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A NEW SALAMANDER OF THE FAMILY BATRACHOSAUIDIDAE FROM THE LATE  
MIOCENE OF NORTH AMERICA, WITH NOTES ON OTHER BATRACHOSAUIDIDS

by

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## ABSTRACT

A new genus and species based on an atlas extends the range of the family Batrachosauroididae into the Clarendonian (Late Miocene) of California. The new taxon was probably amphicoelous and the vertebrae show resemblance to those of *Necturus*. Variation in vomers of *Opisthotriton* is reviewed. Batrachosauroidids are united by the possession of concave, circular atlantal cotyles and a shelf-like odontoid, and by configuration of the toothed cranial bones. Vertebrae are highly variable, ranging from strongly opisthocelous to amphicoelous, and varying in possession and extent of accessory processes. Relationship between proteids and batrachosauroidids is indicated by shared unique characters cranially and by comparison of and inference from vertebral structure and trunk musculature.

## INTRODUCTION

The Batrachosauroididae contains the largest number of species and is the most extensively known of the extinct families of salamanders. It spans a considerable period of time in North America and Europe (Table 1).

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TABLE 1. Stratigraphic occurrence of known taxa of batrachosauroidid salamanders. Some specimens in the Ravenscrag Formation are actually Maestrichtian and some in the Frenchman and Hell Creek formations are lower Paleocene.

	<i>Opiathotriton cf. kayi</i>	<i>Palaeoproteus klatti</i> *** <i>Palaeoproteus gallicus</i> ** <i>Prodesmodon copei</i> *	<i>Perithosauroides problematica</i> *** <i>Batrachosauroides dissimulans</i> ** <i>Batrachosauroides gotoi</i> *
up Miocene md 1r			San Pablo Group*** (California)  Fleming** (Texas) Thomas Farm** Lower Oakville** (Florida) (Texas)
Oligocene			
up Eocene md 1r		Geiseltal*** (Halle)	
	Wasatch (Wyoming)		Golden Valley* (North Dakota)
up Paleocene md 1r	Ravenscrag Paskapoo Polecat Bench (SE Sask.) (Alberta) (Wyoming)  Tongue River (Montana) Ravenscrag Scollard Tullock (SW Sask.) (Alberta) (Montana)	Cernay** (France)	
Maestrichtian	Frenchman Lance Hell Creek (Sask.) (Wyoming) (Montana)	Lance* Hell Creek* (Wyoming) (Montana)	
Campanian	Oldman Judith River Fruitland (Alberta) (Montana) (New Mexico)  Milk River (Alberta)		

Complete or partial skeletons include the following: *Ophisthotriton* cf. *kayi* (see Estes, 1975; also four undescribed Alberta specimens, including part of a skull in a coprolite from the Campanian Upper Milk River Formation, a complete skeleton from the Scollard Formation near the Cretaceous-Paleocene boundary, and several fragmentary specimens from the Paleocene Paskapoo Formation [R.C. Fox, pers. comm.]); *Palaeoproteus klatti* (see Herre, 1935); and a skull, now lost, of *Batrachosauroides dissimulans* described by Taylor and Hesse (1943) and Estes (1969). Including the genus described below, the family now contains five genera, most of which are monotypic, and an undescribed genus from the Upper Cretaceous of France may be in or near the family (R. Estes, pers. comm.).

A study of Upper Miocene trackways from Table Mountain (Peabody, 1959) provides the only published pre-Pleistocene record of fossil salamanders from California, and together with *Taricha oligocenica* (van Frank, 1955) and *T. lindoei* (Naylor, 1979b) marks the only Tertiary record along the western coast of North America. Miocene (late Clarendonian) specimens from California and partial skeletons from the middle Oligocene of Washington are known, but these are also referable to extant genera (Naylor, in prep.). The fossil salamander from the upper Miocene of Stanislaus County, California documents the most recent occurrence of the Batrachosauroididae, and provides a significant range extension for the family.

*Ophisthotriton kayi* has the most extensive occurrence in time and space known for a batrachosauroidid, ranging from the lower Campanian (Fox, 1972) to the Lower Eocene (Wasatch Formation, UCMP collections) in the Western Interior of North America. It is, however, unlikely that the biological species *O. kayi*, which is based on a trunk vertebra from the Maestrichtian Lance Formation of eastern Wyoming (Auffenberg, 1961), actually extends throughout this entire time.

Specimens of the new taxon are catalogued in the Museum of Paleontology, University of California, Berkeley (UCMP), and comparative material from the same institution and from the Department of Geology, The University of Alberta (UA) was also available for study.

#### SYSTEMATIC PALEONTOLOGY

##### CLASS Amphibia

##### ORDER Caudata

##### SUPERFAMILY Proteoidea

##### FAMILY Batrachosauroididae

##### *Peratosauroides*, new genus

*Type species.* -- *Peratosauroides problematica*, new species.

*Etymology.* -- From the Greek *peratos*, on the opposite side or west, with reference to presence on the west side of the Rocky Mountains, and *sauroides* by comparison with *Batrachosauroides* Taylor and Hesse (1943).

*Diagnosis.* -- As for the type and only species.

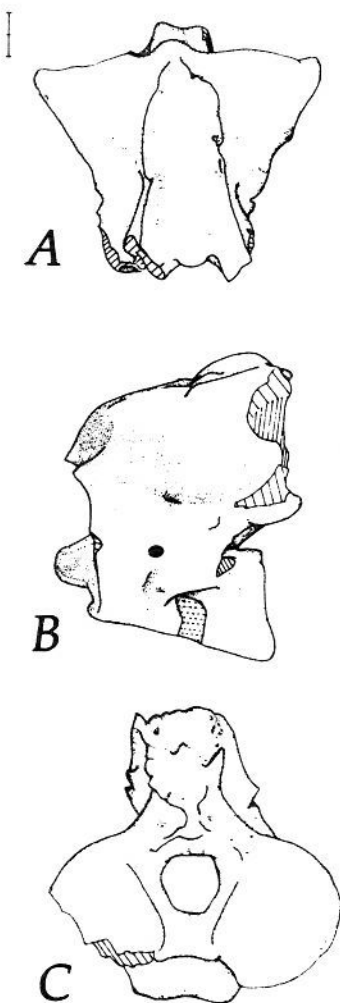


Figure 1. UCMP 75465, an atlas, holotype of *Peratosauroides problematica*; in: A, dorsal; B, lateral; and C, anterior views. Dotted lines indicate area reconstructed in plaster, straight lines represent broken surfaces. Scale is two mm.

*Peratosauroides problematica*, new species

(Fig. 1, Table 1)

*Holotype.* -- UCMP 75465, an atlas.

*Referred specimens.* -- UCMP 123433, a partly broken vertebra from

the mid-trunk region.

*Horizon and type locality.* -- Late Clarendonian (Upper Miocene) "San Pablo" Formation (see discussion); Ingram Creek, site 8, Stanislaus County, California (UCMP locality V-3952).

*Known distribution.* -- Type locality.

*Etymology.* -- From the Greek *problematikos*, problematical, with reference to geographical occurrence and uncertainty as to exact phylogenetic relationship within the Batrachosauroididae.

*Diagnosis.* -- A batrachosauroidid salamander differing from other known species in having the atlantal posterior cotyle set ventral to the anterior cotyles; strong ventrolateral ridges on centrum; large odontoid process; and robust, posteriorly expanded neural spine with a vertical hyperapophyseal area. (The term neural spine here refers to the longitudinal mid-dorsal ridge on the neural arch, the hyperapophyseal area is located directly above the posterior zygapophyses, and the hyperapophyseal spine extends posteriorly from the hyperapophyseal area.)

*Description.* -- The atlas is robust, with large, deeply concave anterior cotyles in the shape of dorsoventrally elongate ovals. The odontoid (= intercotylar) process is a robust shelf that extends from between the anterior cotyles and meets the articular surface of the cotyles with its lateral surfaces. The posterior cotyle is buttressed to the anterior cotyles by a pair of ventrolateral ridges. These ridges continue posteromedially to the rear of the centrum, where they form a pair of small posterior basapophyses. The posterior cotyle is a laterally compressed circle in end view, deeply concave, and with the chordal foramen positioned dorsally just beneath the floor of the neural canal. The shape of the cotyle indicates that the first trunk vertebra was probably amphicoelous.

The neural canal is small and narrow, its lateral walls formed of the anterior cotyles. A small foramen for the first spinal nerve pierces each anterior cotyle anteriorly. The neural arch is capped by a spine, which is thick and expanded dorsally into a roughened surface, to which musculature presumably attached. Posteriorly, the back of the neural spine rises vertically above the posterior zygapophyses. This face is provided with a complex system of ridges and grooves for the attachment of the paired hyperapophyseal ligaments and muscles (Naylor, 1978a).

From the eroded remnant of the left postzygapophysis, the articular facet appears to have been flat and inclined dorsally at the lateral edge.

The single trunk vertebra lacks medial and posterior parts of the neural arch, the right transverse process, and the anterior half of the centrum (Fig. 2). The posterior cotyle is deeply concave, with the chordal foramen set dorsally. A low median ridge is located below the posterior cotyle, but posterior basapophyses are not present. By inference from the structure of the posterior cotyle, the vertebrae were probably amphicoelous (Naylor, 1978a).

The neural canal is low and wide. The roof of the neural arch

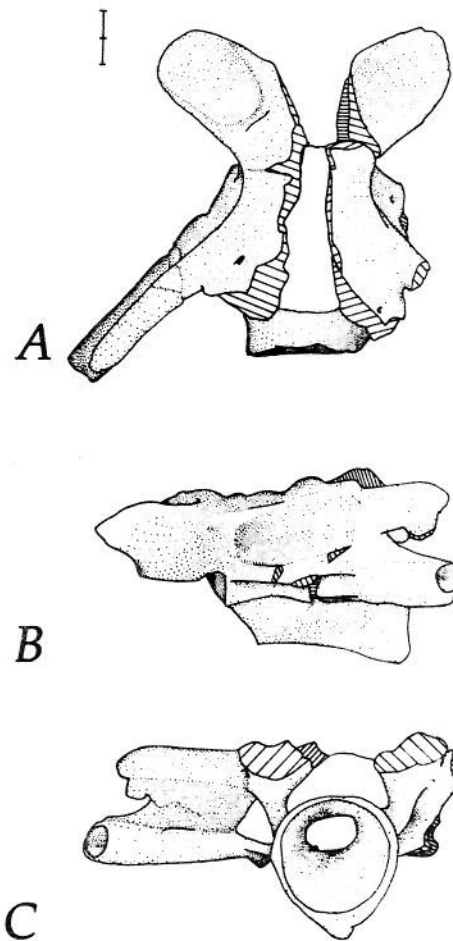


Figure 2. UCMP 123433, trunk vertebra referred to *Peratosauroides problematica*, in: A, dorsal; B, lateral; and C, posterior views. Areas left blank are filled with sediment, straight lines represent broken surfaces. Scale is two mm.

appears to have been flat, but the extent of a neural spine and the shape of the hyperapophyseal spine are unknown. Anterior zygapophyses are large and extend well lateral from their probable origin on the neural arch and anterior cotyle of the centrum. The right prezygapophysis is no longer attached to the vertebra, but is shown in its probable position in Figure 2. Articular facets are circular, but somewhat longer lateromedially than anteroposteriorly, and very slightly dorsolaterally inclined. The size and lateral extent of the prezygapophyses provide confirming evidence that the



column was amphicoelous (Naylor, 1978a). Foramina for spinal nerves are lacking, as is the case in proteids, as well as in other batrachosauroidids (see also Edwards, 1976).

The transverse process is long and forms an acute angle with the centrum. Rib-bearers are bicipital and well-separated, but not greatly divergent, being intermediate in this regard between the condition in *Batrachosauroides dissimulans* and *B. gotoi* (compare Estes, 1969). A sturdy web of bone connects the rib-bearers to each other. The dorsal arm is of notably smaller diameter than the ventral, and the latter parallels the dorsal arm, but is offset anteriorly. A small ventral lamella is formed where the ventral arm attaches to the centrum and subcentral foramina are present.

The flat roof of the neural arch, anterolaterally extended prezygapophyses, and the posterolaterally extending transverse process impart an hour-glass shape to the vertebra in dorsal view.

*Discussion.* -- The two specimens of *Peratosauroides* come from UCMF locality V-3952 (Ingram Creek quarry #2), which is a tan sandstone lentil in conglomerate containing Franciscan detritus, about 10 feet above the top of the Ingram Creek tuffs. The area was referred to as the Tulare Formation by Huey (1948), and is presently considered as part of the San Pablo Group, although most of the latter is marine and lies some distance to the northwest of locality V-3952 (see Clark, 1912; Trask, 1922).

The atlas resembles those of *Batrachosauroides*, *Opisthotriton*, *Prodesmodon*, and *Palaeoproteus* (Fig. 3, also Estes, 1964, 1969; Estes et al., 1967; Naylor, 1979a) in features that are probably uniquely derived for the family. The large, deeply concave anterior cotyles are especially diagnostic in this regard, as is the rudimentary odontoid process. Atlantes of *Piceoerpeton* are similar, but distinct (Naylor and Krause, 1981). The anterior part of the enlarged, dorsally roughened neural spine of *Peratosauroides* resembles that of *Opisthotriton* and *Prodesmodon*, although in the two latter genera the hyperapophysis is low and posteriorly produced (Estes, 1964, 1969; Naylor, 1979a). *Batrachosauroides* departs from the three genera just discussed in lacking an enlarged neural spine, but the condition of its hyperapophyseal spine is unknown. In batrachosauroidids other than *Peratosauroides* the posterior cotyle of the atlas is a short, horizontal continuation from the anterior cotyles. As noted, that of *P. problematica* extends posteriorly and ventrally, but these differences are probably only indicative of generic distinction.

The single vertebra (Fig. 2) of *Peratosauroides* is less clearly batrachosauroidid than is the atlas. The structure is consistent with that of other members of the family, but provides little positive support for inclusion of the new species within the Batrachosauroididae. It resembles vertebrae of *Necturus*, which is probably a derivative from batrachosauroidid ancestry, although this split occurred well before the time of *Peratosauroides* (Estes, 1975; Naylor, 1978a,b). In light of stratigraphy and the differences in atlantal structure, assignment of the new genus to the Proteidae is unlikely.

The presence of *Peratosauroides problematica* in the Miocene of California indicates a long period of isolation from other batrachosauroidids. It is, therefore, possible to account for the

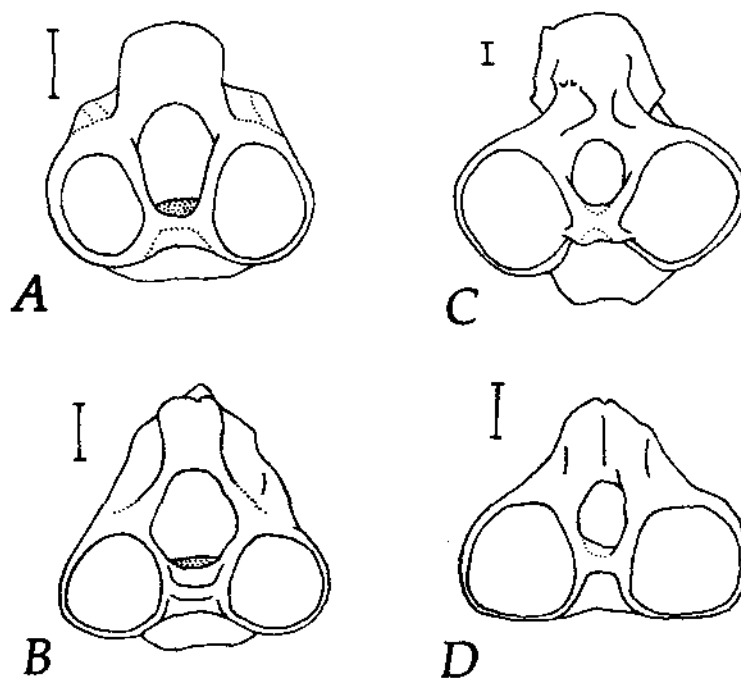


Figure 3. Atlantes of batrachosauroidids sketched in anterior view to indicate variation in the anterior cotyles and neural spine: A, *Prodesmodon copei*, UA 12095, Upper Cretaceous Lance Formation, Wyoming; B, *Opisthotriton kayi*, UA 12096, Upper Cretaceous Oldman Formation, Alberta; C, *Peratosauroides problematica*, UCMP 75465; and D, *Batrachosauroides dissimulans* Middle Miocene Fleming Formation, Texas, redrawn from Estes (1969, fig. 3). Scales are one mm.

differences as owing to a long period of independent evolution in a separate area and environment. If *Peratosauroides* is properly referred to the Batrachosauroididae, the family has a known time range of early Campanian (Late Cretaceous) through to late Miocene, and a correspondingly wide geographic distribution (Table 1).

#### VOMERS OF *OPISTHOTRITON*

A right and left vomer from UCMP locality V-77128 (Lower Paleocene; W.A. Clemens, pers. comm.), Hell Creek Formation of Montana, are referable to *Opisthotriton*, but differ from those presently assigned to *O. kayi*. The two specimens are of the same size and articulate almost perfectly one with the other. Both specimens are broken posteriorly, the left (UCMP 123441, total length 2.95 mm) to a greater extent than is the right (UCMP 123442, total length 3.90 mm).



The posterior length and possible area of articulation to the pterygoids are, therefore, unknown. The teeth are broken from both specimens, leaving only eroded remnants of the pedicles. However, the size and spacing of the teeth that may be inferred from these remains are consistent with the structure of *Opisthotriton kayi* (compare Estes, 1964, fig. 4).

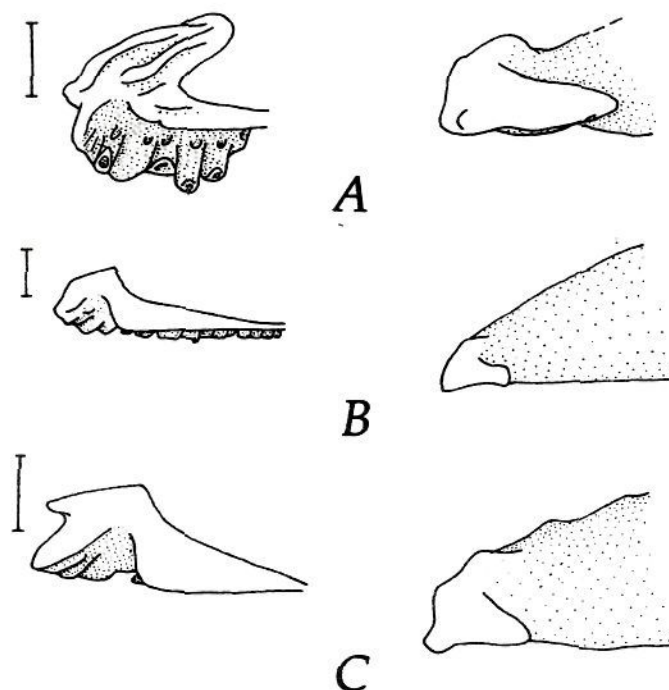


Figure 4. Vomers of batrachosauroidids in medial (l) and dorsal (r) views to illustrate differences: A, *Prodesmodon copei*, UA 12094, Upper Cretaceous Lance Formation, Wyoming; B, *Opisthotriton kayi* UA 16202, Upper Cretaceous Hell Creek Formation, Montana; and C, *Opisthotriton* sp., UCMP 123442, Upper Cretaceous Hell Creek Formation, Montana. Scales are one mm.

In comparison to those of *O. kayi*, the new vomers are small, but solidly built. A narrow, projecting ridge on the anterior and anterolateral edge of each bone is located well above the tooth row. This presumably articulated to the pars palatina of the premaxilla. The anteromedial ascending process (see Estes, 1964) is flattened dorsally and faintly grooved for attachment to the nasal process of the overlying premaxilla. The tooth row is more arched antero-laterally than is the case in other *O. kayi*. Medially, along the edge of the palatal part, the vomer is swollen ventrally, so

as to form a teardrop-shaped area anteromedially in ventral view. Anterior and lateral to this swelling there is a groove next to the tooth row.

Differences between the new vomers and those of *O. kayi* (see Estes, 1964) and *Prodesmodon copei* (see Naylor, 1979a, also Fig. 4) are subtle, but distinct. Vomers of *O. kayi* are relatively large, but thin and delicate, whereas those of *Prodesmodon* are small, but robust, with characteristic tooth bases. The new vomers are intermediate in this regard, being notably more robust than *O. kayi*. *Prodesmodon* differs from both species of *Opisthotriton* in having a more vertically oriented ascending process, which is not dorsally flattened, and which is provided with a system of medial ridges and grooves. The palatal shelf in *Prodesmodon* is also relatively more massive, as is the anterior ridge for attachment to the premaxillary pars palatina. Some vomers referable to *O. kayi* show a trend to development of a medial swelling. In addition, the ascending process of the new vomers is larger and more extensively flattened dorsally.

The new vomers differ significantly from those of *O. kayi* and may indicate the presence of a second species of *Opisthotriton* in the Paleocene of Montana. Continued work in the lowermost Paleocene of the Western Interior of North America should produce additional specimens, and providing a new species for the vomers is premature. However, in living salamanders different species of the same genus are often found in the same geographic regions (e.g., Conant, 1975) and similar situations would be expected to have obtained in the past. Differences among Upper Cretaceous and Paleocene specimens of *Opisthotriton* (Table 1) are evident and detailed work should elucidate the situation.

#### CONCLUSIONS AND SUMMARY

The Batrachosauroididae comprise a well-defined and homogeneous group. Diagnostic characters for the family are to be found in the atlas and toothed bones of the skull (dentaries, premaxillae, and vomers, see Estes, 1969; Naylor, 1979a). Although within the limits of variability encountered in Recent families (Naylor, 1978a), the post-atlantal vertebrae do not provide clearly diagnostic features. Batrachosauroidid atlantes have large, circular, and concave anterior cotyles, with a rudimentary shelf-like odontoid process between (Fig. 3). The condition of the atlantal neural spine is variable: that of *Opisthotriton* is narrow, either high or low, and gently rounded dorsally; in *Prodesmodon* it is a swollen ball; in *Batrachosauroides* the spine is a very low, narrow ridge; whereas that of *Peratosauroides* is thick and dorsally expanded and roughened. These differences presumably reflect variability in the size and orientation of the cranio-mandibularis musculature, and corresponding differences in natural history.

Where known, batrachosauroidid premaxillae have narrow elongate nasal processes (pars facialis), which are in medial contact without the presence of a fontanelle. The pars palatina is weakly developed and the pars dentalis is short. The maxilla possesses a broad, relatively high pars facialis and a short pars dentalis. The vomer has a distinct anterodorsal process, which abuts medially,

and the tooth row parallels that of the premaxilla and maxilla. The shape of the snout closely resembles that of the extant proteids, except that the latter lack all trace of a maxilla. The dentary has a well-developed symphysis, robust non-pedicellate teeth, a deep posterior part with a shallow external depression, and a very shallow dental gutter.

The structure of batrachosauroidid vertebrae exhibits a great degree of interspecific variation. The following genera produce a morphocline with respect to the strength of the anterior ball on the centrum: *Prodesmodon* (strongly opisthocoelous) -- *Opisthotriton* -- *Batrachosauroides* -- *Palaeoproteus* (amphicoelous with some calcified infilling of the anterior cotyle, see Estes et al., 1967). The condition in *Peratosauroides* is uncertain, but based on the structure of the posterior cotyle in UCMP 75465 and UCMP 123433, it can be inferred to have been amphicoelous. Correlative with the degree of opisthocoely is the presence of posterior basapophyses (Naylor, 1978a), these latter structures being present and well developed in *Prodesmodon* and *Opisthotriton* (see Estes, 1964).

By comparison with Recent salamanders, batrachosauroidids have well-developed posterior basapophyseal muscles, as do *Necturus* and *Proteus* which places the Proteoidea with the more derived families -- the Plethodontidae, Salamandridae, and Sirenidae (Naylor, 1978a). Transverse processes are of variable structure, ranging from bicipital, but closely appressed in *Prodesmodon* and *Opisthotriton*, to widely bicipital in *Batrachosauroides gotoi*. Interspecific variation is also observed in the hyperapophyseal spine and subcentral keel (see figures and descriptions in Estes, 1964, 1969). All known batrachosauroidid post-atlantal vertebrae lack spinal nerve foramina.

Batrachosauroidids probably arose from a relatively derived ancestor having posterior basapophyseal musculature (Naylor, 1978a). The earlier species are strongly opisthocoelous, with well-developed posterior basapophyses, and there appears to be a subsequent trend to reduction of both these characters. As argued elsewhere, it seems probable that this family holds the ancestors of the proteids (Estes, 1975; Naylor, 1978a,b), and both taxa are to be classified in the superfamily Proteoidea. Owing to the lack of fossil evidence, evolutionary relationships within the superfamily Proteoidea are uncertain and the ultimate origins are obscure. Nevertheless, taking into account the available data (including stratigraphic occurrences), it is possible to propose tentative hypotheses for future test (see Fig. 5).

Based on vertebral structure, *Prodesmodon* and *Opisthotriton* are closely related and share a common ancestor with no other known batrachosauroidid (Estes, 1964; Naylor, 1979a). The three other batrachosauroid genera occur later in time and exhibit reduction in opisthocoely and loss of posterior basapophyses. *Batrachosauroides* and *Palaeoproteus* closely resemble each other (Estes et al., 1967; Naylor, 1978a, 1979a) and are readily derivable from a structural ancestor represented by *Opisthotriton*, either separately or through a common ancestor. *Peratosauroides* is the most isolated of the family, but is perhaps derivable from within *Batrachosauroides*, although not from either of the presently known species.

Close and unique resemblances in cranial structure between proteids and batrachosauroidids indicate phylogenetic relationship

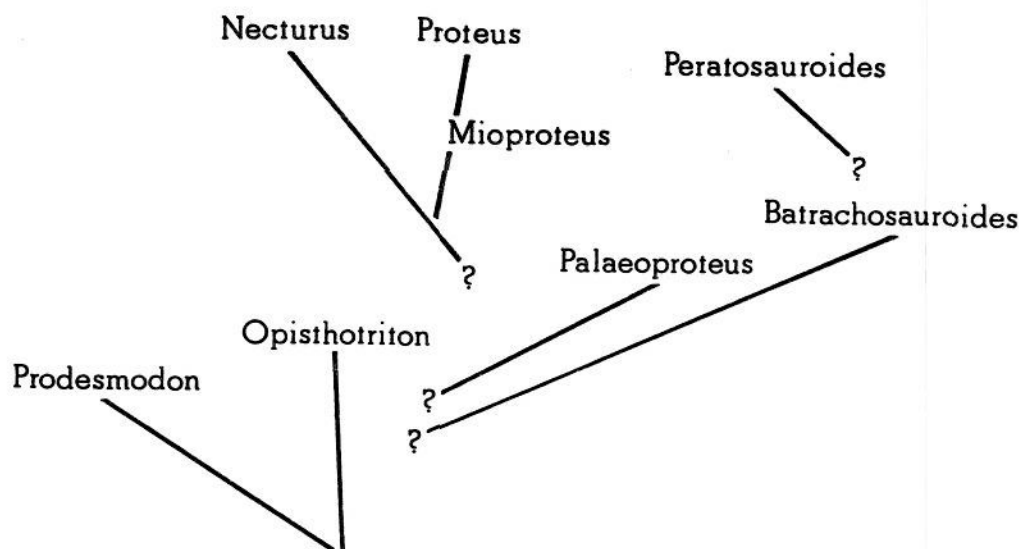


Figure 5. Tentative phylogeny of the Proteidae (*Necturus*, *Proteus*, and *Mioproteus*) and Batrachosauroididae, with genera arranged in rough stratigraphic sequence.

between the families. These characters include a squamosal with a columellar process; presence of only the columella; the structure and relationship of the vomer and palatine, together with the disposition of their associated teeth; the broad, posteriorly produced parasphenoid; and premaxillae with long, separate nasal spines (Estes, 1975; Estes and Darevsky, 1977; Naylor, 1978a, 1979a). Additional support derives from vertebral structure and inferred patterns of trunk musculature in the two families: opisthocoely, posterior basapophyses, posterior basapophyseal muscles, long tubular hyperapophyseal and haemal spines on caudal vertebrae, and lack of post-atlantal spinal nerve foramina (additional discussion in Naylor, 1978a).

Considering stratigraphic positions and morphocline polarities, proteids are derived from within the Batrachosauroididae. *Necturus krausei* from the Paleocene of Saskatchewan (Naylor, 1978b) places a minimum date on this event.

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Editor's Note: Due to an unfortunate publication delay, while this paper was in press, the new taxon presented above was validly published as a redescription attributed to Naylor (1981c, In Press) by Estes (1982, p.37-39). The Naylor (1981c) paper cited above is this *PaleoBios* article. The full Estes reference is: Estes, Richard. 1982 (1981). Gymnophiona, Caudata. in Handbuch der Paläoherpétologie. Gustav Fischer Verlag, Stuttgart and New York. 2: xv,155pp. (This paper was dated 1981, but not actually published until late in 1982.)

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