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## PARRISIA NEOCESARIENSIS, A NEW BATRACHOSAUROIDID SALAMANDER AND OTHER AMPHIBIANS FROM THE CAMPANIAN OF EASTERN NORTH AMERICA

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**ABSTRACT**—The Ellisdale site (Late Cretaceous, Campanian), Monmouth County, New Jersey, has produced the first representative fossil amphibian specimens from the Cretaceous of eastern North America. The known fauna includes indeterminate pelobatid and discoglossid frogs, an amphiimid (cf. *Proamphiuma* sp.), and a sirenian (cf. *Habrosaurus* sp.), however, the most abundant caudate remains are from a previously undescribed genus of batrachosauroidid salamander, herein described as *Parrisia neocesariensis* gen. et sp. nov.

The genus *Parrisia* is established as batrachosauroidid by: an atlas with deeply concave anterior cotyles; lack of a well developed atlantal intercotylar process; and a ring or dome of calcified cartilage on the opisthocoelus vertebral condyles bearing a persistent notochordal pit. It differs from the other members of the family, including *Opisthotriton* and *Prodesmodon* (Late Cretaceous, western North America) by the presence of: unossified neural spine tips; paired caudal intravertebral nerve openings; ventral displacement of the posterior vertebral cotyle relative to the anterior; and a unique dentary morphology.

The occurrence of delicately preserved amphibian fossils in the tidal channel facies at Ellisdale suggests a proximal fauna, which experienced limited post-mortem transport prior to burial. Typically salt-intolerant, these species may have been the residents of a barrier island/spit freshwater slough, an environment which hosts a number of extant amphibian species on the southeastern Atlantic coast of North America today.

### INTRODUCTION

The North American Mesozoic record of lissamphibians is relatively poor, with known occurrences limited to the late Jurassic Morrison Formation of Wyoming (Evans and Milner, 1993); Early Cretaceous Trinity Group of Texas (Goin and Aufenber, 1958); the Late Cretaceous Mesaverde (Armstrong-Ziegler, 1980), Judith River (Sahni, 1972), Lance (Estes, 1964), and Hell Creek Formations of New Mexico, Wyoming and Montana (Estes et al., 1969). Nevertheless, enough specimens are known to demonstrate the presence of a number of extinct and surviving families including the Paleobatrachidae, Discoglossidae, Pelobatidae, Leptodactylidae, and Hylidae among the anurans (Estes and Sanchiz, 1982), as well as Prosirenidae, Sirenidae, and Batrachosauroididae among the caudatans (Estes, 1981).

The Ellisdale Site of the upper Cretaceous (Campanian) of New Jersey revealed for the first time an eastern North American vertebrate microfauna with significant freshwater and terrestrial elements comparable to the relatively productive localities of the western interior of similar age (Grandstaff et al., 1992). The recognition of several new taxa of lacertilians demonstrated a level of endemism that was previously unexpected (Denton et al., 1991; Denton and O'Neill, 1993, 1995). A number of diagnostic amphibian specimens were recognized at the locality in the earliest phases of microfaunal collection and analysis; however, they remained undescribed until this study.

The first fossil amphibians discovered at Ellisdale consisted of two well-preserved atlantes, identified by Richard Estes as comparable to the same elements in the batrachosauroidid genera *Opisthotriton* and *Prodesmodon* respectively (Grandstaff et al., 1992). Continued collecting has revealed the presence of several anuran and caudate taxa, however, the total amphibian fauna remains dominated by the disarticulated remains of a single genus of batrachosauroidid salamander. Dentaries, and numerous well preserved vertebrae from various positions in the spinal column have allowed us to gain a better understanding of the comparative osteology of the Ellisdale salamander, which appears to be a new genus and species.

### MATERIALS AND METHODS

Microfaunal specimens were collected by screen washing of bulk matrix and microscopic sorting, described in detail in previous publications on the Ellisdale Site (Denton and O'Neill, 1995).

Phylogenetic analysis was performed using PAUP version 3.0, run on a Macintosh™ IIxi computer. Multistate characters were ordered where appropriate (see character explanation, Table 1) and free reversibility was allowed. Character polarities were reinforced through the use of an all zero ancestor to root the tree, as well as an unrooted tree with *Scapherpeton* as an outgroup. The exhaustive search option was used to examine all possible tree combinations.

Comparative specimens of *Opisthotriton kayi* used in the description of *Parrisia* were primarily: AMNH 8110, 8112, 8136 (vertebrae), AMNH 8104 (dentary), UCMP 55778 (atlas), UCMP 49504 (dentary), all from the Lance Formation, Late Cretaceous, Wyoming; PU17039 (vertebrae and atlantes), PU18575a-f (vertebrae), PU20559 (mixed specimens), Tongue River Formation, Middle Paleocene, Montana.

**Institutional Abbreviations**—AMNH, American Museum of Natural History; NJSM, New Jersey State Museum; PU, Princeton University Collection, now at Yale Peabody Museum; UCMP, University of California Museum of Paleontology; USNM, United States National Museum.

### GEOLOGY

#### Horizon and Locality

All specimens were collected from the main productive layer of the Ellisdale Site, basal Marshalltown Formation (Late Cretaceous, Campanian), Matawan Group, Upper Freehold Township, Monmouth County, New Jersey.

The geology of the locality has been reported in previous publications (Gallagher et al., 1986; Grandstaff et al., 1992). The Marshalltown Formation is interpreted locally as deposition from a marine transgression along a passive continental margin. Environments ranging from lagoon, to barrier beach and open



FIGURE 1. Anuran ilia from Ellisdale. A, NJSM 15670, distal left ilium of indeterminate discoglossid, arrow indicates acetabular rim. B, NJSM 15035, distal left ilium of indeterminate pelobatid. Both in lateral view.

water are preserved. The main productive layer occurs as an intraformational conglomerate within the lagoonal sequence. It is composed primarily of siderite (clay-ironstone) pebbles, clay, poorly sorted quartz sand and gravel, abundant fossil wood, amber and vertebrate remains. The layer ranges from 3 to 15 centimeters in thickness and has been interpreted as a storm deposit (Gallagher et al., 1986; Tashjian, 1990). Although incompletely characterized, the known lateral extent of the productive layer suggests a debris-choked tidal channel.

#### SYSTEMATIC PALEONTOLOGY

Superorder LISSAMPHIBIA

Order ANURA

Family DISCOGLOSSIDAE

DISCOGLOSSIDAE, gen. et sp. indet.  
(Fig. 1A)

**Material**—NJSM 15670, distal left ilium.

**Description**—The specimen consists of the distal portion of the left ilium, including the entire iliac region of the acetabulum. The presence of a well-defined acetabular rim diagnoses the specimen as a discoglossid. There is an incipient dorsal crest on the iliac shaft, and a reasonably well developed supra-acetabular expansion. The dorsal shaft is broken, but enough is intact to demonstrate the absence of a dorsal tubercle.

**Discussion**—This specimen comprises the only known discoglossid from the Ellisdale site. The absence of a dorsal tubercle is similar to the discoglossid genera *Barbourula* and *Bombina* (Estes and Sanchiz, 1982), however the Ellisdale specimen does not compare favorably in all aspects to any known discoglossid genera. Additional material and further study will be needed to clarify the relationships of this unusual little frog.

Family PELOBATIDAE

PELOBATIDAE, gen. et sp. indet.  
(Fig. 1B)

**Material**—NJSM 15035, distal left ilium.

**Description**—A distal left ilium, missing the posterior su-

pracetabular process, and the dorsal portion of the shaft. The absence of a dorsal tubercle, and presence of a spiral groove in this region diagnose this specimen as a pelobatid.

**Discussion**—NJSM 15035 is one of several well preserved pelobatid ilia that have been found at Ellisdale. Pelobatids (Spadefoot Toads) are an extant family of North American anurans, with *Scaphiopus* the only genus occurring in the continental United States. Their remains are by far the most commonly identified anuran fossils from the Ellisdale site. Unfortunately, pelobatid ilia are not diagnostic beyond family level (Evans and Milner, 1993). Until additional, more nearly complete specimens are recovered, only the presence of the family itself during the Campanian of eastern North America can be verified.

#### Indeterminate Anura

A number of undetermined anuran fossils have been found at the Ellisdale site, which remain to be fully studied. These include several partial urostyles, humeri, femora, and various skull elements. One specimen, NJSM 15918, is a partial maxilla showing a sculptured lateral surface, and may be referable to the discoglossid genus *Scotiophryne*. A number of squamosals also have characteristic sculpture, and seem comparable to *Theatonius*, described by Fox (1976), from the Upper Cretaceous Lance Formation of western North America. A hylid may also be represented. Further study may shed light on these numerous specimens.

Order CAUDATA Oppel, 1811

Suborder PROTEOIDEA (Noble, 1931) emend. Estes, 1981

Family BATRACHOSAUROIDIDEA Auffenberg, 1958

*PARRISIA* gen. nov.

**Type and Only Species**—*Parrisia neocesariensis* sp. nov.

**Locality and Horizon**—Quarry “B”, Quarry “C”, Logjam Quarry, Easter Quarry, at the Ellisdale Site, southwest of Allentown, in Upper Freehold Township, Monmouth County, NJ. Basal Marshalltown Formation, Matawan Group, Campanian (Late Cretaceous).

**Etymology**—In honor of David C. Parris, vertebrate paleontologist, geologist and natural history curator, New Jersey State Museum; and in recognition of his constant encouragement and guidance in the continuing Ellisdale project.

**Diagnosis**—A paedomorphic salamander, with functional anatomy reflecting an aquatic habitus, which is referred to the family Batrachosauroididae on the basis of the following characters: atlas with prominent, deeply concave anterior cotyles; lack of a well developed atlantal intercotylar process (odontoid); a ring or dome of calcified cartilage on the opisthocoelous vertebral condyles, which bear a persistent notochordal pit.

Distinguishable from all other members of the family by the following characters: posterior cotyle of the centrum displaced ventrally relative to the anterior condyle/cotyle when viewed from the lateral aspect; atlantal cotyles surmounted by dorsomedial spinous protuberances; neural spine tips finished in cartilage (unossified); caudal vertebrae with paired intra-vertebral nerve openings; shallow dentary with a smooth lateral surface and an enlarged medial projection of the ventral edge; and teeth mesiodistally compressed. Differs from all other members of the family except *Prodesmodon* in having convex, fully ossified condyles on the cervical and anterior thoracic vertebrae. Differs from all other members of the family except *Paleoproteus* in having a deeply forked atlantal neural spine.

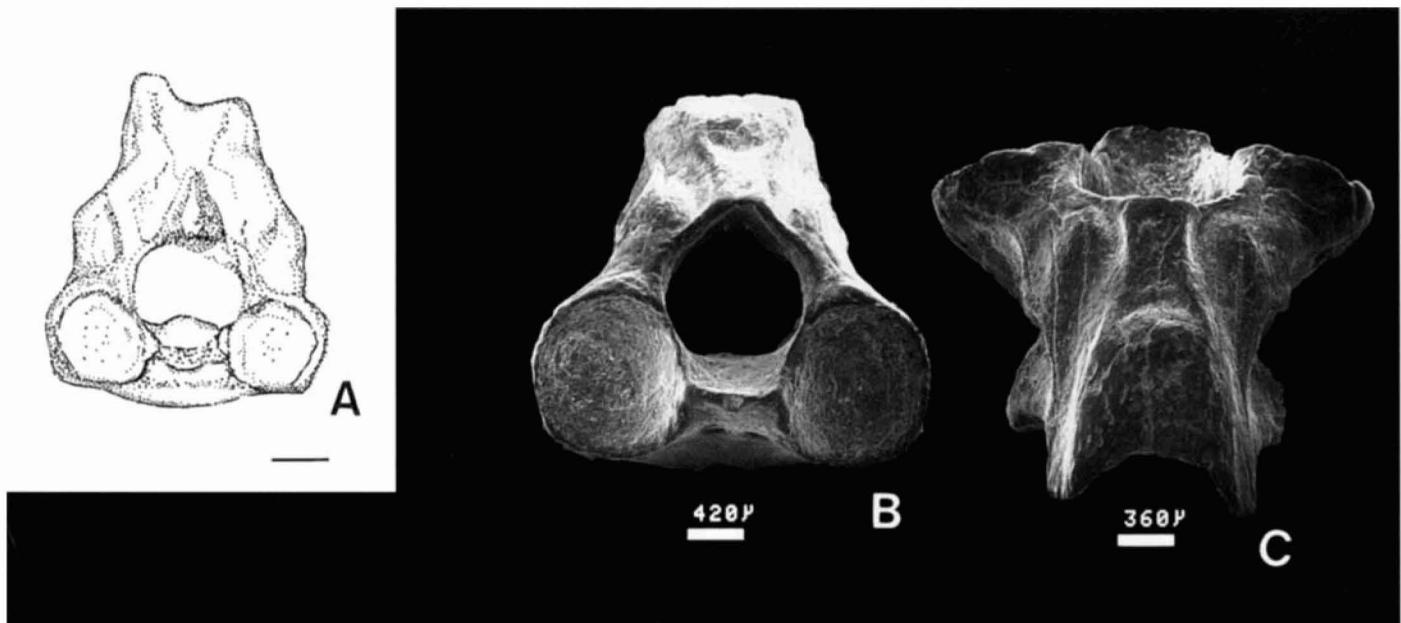


FIGURE 2. Atlantes of *Parrisia neocesariensis*, gen. et sp. nov. A, NJSM 16609, holotype vertebra, anterior view; B, NJSM 14690 b., subadult atlas, anterior view, showing slight dorsoventral elongation of the anterior cotyles; C, NJSM 14690 b., dorsal view, showing broadened ridge on neural spine, deeply forked tip, and slightly protruding tuberculum interglenoideum.

*PARRISIA NEOCESARIENSIS*, sp. nov.  
(Figs. 2–7)

**Holotype**—NJSM 16609, a complete atlas, (Figs. 2A, 3A, C).

**Diagnosis**—As for the genus.

**Locality and Horizon**—As for the genus.

**Etymology**—In honor of the State of New Jersey, the location of the Ellisdale site and the currently known range limit of the species.

**Referred Material**—(All NJSM) 16752, 15875, 15828, 15280, 15651, 14691 (dentaries); 14690B, 16613 (atlas vertebrae); 14207 (2nd cervical vertebra); 16756 (ant. thoracic vertebra); 15042A. (ant. caudal vertebra); 16555 (caudal vertebra); 15042a. (caudal vertebra); 15042 (3 posterior caudal vertebrae).

#### Description

**Atlas**—A number of atlantes are referable to *Parrisia*, the best being a series representing a juvenile (NJSM16613), subadult (NJSM14690B), and the proposed holotype, NJSM16609, from an adult specimen. They are comparable to AMNH8112 and PU20559, atlantes of *Opisthotriton kayi*. All are identifiable as batrachosauroidid by the large, concave anterior cotyles and poorly developed odontoid process (tuberculum interglenoideum). In all specimens the odontoid protrudes slightly as a small ridge, and is located at one third of the height of the cotylar surfaces on either side. *Parrisia* resembles *Opisthotriton* in this respect. It differs from the latter in that at all three growth stages the neural canal is widely open and does not exhibit any lateral compression, although *Opisthotriton* exhibits considerable variability in this character.

The anterior cotylar surfaces of *Opisthotriton* are nearly hemispherical and circular in outline in anterior view, whereas in NJSM16613 they are ovoid (higher than wide), suggesting a comparison with *Prodesmodon* (Appendix 1; character 4). However, there is considerable variation between individual atlantes of *Parrisia*, the cotyles becoming generally more circular and deeply cupped throughout the growth series. We interpret

circular cotyles as the second derived condition of this character, with horizontally flattened cotyles as the primitive condition present in *Scapherpeton*, *Habrosaurus*, *Prosiren*, most non-batrachosauroidid caudates, and some individuals of *Opisthotriton*. Vertically compressed cotyles (as seen in *Prodesmodon*) are coded as the first derived condition, a developmental stage which *Parrisia* appears to pass through in its ontogeny.

The neural spine of *Parrisia* lacks the blade-like central ridge present in *Opisthotriton*, and instead bears a broad flat protuberance, which begins as a paired process lying dorsal to the neural canal, and broadens posteriorly to cover the entire surface of the forked neural spine (Appendix 1; characters 8, 9), a seemingly derived condition in *Parrisia*.

Some of the most profound differences between atlantes of *Parrisia* and *Opisthotriton* are apparent when viewed from the lateral aspect, (Fig. 3, A–D). In NJSM16609, the anterior cotyles are surmounted by paired spinous protuberances, (Fig. 3C, detail 2), forming the medial edge of the neural canal, which are not present in *Opisthotriton*. The neural arch, which forms the vault of the neural canal, extends posteriorly at a 45° angle to the plane of the cotyles, thus leaving an opening on the dorsal surface of the neural canal which extends one third the length of the centrum. In contrast, the anterior edge of the neural arch in *Opisthotriton* extends dorsally in the same plane as the anterior edge of the cotyles. The neural spine in *Opisthotriton* makes a sharp 90° angle at its dorsal edge, (Fig. 3B, detail 1), extending posteriorly, parallel with the axial plane of the centrum. The entire neural spine and arch in *Parrisia* are nearly twice the length of the centrum, extending posteriorly well beyond the edge of the posterior cotyle, and unlike *Opisthotriton* where they end just above the posterior cotylar rim. The posterior cotyle of the NJSM specimen is ventrally directed so that it is at an angle of >20° off the axial plane of the centrum. The only other batrachosauroidid that exhibits this character is the poorly known *Perotosauroides problematica* (Naylor, 1981) from the Late Miocene of California. However *Perotosauroides* also has a robust neural crest, unlike this new genus. In *Opis-*

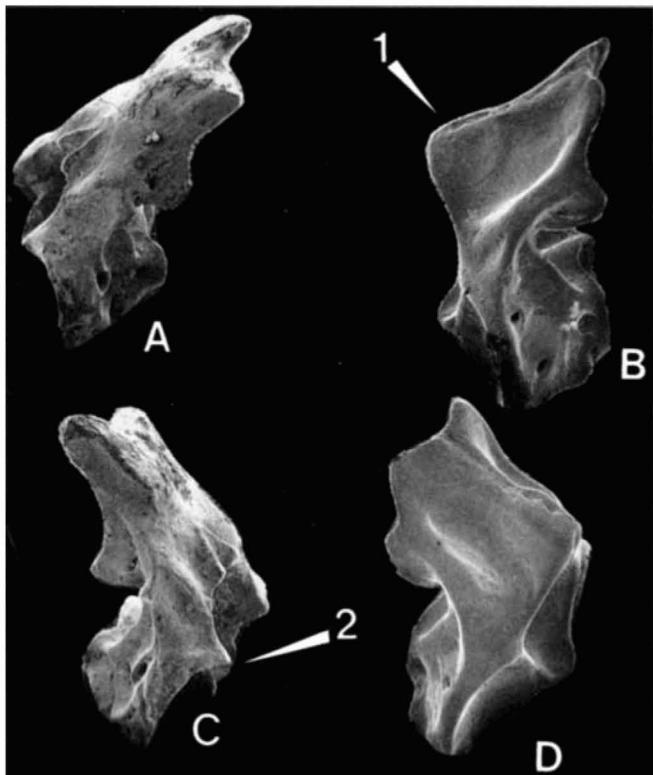


FIGURE 3. Left dorsolateral aspect of batrachosauroidid atlantes. A, NJSM 16609, *Parrisia neocesariensis*, gen. et sp. nov. (holotype). B, PU 20559, *Opisthotriton kayi*, arrow (1) indicates anterior extension of neural arch, absent in NJSM 16609. C, NJSM 16609, right dorsolateral aspect, arrow (2) indicates spinous process above the anterior cotyles, which is not present in D, *O. kayi*, PU 20559.

*thotriton* the posterior cotyle is in line with the anterior cotyles (i.e., on the same plane). The articular surfaces of the posterior zygapophyses of the NJSM specimen are parallel with the axial plane of the centrum. In *Opisthotriton* these same processes extend posterodorsally at a 45° angle. Thus the zygapophyses of the NJSM specimen are more prominent than their equivalent in *Opisthotriton*.

The posterior and ventral aspect of the *Parrisia* specimens are nearly identical to *Opisthotriton*, with the exception of the sub-central foramina, which are perfectly circular and widely spaced in the NJSM specimens. In *Opisthotriton* they are anteroposteriorly elongated, and approach the midline of the centrum more closely, although considerable variation is seen in this genus.

Superficially, the juvenile specimens NJSM16613 and NJSM14690B (Fig. 2B, C), seem to show greater resemblances to *Prodesmodon*, primarily due to the oval shape of the anterior cotyles in early ontogeny. However, all other details of the morphology (e.g., angling of the neural spine, zygapophyseal development and cotylar angulation) predict the final condition in the adult form. The adult specimen exhibits more rounded cotyles, and a general development of spinous processes of the neural arch, presumably for the attachment of the axial cervical musculature.

**2nd Cervical**—NJSM14207, (Figs. 4A, 5B), is a nearly complete opisthocoelous 2nd cervical vertebra, broken on its left side revealing the course of the large intervertebral artery. Anteriorly the condyle is filled with a rounded dome of ossified cartilage. The same vertebra in *Opisthotriton* (PU18575B) shows a thick ring of ossified cartilage, with a large, centrally

located notochordal pit. *Parrisia* shows a tiny, ventrally placed notochordal pit. There is a high neural arch (compressed dorsoventrally in PU18575B), with no sign of any intravertebral nerve openings. The anterior zygapophyses are oriented perpendicular to the sagittal plane, unlike *Opisthotriton* where they are tilted inward at a 45° angle.

Dorsally, NJSM14207 is more antero-posteriorly compressed than the equivalent vertebra in *Opisthotriton*. In *Parrisia*, a strong central ridge runs down the length of the neural arch terminating in an unfinished neural spine. Laterally, both vertebrae show prominent foraminae for the vertebral artery. The neural spine in *Parrisia* is at a higher angle (more prominent) than in *Opisthotriton*. The posterior zygapophyses are weakly developed in *Parrisia* compared to *Opisthotriton*. Ventrally, NJSM14207 shows no trace of the subcentral ridge or keel which characterizes the cervical vertebrae of *Opisthotriton* and *Batrachosauroides* (Estes, 1969). The centrum of the NJSM specimen is more solidly constructed than that of *Opisthotriton*, which is perforated by a number of small foramina. Posteriorly, the cotyle of NJSM14207 is shallower than *Opisthotriton*, and the transverse processes of the neural arch reside at a slightly higher angle.

**Anterior Trunk Vertebra**—NJSM16756, (Fig. 4B), is a nearly complete anterior thoracic vertebra, missing the left transverse process. It is compared to PU18575C and AMNH8136, vertebrae from a similar position in the spinal column of *Opisthotriton*.

Ventrally, NJSM16756 shows a prominent keel, which is most pronounced at midline, but fuses rapidly with the posterior cotyle. In PU18575C the keel runs the entire length of the centrum. The paired basopophyses of the NJSM specimen are strongly appressed to the cotylar cup, actually uniting with its surface posteriorly, and giving the ventral edge a distinctly forked or scalloped appearance, resembling the posterior cotyle of *Pseudobranchus* (Appendix 1; character 15). The widespread occurrence of this morphology in aquatic, non-batrachosauroidid caudates suggests it is a primitive character for the family. In *Opisthotriton* the cotyle is round, with the prominent basopophyses separated from it and projecting ventrally. The transverse processes are directed more posteriorly than in *Opisthotriton*, thus producing a narrow gap between themselves and the posterior zygapophyses. In the NJSM specimen there are paired foramina for the vertebral artery on the anteroventral surfaces of the transverse processes. Anteriorly, NJSM16756 shows a condyle filled with ossified cartilage. A tiny notochordal pit is present near the dorsal edge. This is unlike *Opisthotriton* where the anterior face of the centrum is flattened, with a thick ring of ossified cartilage and a centrally placed notochordal pit. Dorsally, the anterior zygapophyses of *Parrisia* are larger than *Opisthotriton* and more anteroposteriorly elongated. The posterior zygapophyses bear a sharp keel on the entire length of their dorsal surface (pteryophyseal process), a condition seen in the Lance *Opisthotriton* specimen UCMP55821 (Estes, 1964). The neural spine tip is hollow (finished in cartilage). Laterally, the transverse processes of NJSM16756 are bicipital, but webbed with a thin lamina of bone. The ventral lamina of the unbroken transverse process is well developed and more pronounced than in *Opisthotriton*. The closely appressed basopophyses of NJSM16756 project posteroventrally beyond the edge of the cotyle (Appendix 1; character 15). The neural spine in this vertebra is more prominent (angled more dorsally) than in the equivalent vertebra of *Opisthotriton* (Appendix 1; character 16), a character which shows considerable variation among the batrachosauroidids, but is interpreted herein as plesiomorphic for the group on the basis of comparison with *Scapherpeton*.

It is in the lateral view that the strong ventral displacement of the posterior cotyle relative to the anterior condyle is most

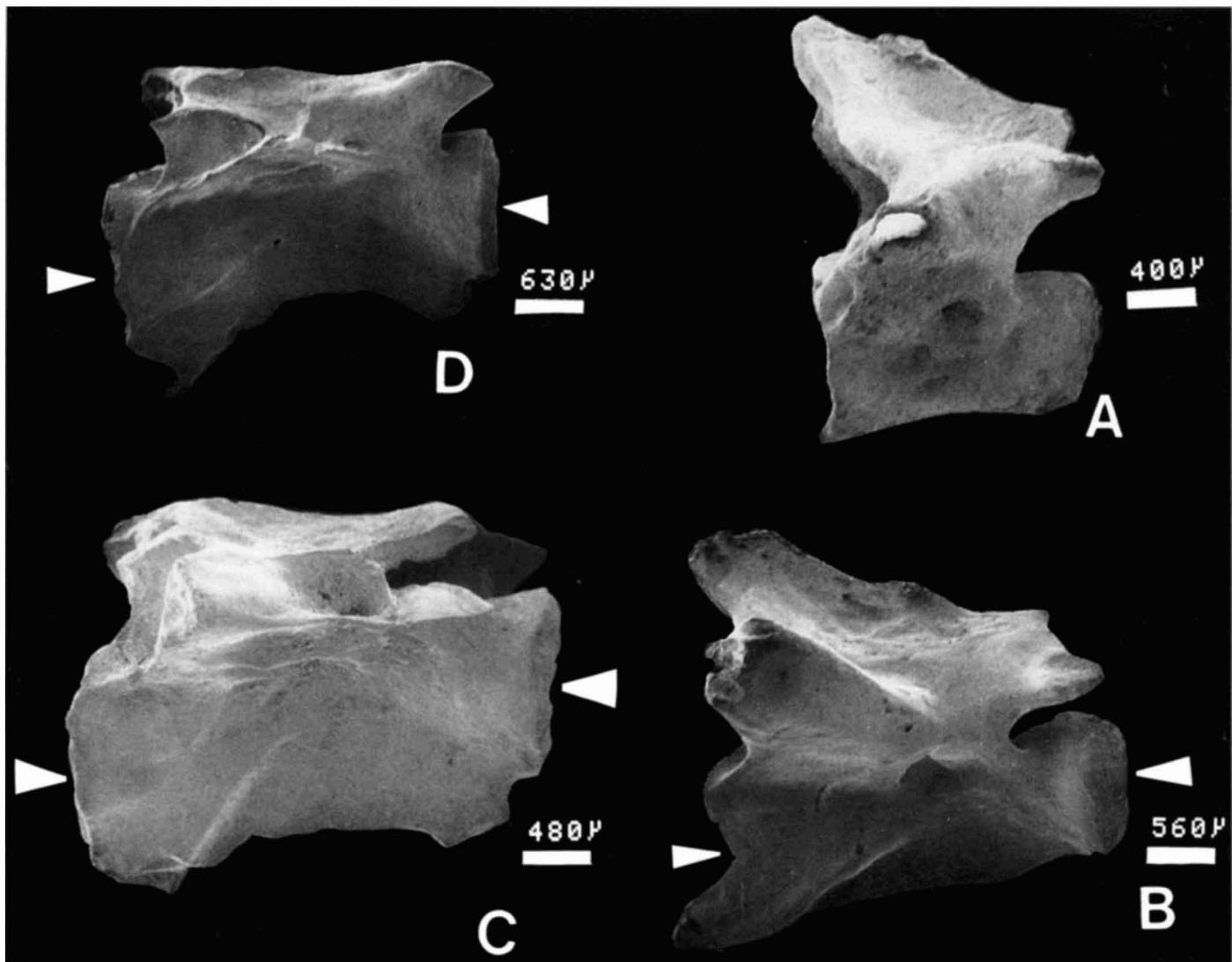


FIGURE 4. *Parrisia neocesariensis*, gen. et sp. nov. Clockwise from upper right; A, NJS 14027, 2nd cervical; B, NJS 16756, anterior thoracic; C, NJS 16555, posterior thoracic; D, NJS 15042a, anterior caudal. All in left lateral view. White arrows in B, C, and D indicate the axis of the condyle and cotyle, showing relative ventral displacement of the posterior face of the centrum.

readily seen (Fig. 4), with the upper edge of the posterior cotyle being in the same plane as the lower edge of the anterior condyle (Appendix 1; character 12). This is the strongest expression of this character in the vertebral series, and is unique to *Parrisia* among the known batrachosauroidids. Thus we interpret it as autapomorphic. Nevertheless, ventral displacement of the posterior vertebral cotyle relative to the anterior cotyle is widespread among other salamander families including the Amblymidae, Plethodontidae, Salamandridae and Sirenidae and serves a functional purpose of increasing the flexibility of the trunk in these elongate caudates.

**Posterior Trunk Vertebra**—NJS 16555, (Figs. 4C, 5A), is a posterior thoracic vertebra. It is comparable to PU 18757D and AMNH 8112, vertebrae from the same approximate position in the spinal column of *Opisthotriton*.

Laterally, the anterior condyle and posterior cotyle of this portion of the vertebral column of *Parrisia* continue to be out of plane with one another, although not as strongly as the anterior thoracics. The posterior cotyle of NJS 16555 is ventrally displaced such that its dorsal margin is on the same plane as the center of the anterior condyle. In the equivalent vertebrae

of *Opisthotriton* they are on the same plane (i.e., the centrum is parallel with the lower surface of the neural arch). In *Parrisia*, the basopophyses descend from the center of the centrum posteriorly towards the edge of the cotyle at a relatively acute angle. The neural spine is more prominent, but lacks the dorsal keel present in *Opisthotriton*. On the posteroventral side of the transverse processes there are paired intravertebral nerve foraminae, which penetrate into the neural canal. These structures are not present in any other member of the family. The subcentral keel, (Fig. 5A), is more pronounced than in the equivalent vertebra of *Opisthotriton*. In the *Parrisia* specimen, the basopophyses are more closely appressed to the cotyle, uniting to form a part of the posterior edge, and define a triangular area on the posteroventral surface of the centrum just anterior to the cotylar edge. In *Opisthotriton* these processes stay separate and distinct along their entire length. Dorsally, the NJS specimen has a weak central ridge, which begins near the center of the neural arch and extends only part of the way up the neural spine. This is unlike the condition in *Opisthotriton*, where the ridge extends the entire length of the neural arch and spine. In *Parrisia* the central ridge is flanked by two accessory ridges

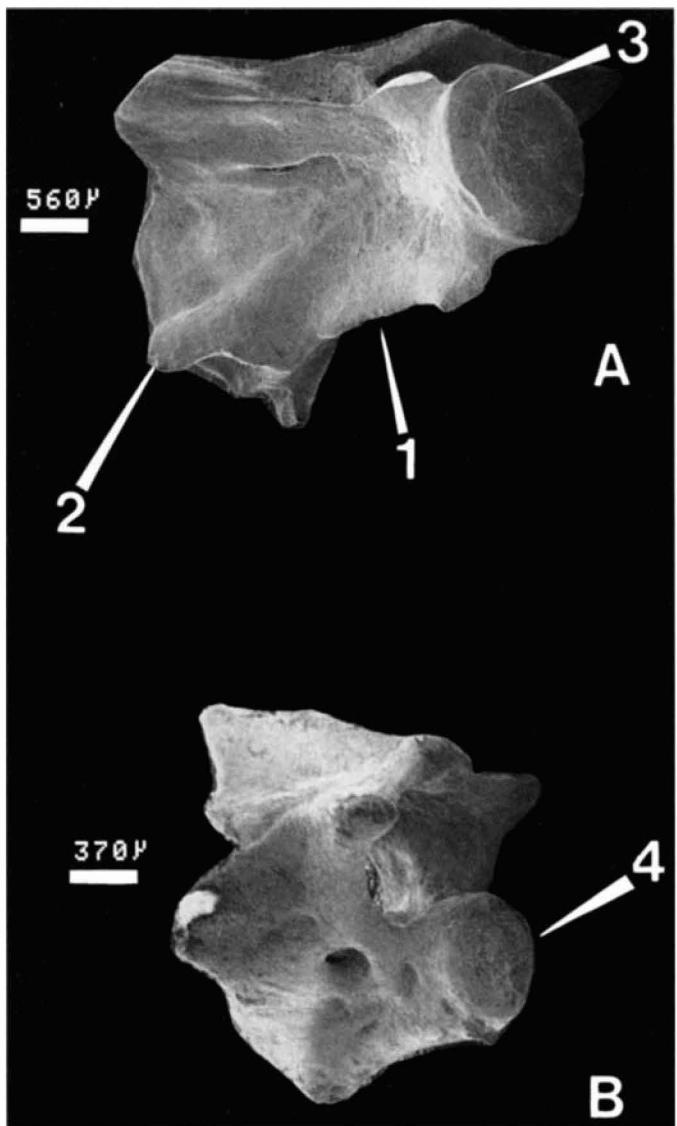


FIGURE 5. Right anteroventral oblique aspect of *Parrisia neocesaricensis*, gen. et sp. nov. A, posterior trunk vertebra, NJSM 16555; B, 2nd cervical vertebra, NJSM 14207. Arrows: 1, ventral keel (hypapophysis); 2, right basopophysis; 3, ring of ossified cartilage surrounding the notochordal pit; 4, anterior vertebra showing dome of ossified cartilage forming the condylar surface, lacking large, centrally placed notochordal pit.

which run parallel to it, and along the length of the neural spine. These accessory ridges are not present in *Opisthotriton*. The anterior zygapophyses are antero-posteriorly directed. The posterior zygapophyses are well separated from the internal edge of the neural arch and lie at the lateral extremity of a curving lamina of bone. They lack pteryphophyses. Anteriorly, the condyle shows a deep notochordal pit and lacks the dome-shaped condyle of the more anterior vertebrae, (Fig. 5B). However, the ring of calcified cartilage surrounding the pit is thicker than the equivalent structure in *Opisthotriton*. The neural canal is more "open" (less dorsoventrally compressed) than in *Opisthotriton*.

**Anterior Caudal Vertebra**—NJSM15042A., (Fig. 4D), is an anterior caudal vertebra, missing the neural spine and the posterior-most portion of the neural arch. It is comparable to PUB18575E, from a similar position in the spine of *Opisthotriton*.

The neural arch of NJSM15042A is preserved intact, with a relatively high vault. The posteromedial internal surface shows the openings of the intravertebral spinal nerve foramina, corresponding to the paired openings on the posteroventral surfaces of the neural arch. The *Parrisia* specimen has a much enlarged ventral keel (hypapophysis) which extends well below the ventral edge of the condyle. The basopophyses, although prominent from the lateral aspect, ascend at a sharp angle to contact the mid-point of the centrum. In *Opisthotriton* they ascend more gradually, contacting the rear edge of the condyle. As in the trunk vertebrae, the basopophyses are generally more closely appressed to the centrum than in *Opisthotriton*. The condyle and cotyle of the NJSM specimen are slightly out of plane. Dorsally, the neural arch lacks a central ridge, and the anterior zygapophyses are more laterally directed than in *Opisthotriton*. Anteriorly, the ring of calcified cartilage on the condyle is relatively thicker than in *Opisthotriton*, however a deep, centrally located notochordal pit is present and the condylar surface is relatively flat, unlike the more anterior vertebrae. The anterior neural arch is flattened, but has a higher vault than the equivalent vertebrae in *O. kayi*. Although there is some variation along the column, both *Parrisia* and *Batrachosauroides* have a higher neural arch than *Opisthotriton* throughout the vertebral series.

**Posterior Caudal Vertebrae**—NJSM 15042 is a mixed lot of bones, containing several broken posterior caudal vertebrae. They are comparable in all aspects to the same vertebra in *Opisthotriton*, with the exception of the presence of paired, intravertebral nerve openings. The most complete specimen has a well developed, prominent neural spine, unfinished with bone, lacks transverse processes, and shows scars for the attachment of a ventral process. The morphology of these bones suggest a tail which was laterally compressed and adapted for swimming.

**Dentary**—Several dentaries are probably referable to the new genus, the best of which is NJSM14691, (Fig. 6 A–C), a partial left dentary. The dentary is broken at the anterior and posterior ends, but seems to suggest that the intact bone was not as deep as is usual for the batrachosauroidids. The symphysis is missing, but referred specimens show that this structure was not enlarged as in *Batrachosauroides*, and more comparable to the symphysis of *Opisthotriton*.

NJSM 14691, (Fig. 6A), is 6mm in length, with three complete teeth. The Meckelian groove is widely open, starting anteriorly at the level of the 7th tooth. The subdental ridge is poorly developed, appearing as a thin shelf beneath the teeth, and unlike most other members of the family where this structure tends to be deep and well developed. There are the lower halves of nine teeth present, and all have broken at an equivalent point, suggesting that an eroded zone in the intact three teeth represents the pedicel, with the remnants of at least 19 teeth in all. The intact tooth bases all show enlarged, lingually directed resorption pits. The teeth are relatively widely spaced, and similar to both *Opisthotriton* and *Paleoproteus* in this respect. The intact teeth extend over one half of their height above the parapet, and all the tooth bases show anteroposterior compression, unlike *Opisthotriton* or *Batrachosauroides*, where they are cone-shaped throughout their length. The crowns of the intact teeth are gently recurved. In many ways the teeth resemble those of *Prodesmodon*.

The lateral wall of the dentary rolls medially where it expands into a large venteromedial shelf (Fig. 6B), forming the floor of the Meckelian groove (Appendix 1; character 1). A similar shelf is seen only in *Paleoproteus* among the Batrachosauroidia, but is also seen in *Necturus* and *Scapherpeton* and is interpreted as plesiomorphic for the family. On the lateral surface there is no sign of any mental foramina, and NJSM14691 shares this characteristic with both *Opisthotriton*, and *Prodesmodon*. Externally, (Fig. 6C), the jaw is concave, with a slight

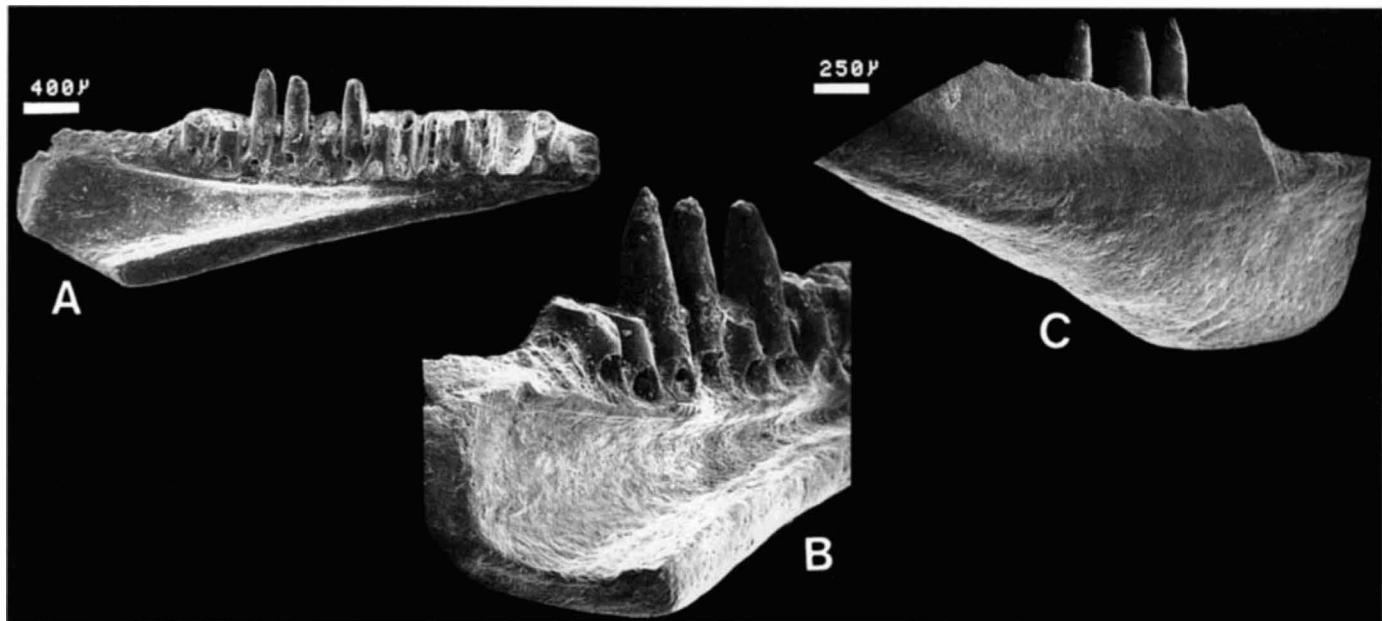


FIGURE 6. NJSM 14691, batrachosauroidid left dentary. A, medial view; B, posterior oblique view, showing enlarged ventromedial shelf and poorly developed subdental ridge; C lateral view showing lack of mental foramina and broken expansion for the "coronoid" process.

convex area starting just below the ninth tooth and extending posteriorly. It is primitive in lacking the deeply excavated external groove seen in both *Batrachosauroides* and *Paleoproteus* (Appendix 1; character 3).

#### Discussion

The family Batrachosauroididae are an extinct group of paedomorphic, presumably aquatic salamanders related to the proteids (Estes, 1981; Naylor, 1981). It is admittedly difficult to analyze the phylogeny of paedomorphic salamanders (Hecht and Edwards, 1976), and therefore both intra- and inter-familial relationships of the batrachosauroidids are not easily resolved. Analysis of inter-familial relationships of these salamanders is further restrained by the relatively poor fossil record of caudates in general. The challenges involved in understanding the Batrachosauroididae and their phylogeny have been discussed by Estes (1969, 1981).

Batrachosauroidids as a group share select "derived" characters with *Necturus*, *Proteus*, the amphiumids, and even *Plethodon*, such as pteryophyseal processes, (Fig. 7A, detail 1), ventral keels, closely approximated rib bearers and ventral laminae, (Fig. 7A, detail 2), of the transverse process. However, these characters are homoplasies in the truest sense, and reflect parallel adaptations in unrelated groups of salamanders. Elongation of the body, reduction or loss of limbs, and corresponding hypertrophy of the axial musculature are a result of an increasingly aquatic habitus, and do not constitute valid synapomorphies, as the most paedomorphic forms among verifiable unrelated families of salamanders all exhibit these characters (Hecht and Edwards, 1976). Nevertheless, pervasive arguments can be made for a "sister group" relationship between the proteids and the batrachosauroidids, although any ancestor/descendant relationship has yet to be established (Estes, 1981; Milner, 1983).

Among the batrachosauroidids, *Parrisia neocesariensis* is most similar to *Prodesmodon* (Cretaceous, N. Amer.) and especially *Opisthotriton kayi* (Cretaceous–Paleocene, N. Amer.). Comparison of these taxa is complicated by the fact that *Opisthotriton* shows considerable variation, especially between the

Cretaceous and Paleocene forms. It has been suggested that the genus should be subdivided into time-distinct species (Naylor, pers. comm.), a contention which is supported by our own observations in conjunction with this study. The Paleocene specimens of *Opisthotriton* are particularly "baroque" in appearance when compared to representative Cretaceous specimens, having more strongly developed subcentral keels, ventral laminae, and muscle attachment processes, all of which suggest a more aquatic habitus. In nearly all aspects the anatomically equivalent bones of *Parrisia* show greater resemblance to the Paleocene *Opisthotriton* than to the Cretaceous specimens. Nevertheless, enough osteological differences are present in the dentary, atlantes and post-atlantal vertebrae of *Parrisia* and *Opisthotriton* to warrant their separation into distinct genera.

It has been postulated that the batrachosauroidids may be descended from a *Scapherpetron* or *Lisserpeton*-like stem neourodele (Estes, 1969; Milner, 1983), although Naylor (1981) has suggested they evolved from an unknown, relatively derived ancestor with well-developed basopophyseal musculature. In either case, *Parrisia* retains a suite of "primitive" characters (i.e., unreversed compared to the more developed paedomorphic batrachosauroidids) including: intravertebral spinal nerve openings in the caudal vertebrae, (Fig. 7B); a poorly developed subdental ridge; an externally rounded, ungrooved dentary, (Fig. 6C); and prominent neural spines unfinished in bone, (Fig. 7A). Phylogenetic character analysis of the Ellisdale salamander suggests it is a primitive sister taxon to all other members of the family (see Appendix, 1, 2, and Fig. 8), sharing several characters with the postulated stem-neourodeles *Scapherpeton* and *Lisserpeton*. Milner's cladistic-vicariance model for salamander biogeographical distributions (1983) proposed a sister-group relationship between the Proteoidea and the "neourodeles" (Plethodontoidae + Salamandroidea). However, the retention of post-sacral intra-vertebral nerve foraminae solely in *Parrisia* among the batrachosauroidids suggests the loss of this character is a valid synapomorphy of the family, and a (neotonous) reversal from the condition which likely existed in the ancestral neourodele. Thus it may be appropriate to redefine a monophyletic "neourodele" clade as consisting of Proteoidea, Pletho-

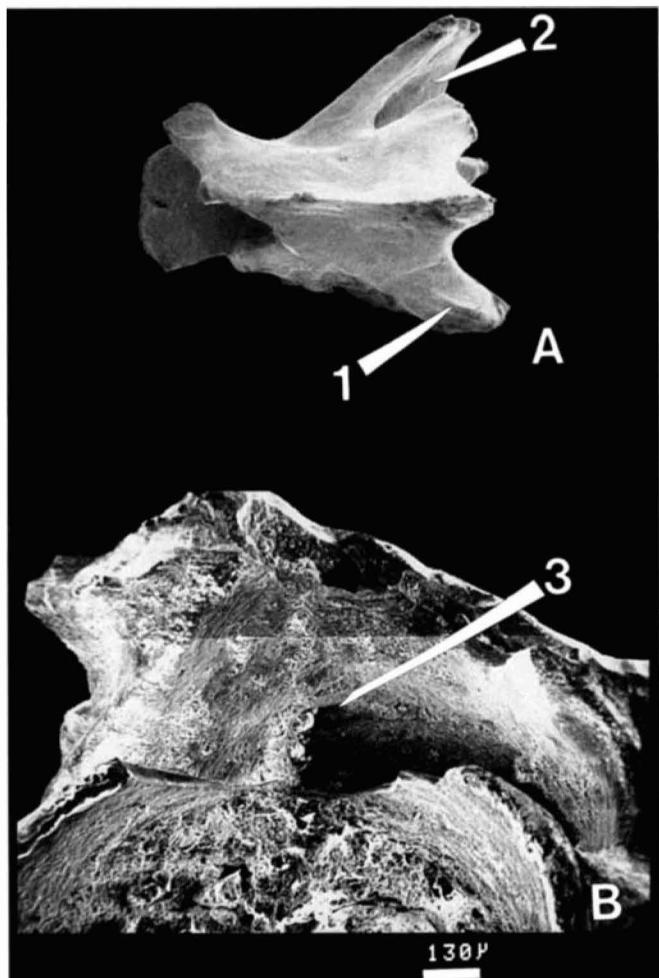
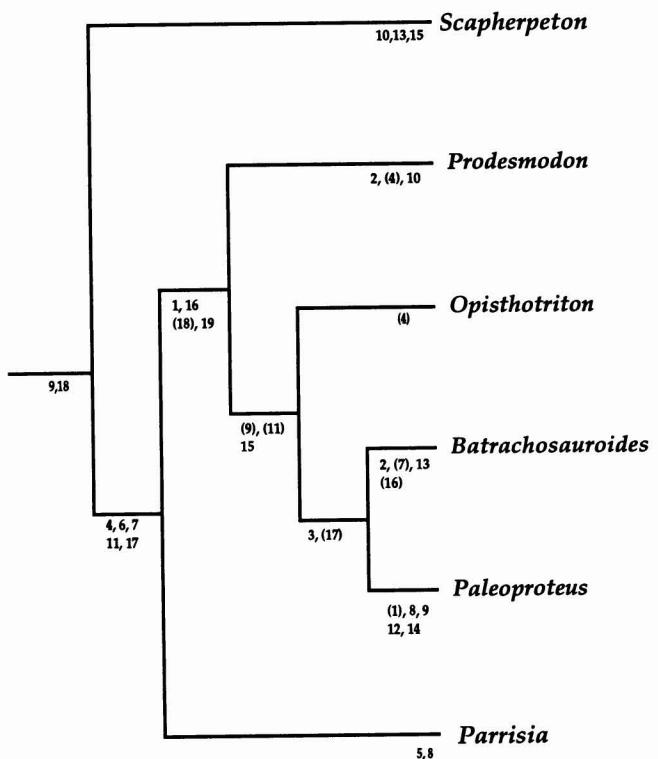


FIGURE 7. *Parrisia neocesariensis*, gen. et sp. nov. A, NJSM 16756, anterior trunk vertebra, dorsal view, showing (1) "pteryophyseal-like" process (ridge) on dorsal surface of postzygapophysis, and (2) ventral lamina of transverse process; B, view into posterior portion of neural canal of NJSM15042a, anterior caudal vertebra showing (3) medial opening of the intra-vertebral nerve foramina.

dontoidea, Salamandroidea, their most recent common ancestor, and all of its descendants.

The batrachosauroidids were strictly holarctic in distribution, appearing in the fossil record during the Late Tithonian (Jurassic–Cretaceous boundary) of Europe (Ensom, et al., 1991; Evans and Milner, 1996), and persisted until at least the Late Miocene of western North America (Naylor, 1981). With the exception of a single occurrence in the Coniacian of central Asia (Nessov, 1988), they were only known from the Mesozoic and early Tertiary of the western interior of North America and western Europe. They lacked any Mesozoic fossil record in eastern North America, although undescribed specimens of cf. *Batrachosauroides* from the Miocene of Delaware were reported (Benson, 1993). The only previously reported batrachosauroidid genera from the Late Cretaceous were *Prodesmodon* and *Opisthotriton*, both from western N. America, and a poorly known and undescribed specimen from Mons, France (Estes, 1981). Thus, *Parrisia neocesariensis* adds significantly to our record of the family, and forms a Mesozoic biogeographic link between the European and western North American forms.

During most of the Cretaceous, the North American continent was divided by a shallow inland sea. Previous workers have



Characters in parenthesis (n) denote reversals

FIGURE 8. Phylogenetic relationships among the Batrachosauroididae. Single most parsimonious cladogram generated using 19 characters (Appendix 1) and 5 genera (Appendix 2) with *Scapherpeton* and an all zero theoretical ancestor as the outgroup. Data analyzed with PAUP 3.0, using the exhaustive search option. Consistency Index = 0.633 (unweighted characters). Character weighting does not affect the apomorphy distribution.

conjectured that the sea did not present significant barrier to faunal interchange (Miller, 1967; Baird and Horner, 1977, 1979; Krause and Baird, 1979). Lack of endemic fossil species would have supported this view, but the hypothesis remained largely untestable due to the unavailability of representative terrestrial assemblages. The identification of a distinct batrachosauroidid genus, dwelling in the coastal swamps and rivers of eastern North America further supports the presence of endemism among the terrestrial fauna of this region (Lillegraven, 1974; Clemens et al., 1979; Grandstaff and Parris, 1993; Denton and O'Neill, 1995). It also suggests that the most recent common ancestor of the North American batrachosauroidids may have evolved prior to Aptian–Albian times, when the epeiric sea divided the continent for the remainder of the Cretaceous.

There seems to have been a relatively low rate of speciation among these salamanders (Estes, 1981), especially if it is accepted that *O. kayi* remained essentially unchanged from the Late Cretaceous through the Late Paleocene. Nevertheless, the presence of diagnostic batrachosauroidid fossils from the Tithonian of Great Britain suggest the most recent common ancestor of the family may have evolved in Laurasia during the Middle Jurassic or earlier (Evans and Milner, 1996). It is probable that when the European Jurassic and Cretaceous specimens are fully described, they will prove to be distinct from *Opisthotriton*, *Prodesmodon*, and *Parrisia*. This would aid in understanding the relationships of *Paleoproteus*, a well known genus from the Lower Tertiary of Europe (Estes et al., 1967), to its allied North American genera of equivalent age.

### Caudata Indet.

Many specimens diagnosed only as "Caudata indet." are present in the Ellisdale collection, and will require further study. Among these are an atlas, NJSM16622, and assorted jaw and skull pieces that have been tentatively identified as cf. *Habrosaurus* sp. Further material will be necessary to determine if these specimens can be positively referred to the characteristic Lance sirenian.

Other specimens have been tentatively identified as comparable to both *Albanerpeton* and *Proamphiuma*, but they are all too incomplete or damaged to make any definite assignments at this time. Additional collecting will be required to shed light on these assorted caudates.

### THE PALEOHABITAT OF THE ELLISDALE AMPHIBIANS, TAPHONOMIC IMPLICATIONS

The Ellisdale site has been interpreted as a sequence of sediments deposited in a backbay or tidal channel setting during a transgressive pulse along a passive continental margin (Gallagher et al., 1986; Tashjian, 1990). Persuasive arguments have been made supporting this model, founded both in the geological evidence (sequence stratigraphy), and the presence of a mixed faunal assemblage consisting of chondrichthyan teeth, fresh and salt water teleost remains, turtles, crocodilians, and dinosaurs.

Considerable disagreement exists on the taphonomic interpretation of the site. It has been proposed that the fauna represents a "taphonomically mature and unquestionably reworked" assemblage (Gallagher, 1993). While most of the Ellisdale megafaunal fossils give considerable evidence supporting pre-burial weathering and transport, the abundant microvertebrate remains do not. Numerous squamate bones are being discovered with teeth, fragile processes, and carbonized soft tissue in place (Denton and O'Neill, 1995). The fossil skeletal remains of the Ellisdale amphibians are also extremely fragile, yet small delicate structures are often preserved completely intact. It is difficult to imagine these bones as having been deposited, fossilized, exhumed, transported, and reburied, without exhibiting far greater damage than is evident. As a result, other authors have not agreed with the "taphonomically mature" interpretation of the site, and have proposed that the visible wear (breakage) occurred prior to burial (Tashjian, 1990; Grandstaff et al., 1992).

In some sites, bones from animals separated by several million years have been reworked and deposited together under estuarine conditions (Frey et al., 1975). But the presence of mixed assemblages does not obviate isochronal mortality or necessarily support an argument towards extensive reworking. The occurrence together of the skeletal remains of animals from disparate environments can just as readily be interpreted as the result of fluvial or tidal transport at times of seasonal floods or periodic storms (Aigner, 1985; Brett et al., 1986). Faunal admixtures of the same sort are present in most of the estuarine and coastal lowland Campanian and Maastrichtian sites of the western interior (Armstrong-Ziegler, 1980; Sahni, 1972; Estes, 1964; Estes and Berberian, 1970), however the fossil remains from these localities are usually interpreted as the result of relatively isochronal mortality.

Both squamates and amphibians are extant members of the coastal lowland fauna of North America today. The large freshwater "sloughs" of the southeastern Atlantic barrier islands and spits are host to several species of toads, frogs, and salamanders including sirenians and amphiumids. In addition, cryptobranchids and *Necturus* range down rivers to the freshwater tidal zones, in some cases only a few miles from the coast itself (Conant, 1958). It is highly probable then, that the dominant Ellisdale squamate *Prototyphlops* was a denizen of the barrier

beach environment, as are teiids of the genus *Cnemidophorus* today. Likewise *Parrisia*, the most abundant amphibian remains at Ellisdale, may be the ecological equivalent to the extant genera of elongated, paedomorphic salamanders *Amphiuma*, *Siren*, and *Pseudobranchus*, which are still found in coastal environments. Thus, significant components of the Ellisdale microfauna may be interpreted as "proximal", on the basis of relative completeness (RC) and relative abundance (RA) of the taxa, using the techniques of Shotwell (1955, 1958, 1963).

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**APPENDIX 1.** List of characters used in the phylogenetic analysis. Character polarity based on prior work (Hecht and Edwards, 1976), (Estes, 1969, 1981), and outgroup analysis (*Scapherpeton*, *Necturus*, and *Plethodon*, respectively). If polarity could not be determined in this manner, loss of a character was accepted as the derived state. Characters listed as “this paper” are explained in detail in the descriptive portion of the text. 0 = primitive condition; 1 = first derived state; 2 = second derived state.

#### Dentary

1. Medial projection of ventral edge of dentary (lingual shelf): present 0; absent 1 (this paper).
2. Tooth shape: pedicillate 0; nonpedicillate 1.
3. Lateral groove on dentary: shallow 0; deep 1 (this paper).

#### Atlas

4. Cotylar shape: horizontally flattened 0; laterally compressed 1; round 2 (this paper).
5. Posterior cotyle ventrally displaced: absent 0; present 1.
6. Cotylar depth: shallow 0; deep 1.
7. Glenoid process: projecting, rounded 0; reduced 1; absent 2.
8. Neural spine: rounded 0; forked 1 (this paper).
9. Neural arch ridge: blade like 0; flattened 1 (this paper).
10. Zygapophyses: large 0; small 1.

#### Vertebrae

11. Condylar condition: amphicoelus 0; semiopisthocoelus 1; fully formed condylar ball 2.
12. Vertebral cotyles: inline 0; posterior cotyle ventrally displaced 1 (this paper).
13. Basopophyses: present 0; absent 1.
14. Basopophyses: posteriorly divergent 0; anteriorly divergent 1.
15. Basopophyses: extending beyond edge of cotyle 0; short, ending at cotyle 1 (this paper).
16. Neural spine: high 0; low 1 (this paper).
17. Ribbearers: bicipittal 0; unicippital 1.
18. Caudal intravertebral nerve opening: Absent 0; Present 1.
19. Neural spine: finished in cartilage 0; ossified 1.

APPENDIX 2. Data matrix showing the distribution of the 19 characters among the five most completely known batrachosauroidid genera as analyzed by PAUP 3.0 software utilizing the “exhaustive search” option. Characters states: 0 = primitive; 1 = first derived state; 2 = second derived state; *Scapherpeton* and an all zero ancestor included in analysis. Characters showing intrageneric variability are coded as the most plesiomorphic condition for the group.

Taxon	Character																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Scapherpeton</i>	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0
<i>Prodesmodon</i>	1	1	0	1	0	1	1	0	1	1	2	0	0	0	0	1	1	0	1
<i>Opisthotriton</i>	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	1	1	0	1
<i>Batrachosauroides</i>	1	1	1	2	0	1	2	0	0	0	1	0	1	0	1	0	0	0	1
<i>Paleoproteus</i>	0	0	1	2	0	1	1	1	0	1	1	0	1	1	1	0	0	0	1
<i>Parrisia</i>	0	0	0	2	1	1	1	1	0	2	0	0	0	0	0	1	1	0	0