresponds to the character number listed (Appendix 1) and the bracketed number at the end of the character

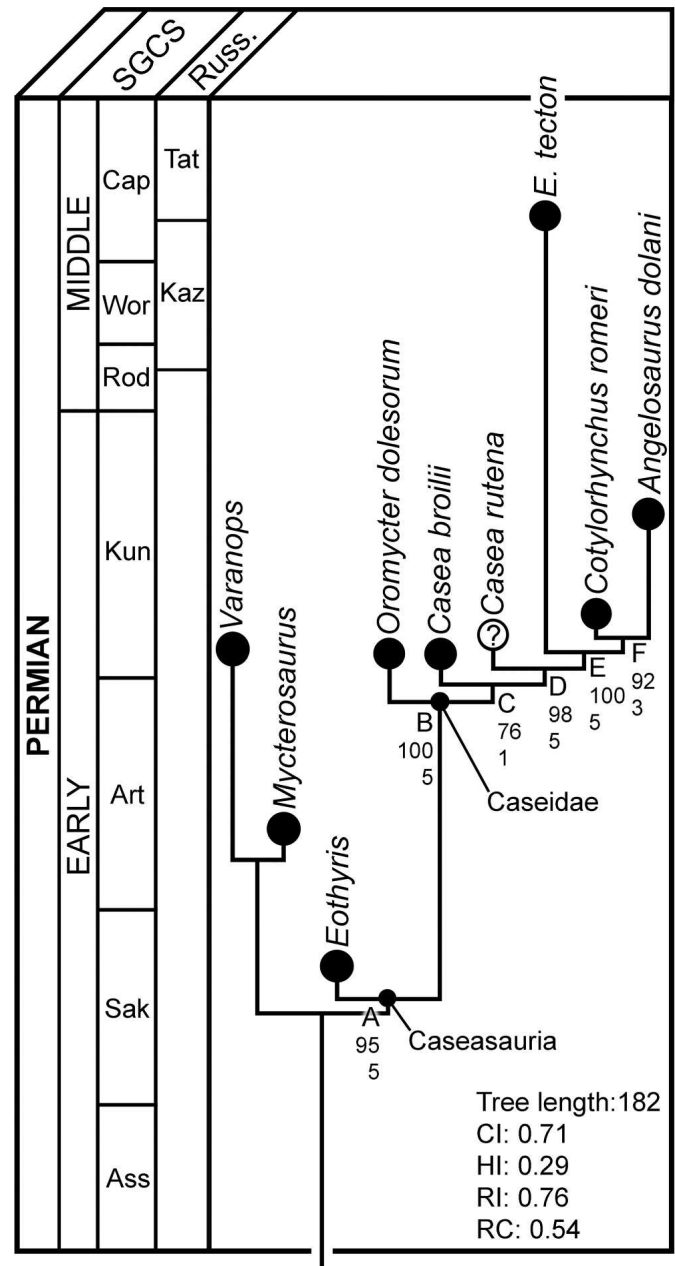


FIGURE 9. A time-calibrated phylogenetic hypothesis for caseid relationships using the most recent correlation of the North American and Russian Permian strata (Lucas, 2004). Stratigraphic data is based on approximate first appearances of each terminal taxon. The precise stratigraphic occurrence of *Casea rutena* is uncertain at this time as it occurs within a unit that spans both the later Early Permian and early Middle Permian. Below each node are the bootstrap support values followed by Bremer decay values. Outgroup taxa, *Diadectes*, *Limnoscelis*, and Reptilia, were rooted at a basal polytomy and are not figured here. **Abbreviations:** Art, Artinskian; Ass, Asselian; Cap, Capitanian; CI, Consistency Index; HI, Homoplasy Index; Kaz, Kazanian; Kun, Kungurian; RC, Re-scaled Consistency Index; RI, Retention Index; Rod, Roadian; Russ., Russian stratigraphy; Sak, Sakmarian; SGCS, Standard Global Chronostratigraphic Scale; Tat, Tatarian, Wor, Wordian.

description indicates the direction of the character transformation.

Clade A (Caseasauria)—Caseasauria, comprised of Eothyrididae and Caseidae (Reisz, 1986), is recovered in the current

analysis and is one of the best-supported clades (95% bootstrap and decay index of five). Caseasauria is diagnosed by five unambiguous synapomorphies:

1. Premaxillary ascending process projects anterodorsally (0→1). Eothyridids and caseids share an anterodorsally directed ascending process of the premaxilla (1), resulting in a forward projecting rostrum that overhangs the tooth row. This feature is much further exaggerated in caseids by an increase in the height of the process, which results in a highly procumbent snout that characterizes the group. This character evolves convergently in the diadectid *Limnoscelis*. The outgroup taxa, excluding *Limnoscelis*, and varanopid synapsids all possess a posterodorsally directed ascending process of the premaxilla (0). This results in the more typical snout profile for basal amniotes and is interpreted as the plesiomorphic condition for amniotes.
 33. Shape of the squamosal wide, with the posterior and temporal margins being subparallel (0→2). The squamosal is a very wide and robust element with subparallel margins in eothyridids and all caseids (2) with the exception of *Ennatosaurus tecton* and *Casea rutena*. *Ennatosaurus tecton* and *C. rutena* possess a much narrower, almost rod-like squamosal morphology (1). The narrow squamosals are considered autapomorphic for these taxa. The morphology of the squamosal in the outgroup taxa and the mycterosaurine varanopid *Mycterosaurus* is wide, but tapers dorsally (0). The derived varanopid *Varanops* exhibits a narrow squamosal like that in *E. tecton* and *C. rutena*; however, this morphology is interpreted as convergent.
 40. Paroccipital processes project posterior to the squamosals, such that they are visible in lateral view (0→1). The paroccipital processes of the opisthotic in caseasaurians project posteroventrally beyond the posterior margin of the skull formed by the squamosals (1). This feature produces an awning-like morphology of the occipital plate with the paraoccipital processes being visible in lateral view. This is the derived condition and autapomorphic for caseasaurians. In all of the outgroup taxa, as well as in varanopids and in basal synapsids in general, the profile of the occiput, including the paraoccipital processes, follows the profile of the posterior margin of the skull closely and does not project beyond the squamosals (0).
 50. Preorbital length of the skull is short, less than 1/3 the total skull length (0→1). The plesiomorphic condition for the length of the preorbital region of the skull is within the range of one-third to one-half the total skull length (0). Reptiles, the diadectomorph *Diadectes*, and varanopids all possess this condition. The preorbital length of caseasaurians is relatively short in comparison to most other basal synapsids, being less than 1/3 the total skull length (1). Shortening of the facial region is a typical modification for herbivorous animals, as it increases the bite force at the front of the jaws and reduces the speed of closure of the mouth (Kemp, 1982). The appearance of this feature at the caseasaur node (Node A) and the exaggeration of it at the caseid node (Node B) suggests a transition to an herbivorous diet.
 58. Coronoid eminence of the lower jaw is located at a level approximately 40% from anterior end of the lower jaw (0→1). The coronoid eminence is located within the anterior half of the lower jaw in caseasaurians, at approximately the 40% mark of the jaw's length (1). This is a much more anterior location than is typical for basal synapsids and reptiles. The outgroup taxa, excluding *Diadectes*, and varanopids exhibit the plesiomorphic state whereby the coronoid eminence is located within the posterior third of the lower jaw (0). Edaphosaurids, as well as *Diadectes* also possess an anteriorly located coronoid eminence. This morphology evolved convergently in these taxa and is likely related to improving jaw mechanics associated with herbivory (Kemp, 1982).
- Clade B (Caseidae)**—Caseidae is also well supported (100% bootstrap and decay index of 5) and is more closely related to Eothyrididae than to other eupelycosaurians (e.g. varanopids) as previously suggested by Reisz (1986). Five unambiguous synapomorphies diagnose Caseidae:
17. Medial projection of the lacrimal contributes to narial emargination (0→1). A derived feature of the caseid cranium is the development of a medial shelf emarginating the external naris, formed by some or all of the circumnarial elements. The absence of a medial shelf is the plesiomorphic condition (0), being absent in eothyridids, varanopids, and the outgroup taxa. The degree of development of the emargination varies within Caseidae, including variation in the number of circumnarial elements contributing to this feature. All caseids possess at least a minor contribution from the lacrimal (1). This suggests the early development of this feature of caseids began with a modified lacrimal and was followed by the other elements later, given the current hypothesized relationships within Caseidae.
 53. Absence of an anterior tapering of the lower jaw (0→1). The shape of the lower jaw unites caseids. There is little to no anterior tapering of the lower jaw in lateral view (1). This morphology is achieved by the fairly consistent depth of the anterior portions of the dentary and the deepening of the splenial anteriorly. This morphology evolved convergently in the diadectomorph *Limnoscelis*. Similarly, edaphosaurids possess a relatively deep anterior portion of the lower jaw compared to most basal synapsids, suggesting that this may be an adaptation to an herbivorous diet. All other outgroup taxa and varanopids possess a lower jaw that tapers anteriorly (0).
 68. First premaxillary tooth is the largest in the tooth row (1→0). The first premaxillary tooth in all known caseids is the largest in the tooth row and subsequent teeth decrease in size posteriorly (1). In *Oromycter dolesorum*, the first tooth is slightly shorter than the second; however, upon close examination, the first tooth appears to be heavily worn and actually has a much broader base, making it overall more robust than any other preserved tooth. This strongly contrasts with the condition seen in nearly all other reptiles and basal synapsids in which the first tooth is not the largest (0). In most basal synapsids the caniniform region boasts the largest tooth. In forms lacking a caniniform region, such as edaphosaurids, the first tooth is either equal to, or less than, the size of the other teeth in the row.
 72. Shape of the lingual surface of the marginal dentition is spatulate (0→1). Caseids possess highly complex and adapted marginal dentitions related to their diet. Apically the lingual surfaces of the teeth flatten out and become strongly spatulate in morphology (1). Although this general morphology has evolved convergently in several reptilian lineages, it is highly diagnostic for caseids in the context of basal synapsids. All outgroups examined here, with the exception of the apparently uniquely evolved dental morphology in *Diadectes*, possess conical teeth with convex lingual surfaces (0), which is interpreted as the plesiomorphic condition.
 73. Marginal dentition with lingual shoulder and lingual curvature (0→1). In all caseids, the crowns of the marginal dentition possess an expansion, or shoulder on the lingual surface and are curved lingually (1). There is variation in the point of onset and the degree of the curvature among caseids. In *Cotylorhynchus romeri* the curvature is limited to the apices

of the crowns. Where as in *Ennatosaurus tecton*, the curvature initiates just apically to the expanded waist and tends to be greater in degree. The teeth of the outgroup taxa and varanopids possess the plesiomorphic condition in which no shoulder is present and the teeth are curved posteriorly or not at all (0).

Clade C—This clade is diagnosed by the possession of only a single unambiguous cranial character, likely due to the highly fragmentary nature of *Oromycter dolesorum*. This is the most weakly supported node with bootstrap support of only 76% and a Bremer decay index of one. The following single derived character diagnoses node C:

7. Presence of a vertical medial flange on the maxilla that emarginates the posterior of the external naris (0→1). In all caseids of Clade C the maxilla contributes to the emargination by forming the posterior portion (1). The absence of a maxillary contribution (0) is interpreted as the plesiomorphic condition. With the appearance of the maxillary contribution come the contributions from the premaxillary and nasal at Node C. This feature was formerly considered to be a diagnostic feature for all caseids (Romer and Price, 1940; Olson, 1968; Reisz, 1986), and thus, the diagnosis for Caseidae is modified here.

Clade D—This clade divides the putative sister taxon relationship between the two *Casea* species (Sigogneau-Russell and Russell, 1974) resulting in a paraphyletic *Casea*. This topology is particularly well supported with a bootstrap value of 98% and has the highest Bremer decay index of 5. As such, a reevaluation of *C. rutena* is in preparation. Six unambiguous cranial synapomorphies diagnose this node:

9. Tallest point of the postnarial process of the maxilla is anteriorly located (0→1). This character describes the location of the apex of the postnarial process of the maxilla and is independent of its shape (character eight). In *Oromycter dolesorum* and *Casea broilii*, the apex of the postnarial process of the maxilla occupies a central position below the orbitonarial bar (0). The location of the apex transforms at Node D becoming more anterior (1). In *Casea rutena* the apex of the rounded postnarial process is located anteriorly. In *Ennatosaurus tecton* and *Cotylorhynchus romeri* the pointed tip of the postnarial process actually contributes to the posterior margin of the external naris. In other basal synapsids, when a postnarial process is present, as in varanodontine varanopids, it assumes the plesiomorphic condition of being centrally located.

14. Postparietal contributes to the posttemporal foramen (0→1). The contribution of the lateral ramus of the postparietal to the border of the posttemporal foramen (1) is a feature unique to the caseids of Clade D. This feature appears to be related to the increase in the lateral extent of the postparietal and not a decrease in the distance between the posttemporal foramina. *Cotylorhynchus romeri* has a much wider supra-occipital, and thus, a greater distance between the foramina than that in *Casea rutena*, and yet in both taxa the postparietal extends to the posttemporal foramen. The postparietal is laterally restricted in all of the other taxa included in the current analysis and does not contribute to the border of the posttemporal foramen (0).

16. The lacrimal is taller than it is long (0→1). In the two most basal caseid taxa, as well as *Eothyris*, varanopids, and the outgroup taxa, the lacrimal is a short element that is longer than it is tall (0). *Casea rutena* exhibits a morphology that could be considered intermediate between these basal forms and the condition seen in *Ennatosaurus tecton* and *Cotylorhynchus romeri*, as it is not quite as slender as in these latter forms. However, the lacrimal in *Casea rutena* is still taller than it is long, which is interpreted as the derived condition

here (1). This shift in lacrimal morphology may be related to the enlargement of the external naris and orbit at the expense of the lacrimal and other orbitonarial bar elements.

28. The supratemporal is large and elongate, approximately the midline length of the parietal (0→2). The supratemporal of the caseids basal to Node D, eothyridids, and outgroup taxa is broad and shorter than the length of the parietal at its midline (0). The morphology of the supratemporal is also broad in members of Clade D but transforms from the plesiomorphic condition to become an elongate element, roughly the length of the parietal at the skull-table midline (2). Varanopids and the other more derived basal synapsid groups possess a relatively elongate supratemporal in comparison to the length of the parietal; however, it is much more slender and almost splint-like, residing in a groove within the posterior flange of the parietal (1).

29. The length of the lateral temporal fenestra is greater than 30% of the length of the skull (1→2). The outgroup taxa in this analysis possess no lateral temporal fenestra (0). Within synapsids a single temporal fenestra is present and varies greatly in its size relative to the skull length. A large lateral temporal fenestra relative to the skull length is characteristic of all caseids. However, there is a trend within caseids to enlarge the size of the fenestra even further. The length of the lateral temporal fenestra increases at Node D from a moderate size relative to the skull length, roughly between 15–25% of the total skull length (1), which is considered the plesiomorphic condition for synapsids, to a length greater than 30% of the skull length (2). This transformation to a very large temporal fenestra evolves convergently in the more derived varanodontine varanopids from a smaller sized fenestra.

55. Splenial is dorsoventrally deepened at the symphysis (0→1). The plesiomorphic shape of the splenial is a uniform thickness when viewed in lateral aspect (0). Caseids of Clade D possess a splenial that deepens at the mandibular symphysis. *Casea rutena* exhibits the least deepening, with only a minor increase in the thickness. *Ennatosaurus tecton* and *Cotylorhynchus romeri* exhibit a great increase, nearly doubling in thickness anteriorly. This reduces the proportion of the contribution of the dentary to the symphysis and it increases as well the overall depth of the lower jaw anteriorly.

Clade E—This clade includes the most derived clade consisting of *Angelosaurus dolani* and *Cotylorhynchus romeri*, as well as its sister taxon, *Ennatosaurus tecton*. This node is very well supported with a bootstrap support value of 100% and a decay index of 5. The greatest number of unambiguous synapomorphies (11), seven of which are cranial, characterizes this node. The seven unambiguous cranial synapomorphies are:

5. External naris greater than 75% or equal to the height of the orbit (0→1). Caseids in general are characterized by hypertrophied external nares in comparison to eothyridids and other basal synapsid groups. However, the caseids of Clade E further increase the size of the external naris relative to the orbit. In *Oromycter dolesorum*, *Casea broilii*, and *C. rutena* the height of the external naris is between 30% and 75% of the height of the orbit (0), though all taxa are on the upper end of this range. In the caseids of Clade E the external naris height is greater than 75% of the height of the orbit (1). In *Cotylorhynchus romeri* the external naris is nearly equal in height to the orbit.

8. Postnarial ascending process of the maxilla is present and pointed dorsally (1→2). The presence of a postnarial process of the maxilla is the derived condition for many basal synapsid groups, and its absence (0) is considered plesiomorphic in the current analysis. The dorsal margin of the post-narial

process may be rounded (1) as it is in *Oromycter dolesorum*, *Casea broilii*, and *C. rutena*, or pointed as it is in the more derived caseids. This pattern of morphology of the postnarial process evolves convergently in the derived varanodontine varanopids.

12. Ventral edge of the maxilla is slightly to strongly convex (0→1). Among all the taxa considered here, the possession of a convex ventral margin of the maxilla (1) is unique to members of Clade E. The plesiomorphic condition from which the convex morphology evolved is that of a straight ventral margin (0). A convex ventral margin of the maxilla does, however, evolve convergently in other basal synapsid groups that were not considered here, such as ophiacodontids and sphenacodontids.
20. Dorsal ramus of the jugal is greater than or equal to 50% of the height of the orbit (0→1). The plesiomorphic condition for the dorsal ramus is wide, with a maximum dorsal extent less than 50% of the orbit height (0). There is a dramatic change in the morphology of the dorsal ramus at Node E to a tall, narrow, slender shape that extends to 50% or more of the orbit's maximum height (1). This condition evolves convergently in the small mycterosaurine varanopid, *Mycterosaurus*, and appears to be autapomorphic for this taxon.
22. Well-defined right angle on the postorbital formed between the skull table and the temporal portion (0→1). The transition between the skull table and the lateral surface of the skull is smooth and round in diadectomorphs, excluding *Diadectes*, reptiles, eothyridids, and caseids basal to Clade E, as indicated by the absence of a well-defined angle on the postorbital (0). Within Caseidae this smooth shape transforms into a well-defined right angle on the postorbital (1) in members of Clade E. This results in the more box-like appearance of the skull that characterizes these forms. This morphology of the postorbital evolves convergently in varanopids.
38. Anterolateral dental field on the palate is reduced and does not reach the basicranial area (0→1). The pattern of the palatal dentition is reduced within Caseidae from a nearly ubiquitous distribution to one possessing three discrete fields: a medial field, anterolateral field, and one along the transverse flange of the pterygoid. At Node E the anterolateral field is further reduced, such that it does not reach the basicranial area (1). In *Casea rutena* the anterolateral and medial fields are confluent and together they extend posterior to reach a point in line with the basicranial articulations (0). This is interpreted as the plesiomorphic condition and is also that exhibited by eothyridids, varanopids, and the outgroup taxa.
49. Lateral temporal fenestra is subrectangular in shape (1→3). The plesiomorphic condition for the shape of the lateral temporal fenestra when present (absent = 0) is subcircular (1). This condition is retained in basal caseids and transforms in members of Clade E to a subrectangular shape (3). The temporal fenestra is gradually enlarged, moving crownward through the caseid phylogeny, and the transformation in shape contributes to the overall enlargement of the fenestra. This shape is not observed in any other basal synapsid group considered here, making it autapomorphic for the group. In varanopids the shape of the fenestra is transformed from the plesiomorphic subcircular shape to one that is similarly subrectangular, but differs significantly from that of caseids in the presence of an acute angle in the posteroventral corner of the fenestra (2).

Clade F—The final and most derived clade is composed of a sister-taxon relationship between the two youngest North American caseids, *Angelosaurus dolani* and *Cotylorhynchus romeri*. Clade F has a 92% bootstrap support and a decay index of 3. Only four unambiguous characters diagnose this clade, two

of which are postcranial. Both of the unambiguous cranial characters are homoplasious with the plesiomorphic condition expressed in varanopids and the outgroup taxa (and in *Eothyris* for character 41). The two cranial characters are:

36. Two anterior fields of palatal dentition are separate anteriorly (1→0). The plesiomorphic condition for basal amniotes is separate left and right palatal dentition fields (0). The palatal dentition of basal caseids is extensive and covers much of the palate, as in *Casea broilii* (Williston, 1910) and *C. rutena* (Sigogneau-Russell and Russell, 1974), where the two fields can be seen converging anteriorly (1). *Angelosaurus dolani* and *Cotylorhynchus romeri* of Clade F convergently evolve the plesiomorphic condition for amniotes in which the left and right palatal dentition fields do not meet anteriorly. The condition in *Ennatosaurus tecton* is difficult to determine in PIN 4543/1; however, Olson (1968) reconstructed largely separate dental fields meeting along a thin line at the pterygoid-palatine suture, thus demonstrating the derived condition.
37. Transverse flanges of the pterygoids are directed laterally or slightly posterolaterally (1→0). The transverse flanges of the pterygoids in both *Angelosaurus dolani* and *Cotylorhynchus romeri* are directed posterolaterally (0), which is the plesiomorphic condition. Caseids basal to Clade F possess transverse flanges that are directed straight laterally or slightly anterolaterally (1) and this is considered the derived condition that evolved convergently in *Diadectes*. The caseids of Clade F, therefore, evolve the plesiomorphic condition convergently.

Evolutionary Patterns Within Caseidae

The phylogenetic hypothesis recovered here offers new insights into the interrelationships of several of the better-known caseid taxa. The current phylogeny contradicts and/or revises earlier hypotheses, including the hypothesized sister taxon relationship between *Ennatosaurus* and *Cotylorhynchus* (Olson, 1962) and the identity of the most basal member of Caseidae.

Phylogenetic Position of *Ennatosaurus tecton*—The current phylogenetic results posit *Ennatosaurus tecton* as the sister taxon to the clade containing *Cotylorhynchus romeri* and *Angelosaurus dolani* (Clade F). Seven derived cranial synapomorphies (characters 5, 8, 12, 20, 22, 38, and 49) diagnose the clade including *E. tecton*, *C. romeri*, and *A. dolani* (Clade E). *Cotylorhynchus romeri* and *A. dolani* convergently acquire the plesiomorphic condition for two cranial characters (characters 36 and 37), thus uniting *C. romeri* and *A. dolani* as sister taxa (Clade F) more closely related to each other than either are to *E. tecton*. This result conflicts with earlier predictions of a sister taxon relationship between *Ennatosaurus* and *Cotylorhynchus* by Olson (1962). However, close examination of the data reveals there is weak support for linking *Cotylorhynchus* and *Angelosaurus* (Clade F).

Angelosaurus dolani cannot be scored for any of the seven cranial synapomorphies of Clade E because of its highly incomplete cranium. It is more parsimonious to assume *A. dolani* also shares the derived state of the seven characters with both *E. tecton* and *C. romeri* given the topology, which is ultimately the product of the two cranial apomorphies discussed above. It is therefore uncertain whether *A. dolani* truly possesses any of these characters. It might be the case, however, that *E. tecton* and *C. romeri* actually exclusively share some or all of the characters diagnosing Clade E. The exclusive sharing of two or more characters would then yield a substantially different topology. Only more complete specimens of *A. dolani* could confirm or refute this topology. Currently Olson's (1962) earlier prediction that,

had *E. tecton* been found in North America it would have been made congeneric with *Cotylorhynchus*, is not supported.

The current phylogenetic hypothesis also produces a relatively long ghost lineage for *Ennatosaurus tecton* compared to other caseid lineages, spanning approximately ten million years (Fig. 9), under the most recent hypothesis for stratigraphic correlation between North America and Russia (Lucas, 2004). *Cotylorhynchus romeri* and *Angelosaurus dolani* come from horizons within the middle and upper parts of the Lower Permian strata of Texas and Oklahoma. Although the precise ages of the strata containing these taxa are uncertain, they are all well below the base of the Middle Permian (Lucas, 2004). Given our cladogram, the divergence of the lineage leading to *E. tecton* must have occurred during the Early Permian. The majority of Russian Permian tetrapod beds have been shown to be of late Kazanian and early Tatarian age (late Middle Permian; Lucas, 2004), with only a rare amphibian-dominated assemblage, the Inta Assemblage, corresponding to the early Middle Permian (Lozovsky, 1992, 2003; Kotlyar, 2000). A series of core samples taken from the fossiliferous strata along the Kimgha, Vashka, and Mezen rivers (V. Lozovsky, pers. comm.) reveals a southeastern younging trend from the late Kazanian to the early Tatarian. The Nysagora locality (4543), from which the current specimen of *Ennatosaurus tecton* was recovered, lies within the earliest early Tatarian age equivalency, virtually on the boundary between the Kazanian and Tatarian (V. Lozovsky, pers. comm.). The Russian Permian assemblages are also therapsid-dominated, as they record the early radiation and subsequent domination of therapsids. The therapsid-dominated assemblages are a dramatic shift from the older pelycosaur-dominated assemblages of the Lower Permian in North America. The details of the actual shift remain enigmatic as these two Permian assemblage types appear to be separated by a global hiatus in the fossil record (Lucas, 2004), which spans much of the transition period. The presence of *Ennatosaurus tecton* in the Russian therapsid-dominated assemblages provides important insight into the final stages of this global faunal turnover. We therefore see that caseids are among the few basal synapsids to persist into the therapsid-dominated communities, and were among the last to disappear in the Middle Permian.

Interestingly, the disappearance of caseids in Russia appears to be closely timed with the appearance of pareiasaurian parareptiles. Pareiasaurs, like caseids, are medium- to large-sized animals with an overall similar gross morphology. They share with caseids the leaf-like tooth morphology and large, barrel-like torso, suggesting similar herbivorous lifestyles. Pareiasaurs begin their early history in South Africa with the basal members *Bradyosaurus* and *Embrithosaurus* from the Middle Permian *Tapinocephalus* Assemblage Zone (Rubidge, 1995, 2005; Lee, 1997). They persisted in South Africa until the Late Permian, as indicated by the presence of such taxa as *Pareiasaurus* and *Anthodon* from the *Cistecephalus* and *Dicynodon* assemblage zones (Rubidge, 1995). Pareiasaurs appear in northern Europe in the Late Permian. The Scottish pareiasaur *Elginia mirabilis* comes from a formation considered to be latest Tatarian in age (Benton and Walker, 1985; Spencer and Lee, 2000) and the two Russian genera *Scutosaurus* and *Deltavjatia* also come from the Tatarian horizons (Ivakhnenko et al., 1997; Kordikova and Khlyupin, 2001). The highly similar dental morphology between caseids and pareiasaurs suggests a similar resource was utilized in these two groups. A potential brief period of overlap between these two groups (if PIN 4653/2 is a pareiasaur and not a caseid) in addition to their apparent mutual exclusivity may be the result of a competitive exclusion event (see Hardin, 1960; Armstrong and McGehee, 1980).

Phylogenetic Position of *Oromycter dolesorum*—The most recent addition to Caseidae is an animal based on fragmentary remains recovered from the Richards Spur locality in Oklahoma.

The new taxon, named *Oromycter dolesorum*, consists of isolated cranial elements, as well as several postcranial elements that include a caudal vertebra and phalanges (Reisz, 2005). This is the first new caseid taxon to be named since Sigogneau-Russell and Russell (1974) described *Casea rutena* from France.

Despite the absence of a previous caseid phylogenetic analysis, *Casea broilii* was considered for a long time to be the most basal member of the group primarily because of its lowest stratigraphic appearance (Olson, 1954; Reisz, 1986) and because of the possession of several primitive features (Romer and Price, 1940; Olson, 1968; Reisz, 1986), including the retention of coronoid dentition, extensive palatal dentition, and the dubious feature of its small size (Romer and Price, 1940). However, in the current analysis, *O. dolesorum* replaces *C. broilii* as the most basal member of the clade.

Many of the primitive features retained in *Casea broilii* cannot be assessed in *Oromycter dolesorum* because of the fragmentary condition of the latter. Features that *O. dolesorum* does share with *C. broilii* include the plesiomorphic shape of the maxillary postnarial process and the lacrimal (characters 8 and 16). Reisz (2005) identified several additional plesiomorphic features present in *O. dolesorum* that appear in the derived condition in *C. broilii* and all other caseids. These include the absence of a contribution to the narial emargination by the maxilla and the absence of complex apical cuspsules on the marginal dentition seen in all other caseids, thus leading Reisz (2005) to suggest that *O. dolesorum* probably occurred at the base of Caseidae. Reisz's (2005) hypothesis is supported by the current phylogenetic analysis. When these characters of the maxilla and teeth (characters 7 and 70), which were suggested to indicate a basal position of *Oromycter dolesorum*, are optimized on the tree, we see that *O. dolesorum* retains the plesiomorphic condition exhibited by *Eothyris*, varanopids, and all of the outgroup taxa.

The basal position of *Oromycter dolesorum* is also supported by its early occurrence in the fossil record. *Oromycter dolesorum* comes from the Richards Spur locality, Oklahoma, where the precise age is uncertain because of the geologically isolated nature of the fissure-fill rock containing the fossils. There is strong support from the taxa present at Richards Spur, however, for an age equivalency with that of the *Cacops* bonebed of Texas (Sullivan and Reisz, 1999; Maddin et al., 2006). The *Cacops* bonebed is the only known locality to produce *Casea broilii*. This means *O. dolesorum* occurs at least as early as *C. broilii* and that the topology is stratigraphically consistent (Huelsenbeck, 1994).

Evolution of Complex Dentition in Caseids—Olson (1962:fig. 64) suggested, after looking at the marginal dentition of *Cotylorhynchus romeri*, *Cotylorhynchus hancocki*, and *Ennatosaurus tecton*, in combination with their increasingly younger ages, that the pattern of apical complexity represented a unidirectional, graded morphological series of increasing complexity. The tips of the teeth of *C. romeri* are described as simple with no cuspsules, those of *C. hancocki* are described as possessing three moderately developed cuspsules, and those of *E. tecton* are described as possessing five strongly developed cuspsules (Olson, 1962). However, in light of the topology obtained here and with the addition of new caseid taxa, Olson's model is shown to be unsupported.

First, closer examination of the marginal dentition of *Cotylorhynchus romeri* reveals a more complex apical morphology than Olson described. Despite substantial wearing on many of the teeth, three longitudinal cuspsules are present on several teeth, most notably on the posterior teeth, in OMNH 04329. Second, the current phylogenetic hypothesis does not place *Ennatosaurus tecton* at the top of an evolutionary series, above *Cotylorhynchus romeri*, and presumably *Cotylorhynchus hancocki*, if proven to be a valid taxon. Rather, the lineage leading to *E. tecton* comes out more stemward to the putative *Cotylorhynchus* clade.

When dental complexity is optimized onto the current topol-

ogy (Fig. 10), there are two most-parsimonious patterns of the evolution of apical complexity (character 70). In the first pattern five or more cuspules appear on the stem of Clade C and three cuspules evolve convergently in both *Casea broilii* and *Cotylorhynchus romeri*. In the second pattern three cuspules appear on the stem of Clade C, five or more cuspules appear on the stem of Clade D, and the dentition of *Cotylorhynchus romeri* experiences a reversal back to the three cuspule condition exhibited by *Casea broilii*.

In both of these scenarios tooth complexity contains homoplasy, either via convergent evolution (pattern 1) or via character state reversal (pattern 2). These findings, in addition to known ontogenetic variation in tooth complexity in early amniotes (Lee 1997), suggest the loss and acquisition of apical cuspules may occur frequently and that similar morphologies have a high likelihood of lacking homology. Therefore, the use of this character in phylogenetic analyses should be pursued with caution.

CONCLUSIONS

The cranial anatomy of *Ennatosaurus tecton*, a caseid from the upper Middle Permian of Russia, was described in detail and reconstructed. A first phylogenetic analysis of Caseidae placed *Ennatosaurus tecton* as the sister taxon to a clade of two Lower Permian North American taxa, resulting in a long ghost lineage for *E. tecton*. The recently discovered *Oromycter dolesorum* replaced *Casea broilii* as the long time basalmost member of Caseidae. In addition, a paraphyletic *Casea* was obtained, and closer examination may lead to the reassignment of the French caseid, *Casea rutena*, to a new genus.

The varying complexity of tooth morphology in caseids was examined in the context of the new phylogeny. When optimized

onto the tree, tooth morphology is homoplasious either via convergence or a reversal in *Cotylorhynchus romeri*. This reveals the potentially unreliable nature of tooth morphology as a phylogenetic indicator especially as a unidirectional character in caseids, and possibly in amniotes as a whole.

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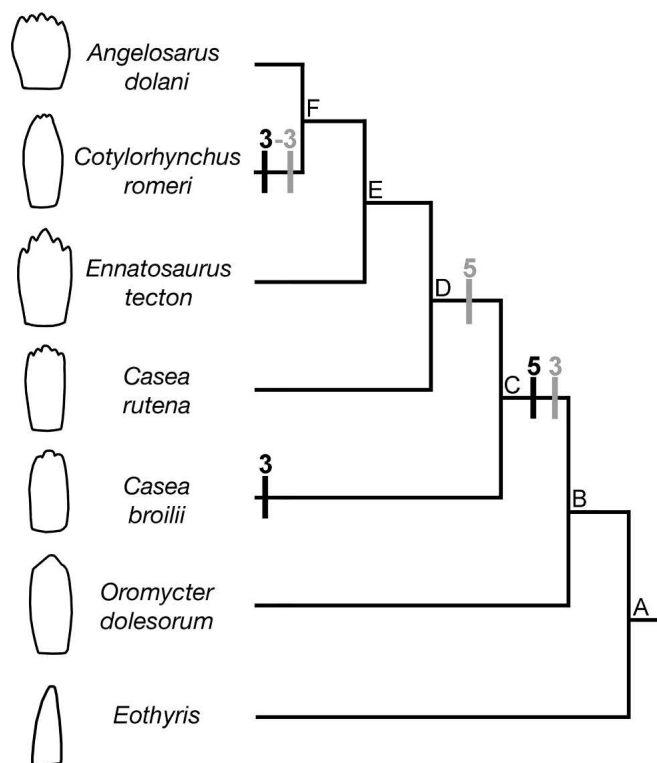


FIGURE 10. Pattern of apical dental complexity evolution in caseids based on the current phylogenetic hypothesis. The two most parsimonious optimizations, as discussed in the text, reveal evolution of tooth complexity is homoplasious via either convergent evolution (pattern 1, black) or a reversal (pattern 2, grey).

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APPENDIX 1. Description of characters used in phylogenetic analysis.

SKULL ROOF

- 1) Shape of premaxillary ascending process: slopes posterodorsally from tooth row (0); projects anterodorsally to overhang tooth row (1).
- 2) Shape of the antorbital region: maxilla slopes dorsolaterally, overhanging tooth row (0); maxilla slopes dorsomedially (1).
- 3) Subnarial foramina on dorsal edge of maxilla: small or absent (0); present and large (1).
- 4) External naris length: small, less than 25% preorbital length (0); moderate, 25–50% preorbital length (1); long, greater than 50% preorbital length (2).
- 5) External naris height: 30–75% of orbital height (0); greater than 75% or equal to orbital height (1).
- 6) Contribution of nasal to external naris: confined dorsally (0); blade-like, anteroventral portion of narial emargination (1).
- 7) Medial flange on maxilla forming vertical wall emarginating external naris: absent (0); present (1).
- 8) Postnarial ascending process of maxilla: absent (0); present and rounded dorsally (1); present and pointed dorsally (2).
- 9) Position of apex of postnarial ascending process of maxilla: process absent (0); tallest point located centrally (1); tallest point located anteriorly (2).
- 10) Length of posterior ramus of maxilla: confined to suborbital region (0); continues posteriorly beyond orbital region (1).
- 11) Dentition on posterior ramus of maxilla: present to posterior margin of orbital exclusively (0); terminates under postorbital bar (1); continues posterior to postorbital bar (2).
- 12) Shape of ventral edge of maxilla: straight (0); mildly to strongly convex (1).
- 13) Maxilla-quadratojugal contact: absent, jugal reaches ventral margin of skull in lateral view (0); present, jugal excluded from ventral margin of skull in lateral view (1).
- 14) Postparietal contribution of margin of posttemporal fenestra: absent (0); present (1).
- 15) Postorbital contribution to skull table: large, wide (0); small, narrow (1).
- 16) Shape of lacrimal: dorsoventral dimension less than length (0); dorsoventral dimension greater than length (1).
- 17) Lacrimal contribution to medial emargination of external naris: absent (0); present (1).
- 18) Jugal-squamosal contact below level of orbit: absent (0); present (1).
- 19) Morphology of anterior ramus of jugal: thin, sliver-like (0); thick and robust (1).
- 20) Height of dorsal ramus of jugal: less than 50% height of orbit and broad (0); greater than or equal to 50% height of orbit and slender (1).
- 21) Height of lateral temporal fenestra: lateral temporal fenestra absent (0); short, temporal fenestra height to temporal roof height ratio 0.5 or less (1); tall, temporal fenestra height to temporal roof height ratio 0.575 or greater (2).
- 22) Postorbital shape: smoothly rounded between skull table and temporal portions (0); right angle formed between skull table and temporal portions (1).
- 23) Extent of the contribution of frontal to orbital rim: none or small, less than 1/10 maximum orbital length (0); large, more than 1/5 maximum orbital length (1).
- 24) Size of pineal foramen: maximum diameter less than that of foramen magnum (0); maximum diameter equal to or greater than that of foramen magnum (1).
- 25) Frontal:parietal ratio of lengths at midline: frontal less than 1.5 times parietal length (0); frontal greater than 1.6 times parietal length (1).
- 26) Position of pineal foramen on parietal suture: anteriorly located on parietal suture (0); centrally located on suture (1); near posterior of parietal suture (2).
- 27) Postorbital-supratemporal contact: present (0); absent, postorbital reaching level of supratemporal (1); absent, postorbital and supratemporal widely separated (2).
- 28) Supratemporal shape: broad, subrectangular, superficial bone on skull roof, length less than that of parietal at midline (0); small splint-like element in groove in parietal (1); large, elongate, roughly equal in length to parietal at midline (2).

- 29) Length of lateral temporal fenestra: absent (0); moderate, between 15–25% of total skull length (1); large, greater than 30% of total skull length (2).

PALATE

- 30) Dentition on cultriform process of parasphenoid: absent (0); present (1).
 31) Parasphenoid body shape: wide, maximum width greater than length from basipterygoid processes to basioccipital (0); narrow, length greater than width (1).
 32) Posterior-most location of parasphenoid dentition: present anterior to transverse flange of pterygoid exclusively (0); posterior to transverse flange of pterygoid (1); teeth absent on body (2).
 33) Squamosal shape: wide and tapering dorsally, ventral sutural surface longer than dorsal sutural surface (0); narrow, occupying less than 30% of temporal length and columnar (1); wide, posterior and temporal edges of squamosal subparallel (2).
 34) Position of basicranial joint: in line with or posterior to transverse flange of pterygoid (0); anterior to transverse flange of pterygoid (1).
 35) Shape of basipterygoid process: wing-like, articulating surface along anterior edge (0); knob-like, articulating surface located anterolaterally (1).
 36) Distribution of palatal dentition: two anterior fields separate (0); two anterior fields confluent (1).
 37) Shape of transverse flange of pterygoid: directed laterally or posterolaterally (0); directed anterolaterally (1).
 38) Anterolateral dental field on pterygoid: extending to basicranial area (0); reduced, not reaching basicranial area (1); absent (2).

OCCIPUT

- 39) Location of paroccipital process: confined between squamosals, not visible in lateral view (0); posterolateral flange projecting posterior to squamosals, visible in lateral view (1).
 40) Paroccipital process of opisthotic-supraoccipital contact: unfused (0); fused (1).
 41) Direction of occiput: directed vertically (0); inclined anterodorsally (1).
 42) Direction of occipital condyle: directed posteriorly (0); directed sharply ventrally (1).
 43) Postparietals: unfused (0); fused (1).

GENERAL SKULL

- 44) Height of zygomatic arch: inapplicable (0); narrow, less than 30% height of lateral temporal fenestra (1); deep, greater than 50% height of lateral temporal fenestra (0).
 45) Lateral temporal fenestra: absent (0); present (1).
 46) Longitudinal location of jaw articulation: at level of occipital condyle (0); far posterior to occipital condyle (1).
 47) Dorsoventral location of jaw articulation: at level of tooth row (0); below level of tooth row (1).
 48) Skull ornamentation: absent (0); present (1).
 49) Lateral temporal fenestra: fenestra absent (0); subcircular (1); subrectangular, posteroventral margin forming acute angle (2); subrectangular (3).
 50) Preorbital length of skull: short, less than 1/3 total skull length (0); moderate, between 1/3 and 1/2 skull length (1); long, equal to or greater than 1/2 skull length (2).
 51) Head size: large, greater than 30% presacral length (0); small, less than 20% presacral length (1).
 52) Frontal length:width ratio: less than 3.3 (0); greater than 3.5 (1).

LOWER JAW

- 53) Lower jaw shape: lower jaw tapers anteriorly, symphysis thinnest portion of jaw (0); anterior region nearly as deep as mid-tooth row (1).
 54) Snout proportions: wider than tall (0); taller than wide (1).
 55) Splenial dorsoventrally deepened at symphysis: absent (0); present (1).
 56) Cross-sectional shape of ventral border of angular: ventral margin ridged (0); ventral margin smoothly rounded (1).
 57) Splenial contacting posterior coronoid: absent (0); present (1).

- 58) Position of coronoid eminence of lower jaw: within posterior 1/3 of lower jaw (0); approximately at 40% from anterior of total jaw length (1).
 59) Composition of mandibular symphysis: dentary and splenial (0); dentary only (1).
 60) Size of Meckelian foramen: small, less than 10% jaw length (0); large, greater than 25% jaw length (1).
 61) Number of coronoids in lower jaw: two (0); one (1).
 62) Coronoid dentition: absent (0); present (1).

MARGINAL DENTITION

- 63) Premaxillary tooth number: two (0); three (1); four or greater (2).
 64) Maxillary tooth number: 8–17 teeth (0); 22–28 teeth (1).
 65) Number of precaniniform maxillary teeth: inapplicable, no canines (0); zero or one precaniniforms (1); three precaniniforms or greater (2).
 66) Secondary enlargement in tooth row posterior to caniniforms: absent (0); present (1).
 67) Recurvature of marginal teeth: absent (0); present, apex posteriorly recurved (1); highly posteriorly recurved, apex approximately 80–90 degrees from vertical (2).
 68) Relative size of premaxillary tooth #1: premaxillary tooth #1 largest in tooth row (0); premaxillary tooth #1 not largest (1).
 69) Caniniform teeth: absent to weakly differentiated (0); present as 2 large maxillary teeth (1); present as enlarged tooth “region”, but two pronounced caniniforms absent (2).
 70) Number of apical cusps on teeth: single cusp (0); three cusps (1); greater than three cusps (2).
 71) Bone forming dorsal margin of coronoid region: post-dentary bone (e.g., coronoid, surangular) (0); dentary (1).
 72) Shape of lingual surface of marginal dentition: conical, convex (0); spatulate (1).
 73) Shoulder on lingual surface: absent (0); present, with lingual curvature (1).

AXIAL SKELETON

- 74) Shape of dorsal neural arch: not swollen or buttressed (0); swollen or buttressed (1).
 75) Number of sacral vertebrae: two or fewer (0); three or greater (1).
 76) Sacral rib articulation: 2nd rib primarily braces first, contact with ilium minimal (0); all ribs attach directly to ilium (1).
 77) First sacral rib shape: forms flat plate distally (0); U-shaped distally, extremely broad (1).
 78) Sacral rib, mode of attachment to vertebrae: sutural in adult (0); fused in adult (1).
 79) Expanded rib cage: absent, dorsal ribs restricted ventral to transverse processes (0); present, dorsal ribs rising above transverse processes (1).
 80) Size of axis neural spine: large, maximum anteroposterior length greater than that of axis centrum length (0); small, maximum anteroposterior length less than that of axis centrum length (1).

PECTORAL GIRDLE

- 81) Angle of head of interclavicle: low angle, shallow (0); steep angle, sharply upturned anteriorly (1).
 82) Shape of ventral plate of clavicle: narrow, only slightly wider than dorsal process (0); broad, much wider than dorsal process (1).
 83) Posterior coracoid triceps process: absent (0); present (1).
 84) Supraglenoid foramen of scapula: absent (0); present (1).
 85) Number of scapulocoracoid ossifications: two (0); three (1).
 86) Notch in anterior edge of scapula: absent (0); present (1).

FORELIMB

- 87) Ectepicondylar foramen of humerus: absent (0); present (1).
 88) Distinct shaft on humerus: absent (0); present (1).
 89) Number of manual phalanges in digit II: three (0); two (1).
 90) Number of manual phalanges in digit III: four (0); three (1).
 91) Number of manual phalanges in digit IV: five (0); four or fewer (1).
 92) Number of manual phalanges in digit V: three (0); two (1).
 93) Ratio of length of 4th metacarpal to radius: less than 25% (0); between 30% and 45% (1); greater than 50% (2).

- 94) Metapodial shape: long and slender, two to three times longer than maximal width (0); short and fat, with small diaphysis (1).
- 95) Shape of ungual phalanx: strongly recurved (0); weakly recurved (1).

- chium, lacking enlarged region on pubis (0); enlarged symphyseal region on pubis (1).
- 100) Lateral pubic tubercle: absent (0); present (1).
- 101) Pectineal ridge of pubis: absent (0); present (1).

PELVIC GIRDLE

- 96) Plate-like dorsal process of ilium: absent, height above center of acetabulum less than 50% length to distal tip of posterior process (0); present, height above acetabulum greater than 75% length to posterior process (1).
- 97) Length of posterior process of ilium: confined above acetabulum (0); projecting posterior to acetabulum (1).
- 98) External shelf on lateral surface of ilium: absent (0); present (1).
- 99) Puboischiatic symphysis: evenly distributed between pubis and is-

HIND LIMB

- 102) Shape of posterior ridge of femur: absent, internal fossa without posterior border (0); present, Y-shaped trochanter formed proximally (1).
- 103) Number of pedal phalanges in digit II: three (0); two (1).
- 104) Number of pedal phalanges in digit III: four (0); three (1); two (2).
- 105) Number of pedal phalanges in digit IV: five (0); two (1).
- 106) Number of pedal phalanges in digit V: four (0); three (1); two (2).

APPENDIX 2. Character-taxon data matrix for phylogenetic analysis of caseid relationships. **Abbreviation:** a, polymorphic character.

	10	20	30	40	50
Reptilia	0?00000000	00000?01?0	00100a2a00	120000000a	0000000000
<i>Diadectes</i>	0000000000	00000?01?0	0101120000	0200001201	0110001100
<i>Limnoscelis</i>	1000000000	00000?01?0	0000010000	00?0000200	0110000002
<i>Mycterosaurus</i>	0101000111	2010100111	2111021111	0000000?01	1001100010
<i>Varanops</i>	0100000211	2010100010	2111122121	01100?0001	10?1110020
<i>Eothyris</i>	10010?0111	0010000100	100101001?	0?2000??11	1?02100?11
<i>Oromycter</i>	1?0??01111	?01??01???	???????????	???????????	????????1??
<i>Casea broilii</i>	?0?20?1111	101000?0?0	10?1000011	0021?11011	1112101111
<i>Casea rutena</i>	1012011121	1011011000	2001000221	0011111011	1111101111
<i>Cotylorhynchus</i>	1012111221	1111011001	2102000221	0?21100111	1101101131
<i>Angelosaurus</i>	???????????	???????????	???????????	00?1100??1	11?????????
<i>Ennatosaurus</i>	1012111221	1111011011	211100022?	1?1??11111	1?01101131

	60	70	80	90	100
Reptilia	0000001000	1a2?a001a0	000a001100	0a01100100	00100010aa
<i>Diadectes</i>	0000000101	102000010?	0101000110	0?01000000	00?1111111
<i>Limnoscelis</i>	0110101001	0010000000	000101?100	?101000000	0011111110
<i>Mycterosaurus</i>	0101???????	??11202120	?0000?1?0?	????0?01??	???0?01?01
<i>Varanops</i>	010101?010	?021202120	?000011100	01011001??	?020101000
<i>Eothyris</i>	?00000?100	0010111110	000???????	???????????	???????????
<i>Oromycter</i>	??1???????	??10000000	?11???????	???????????	???????????
<i>Casea broilii</i>	101000?100	0100000001	1110110111	11101001??	??10011000
<i>Casea rutena</i>	1010101100	0?20000002	1110??0?01	?11??1100	101111?0??
<i>Cotylorhynchus</i>	1010101100	1010000001	0110110111	1010111111	1101110000
<i>Angelosaurus</i>	???????????	???0?00???	?11011011?	10101111??	??01110000
<i>Ennatosaurus</i>	101010?100	??00000002	111011011?	?110100111	?101?10000

	106
Reptilia	1?0000
<i>Diadectes</i>	010000
<i>Limnoscelis</i>	010000
<i>Mycterosaurus</i>	?1?????
<i>Varanops</i>	110000
<i>Eothyris</i>	???????
<i>Oromycter</i>	???????
<i>Casea broilii</i>	10??01
<i>Casea rutena</i>	???????
<i>Cotylorhynchus</i>	101111
<i>Angelosaurus</i>	101212
<i>Ennatosaurus</i>	101112