

## SUPPORTING INFORMATION (SI)

## TAXON SAMPLING:

**Hynobiidae:** The family includes 54 species in ten genera (AmphibiaWeb, 2012). Besides the type genus *Hynobius*, *Onychodactylus* is included in our data matrix as a basal taxon of the family (e.g., Zhang et al., 2006). The fossil record of Hynobiidae is extremely poor, with only fragmentary material known from the upper Pliocene of Kazakhstan (Averianov and Tjudkova, 1995), and from the upper Miocene and lower Pleistocene of Romania (Venczel, 1999). More recently, the Early Cretaceous *Liaoxitriton* from China has been recognized as a stem-group taxon of the family (Chen and Gao, 2009).

**Cryptobranchidae:** The family consists of three species in two genera (AmphibiaWeb, 2012). We included both *Cryptobranchus* and *Andrias* in our data matrix. In addition, the Middle Jurassic fossil taxon *Chunerpeton* (Gao and Shubin, 2003) from China is also included in this study. The latter taxon was named and described based on well-preserved specimens from the Daohugou site near Ningcheng, Inner Mongolia. The fossil beds exposed at the Daohugou site were mistakenly correlated with the Early Cretaceous Yixian Formation (Wang et al., 2000), but have been consistently dated as 164-165 Ma by independent research groups (Chen et al., 2004; Liu et al., 2006; Yang and Li, 2008), and thus are Middle Jurassic (Bathonian-Callovian) in age.

**Dicamptodontidae and Rhyacotritonidae:** The family Dicamptodontidae, commonly known as Pacific giant salamanders, includes four living species in the single genus *Dicamptodon* (AmphibiaWeb, 2012). In addition, *Dicamptodon* is recorded by fossil material from the Paleocene of Alberta, Canada (Naylor and Fox, 1993). Several other fossil taxa (*Bargmannia* from the Miocene of Slovakia, *Chrysotriton* from the lower Eocene of North Dakota, *Geyeriella* and *Wolterstorffiella* from the upper Paleocene of Germany) were previously assigned to the Dicamptodontidae solely based on the position of spinal nerve foramina (Estes, 1981; Roček, 1994), but these are currently treated as enigmatic forms with uncertain taxonomic positions (Milner, 2000; Venczel, 2008). Among these, the generic name *Bargmannia* Herre, 1955 has been found to be a junior homonym of the siphonophore *Bargmannia* Totton, 1954 (Naish, 2008). In any case, these problematic fossil taxa are not included in our phylogenetic analysis because of their uncertain taxonomic status (see Milner, 2000 for discussion).

The monotypic family Rhyacotritonidae has four living species in the genus *Rhyacotriton* (AmphibiaWeb, 2012). Known as the torrent salamanders of the Pacific northwest region of the United States, *Rhyacotriton* was previously classified in Dicamptodontidae or Ambystomatidae, but has been formally recognized as the type genus of the Rhyacotritonidae by Good and Wake (1992). No fossils referable to the Rhyacotritonidae are known.

**Salamandridae:** The family Salamandridae was traditionally subdivided into the “true salamanders” and the “newts,” but these informal groups have been formally recognized as the subfamilies Salamandrinae and Pleurodelinae, respectively (Dubois and Raffaëlli, 2009) based on the molecular analysis of Zhang et al. (2008). In addition, a third subfamily (Salamandrininae) has also been recognized to include *Salamandrina* and the Oligocene fossil genus *Archaeotriton* (Dubois and Raffaëlli, 2009). Our data matrix included three taxa of the family group: *Taricha* and *Tylototriton* as representatives of the Pleurodelinae, and *Salamandra* as the representative of

the Salamandrinae. *Taricha* has a fossil record extending to the Oligocene in North America, and both *Salamandra* and *Tylotriton* have been recorded from the Eocene of Europe (Estes, 1981; Venczel, 2008).

**Amphiumidae:** The family includes the genus *Amphiuma*, with three living species and a Paleocene occurrence of the genus. All taxa are North American in distribution (Estes, 1981). The earliest record of the family is documented by *Proamphiuma* from the latest Cretaceous (see Gardner, 2003b). The fossil taxon *Paleoamphiuma* from the Eocene Green River Formation was reported as an amphiumid in the original publication (Rieppel and Grande, 1998), but a recent review of the fossil material has shown it may be a sirenid (Gardner, 2003b). Since a formal revision of the taxon is in progress, this significant taxon is excluded from our analysis until the correct information concerning it is available in publication. Nonetheless, inclusion or exclusion of this fossil taxon has no effect on the stratigraphic range of the family Amphiumidae or Sirenidae, as both families have an early record back to Cretaceous time (Estes, 1981; Milner, 2000; Gardner, 2003a, b).

**Proteidae:** This is a small family including only the genera *Necturus* and *Proteus*. The former genus has five living species in North America, and the latter a single species known from Europe (AmphibiaWeb, 2012). Both genera are included in our data matrix. *Necturus* has a fossil record extending to the Paleocene in North America (Naylor, 1978a), and *Proteus* to the Pleistocene in Europe (Estes, 1981). In addition, fragmentary fossil material has been described under the names *Mioproteus* and *Orthophya* from the Miocene of North Caucasus, Germany, and Hungary (Estes and Darevsky, 1977; Estes and Schleich, 1994; Roček, 2005), and from the Pliocene of Poland (Młynarski et al., 1984). These Neogene fossil proteids are not included in our phylogenetic analysis because both taxa are poorly diagnosed, being based on fragmentary material.

**Sirenidae:** Another small family, consisting of *Siren* and *Pseudobranchius*, each with two species (AmphibiaWeb, 2012). The fossil record of the family is poor, with *Habrosaurus* as the only well-known genus, based on material from the Late Cretaceous (middle Campanian) and middle Paleocene of North America (Gardner, 2003a). Two Gondwanan fossil salamanders, *Kababisha* (Cenomanian, Sudan) and *Noterpeton* (Maastrichtian, Bolivia), each based on fragmentary material, were regarded as possible sirenids (Evans and Werner, 1996), but a recent review of the evidence has excluded these enigmatic taxa from the Sirenidae (Gardner, 2003a).

**Plethodontidae:** Commonly known as “lungless salamanders,” the Plethodontidae are by far the most species diverse group of salamanders, having 419 species recognized at present (AmphibiaWeb, 2012). The family consists of two subfamilies, Hemidactyliinae and Plethodontinae. Two taxa are included in our data matrix, *Plethodon* and *Desmognathus*, both from the subfamily Plethodontinae.

**Ambystomatidae:** The family includes a single genus *Ambystoma*, with 32 extant species named and described so far (AmphibiaWeb, 2012). Among these, *Ambystoma mexicanum* is probably the best-known salamander taxon with over thousand publications on various aspects of the famous salamander species. The earliest fossil record of the family is described under the name *Ambystoma tihenii* based on fossils from the lower Oligocene of Saskatchewan in western Canada

(Holman, 1968; Estes, 1981). Although classified in the Ambystomatidae, the ichnogenus *Ambystomichnus* Peabody, 1954 is known by trackways from Paleocene beds in Montana (Gilmore, 1928; Peabody, 1954) and Eocene beds of Wyoming (Foster, 2001). Because no character in our data matrix can be scored for *Ambystomichnus*, the ichnotaxon is excluded from our phylogenetic analysis.

**Mesozoic Fossil Taxa:** In the past decade, a number of crown-group salamanders have been named and described based on the material from Jurassic and Cretaceous deposits in China. Several of these taxa are included in our data matrix: *Chunerpeton*, *Pangerpeton*, *Liaoxitriton*, and the new taxon *Beiyanerpeton*. Several other taxa (e.g., *Laccotriton*, *Sinerpeton*, and *Jeholotriton*) are excluded from this analysis because they are anatomically uncertain and are currently under taxonomic revision.

Among Mesozoic salamanders known from North America, *Iridotriton* was described as a putative salamandroid based on a partial skeleton from the Upper Jurassic Morrison Formation (Evans et al., 2009). The Morrison Formation has yielded  $^{40}\text{Ar}/^{39}\text{Ar}$  dates of 148-150 Ma (Kowallis et al., 1998), and thus, is Tithonian in age (International Commission on Stratigraphy, 2009). This Jurassic taxon (78% missing data in our data matrix) is included in our phylogenetic analysis because of its age, biogeographic significance, and its putative salamandroid affinity as described in the original publication.

Among the Mesozoic salamanders known from Europe, *Valdotriton* from the Lower Cretaceous (Barremian) of Spain represents an important record (Evans and Milner, 1996), and this taxon is included in our analysis as a fossil representative of the Salamandroidea. Among the several salamanders known from the Kirtlington Quarry (Evans and Milner, 1994), *Marmorerpeton* and the undescribed “salamander A” are non-crown group salamanders (Evans and Milner, 1996; Milner, 2000). Also from the Kirtlington Quarry, the so-called “salamander B” is mentioned as a possible “crown-salamander” (Milner, 2000), but cannot be incorporated into a phylogenetic analysis before its nomenclatural status is established by formal publication with illustration and description of the specimens.

#### CHARACTER CODING:

The characters used in the phylogenetic analysis include both binary and multistate alternatives (e.g., Siddall and Jensen, 2003). Coding of skeletal characters for extant salamanders is based on information from representative specimens of each group and data published in the literature, with the sources of information as listed below. Since the impact of polymorphic characters on phylogenetic results differs among datasets and methods (Wiens, 1995), we have chosen to code the characters as observed from specimens. Inapplicable character states are treated as unknown using the reductive coding method (see Strong and Lipscomb, 2005).

*Karaurus*—Ivachnenko (1978); Estes (1981: fig. 1); Milner (2000: fig. 4); Averianov et al. (2008).

*Hynobius*—Sato (1943); Carroll and Holmes (1980); Fei et al. (2006).

*Onychodactylus*—Sato (1943); Rose (2003); Wang et al. (2004); Fei et al. (2006); AmphibiaTree (2007).

*Cryptobranchus*—Cope (1889); Rose (2003).

*Andrias*—Sato (1943); Greven and Clemen (1980: teeth); Rose (2003).

*Dicamptodon*—Ashley-Ross (1992); Rose (2003); Wake (2001): *Dicamptodon ensatus* (on-line), Digital Morphology. Accessed April 23, 2010 at [http://digimorph.org/specimens/Dicamptodon\\_ensatus/](http://digimorph.org/specimens/Dicamptodon_ensatus/).

*Ambystoma*—Worthington and Wake (1971); Carroll and Holmes (1980); Ashley-Ross (1992); Rose (2003); Digimorph Staff, 2008: *Ambystoma tigrinum* (on-line), Digital Morphology. Accessed April 23, 2010 at [http://digimorph.org/specimens/Ambystoma\\_tigrinum/head/](http://digimorph.org/specimens/Ambystoma_tigrinum/head/).  
AmphibiaTree, 2008: *Ambystoma gracile* (on-line), Digital Morphology. Accessed April 23, 2010 at [http://digimorph.org/specimens/Ambystoma\\_gracile/head/](http://digimorph.org/specimens/Ambystoma_gracile/head/).

*Amphiuma*—Cope (1889); Carroll and Holmes (1980); Gardner (2003b); Rose (2003); also based on information from UA 14364 (dry skeleton of skull and postcranium, comparative specimen in UALVP collections).

*Plethodon*—Cope (1889); Wake (1963, 1966); Trueb (1993).

*Desmognathus*—Cope (1889); Wake (1966); Trueb (1993).

*Rhyacotriton olympicus*—Cloete (1961); Srinivasachar (1962); Worthington and Wake (1971); Wake (1980).

*Rhyacotriton variegatus*—Rose (2003); AmphibiaTree, 2007. *Rhyacotriton variegatus* (on-line), Digital Morphology. Accessed March 16, 2010 at [http://digimorph.org/specimens/Rhyacotriton\\_variegatus/head/](http://digimorph.org/specimens/Rhyacotriton_variegatus/head/).

*Salamandra*—Bolkay (1927); Francis (1934); Rose (2003); and other sources as cited below in the character descriptions.

*Taricha*—Digimorph Staff, 2008. *Taricha torosa* (on-line), Digital Morphology. Accessed April 24, 2010 at [http://digimorph.org/specimens/Taricha\\_torosa/head/](http://digimorph.org/specimens/Taricha_torosa/head/).

*Tylototriton*—Coding the characters for this taxon is based on Bolday (1927); Rose (2003); Yu and Zhao (2007); Zhao et al. (2009).

*Necturus maculosus*—Coding of the characters for this taxon is based on information from Cope (1889); Evans (2003); Rose (2003).

*Proteus*—Source of information on this taxon includes: Kingsbury and Reed (1908); Sket and Arntzen (1994); Rose (2003); Larson et al. (2006).

*Siren*—Cope (1889); Reilly and Altig (1996); Gardner (2003a: text-fig. 2-3); Rose (2003).

AmphibiaTree, 2008. *Siren lacertina* (on-line), Digital Morphology. Accessed April 24, 2010 at [http://digimorph.org/specimens/Siren\\_lacertina/head/](http://digimorph.org/specimens/Siren_lacertina/head/).

*Pseudobranchius*—Duellman and Trueb (1986: fig. 13-3G); Rose (2003); Gardner (2003a: text-fig. 3).

In addition, characters of limb structure are coded based on information from various sources, including Shubin and Wake (1996, 2003).

## PHYLOGENETIC ANALYSIS AND RESULTS:

The data matrix constructed for the phylogenetic analysis of this study contains 26 basic taxa (including *Karaurus* as the outgroup) coded across 105 characters (Table S1). Our sampling of taxa is explained above, and the characters used in the analysis are described below. The constructed dataset contains nine characters that are phylogenetically uninformative because of their apomorphic status a single taxon or lack of variation in the scope of this study. These characters (11, 18, 47, 50, 72, 73, 92, 93, 103) were excluded from the analysis, but are retained in the dataset for possible expansion of taxon sampling in future studies. All characters were unordered and equally weighted in the initial analysis, but character re-weighting was imposed for a further step analysis of the dataset (see below).

It is well understood that outgroup comparison can effectively determine the evolutionary polarity of characters in a given ingroup clade (Fitch, 1971; Watrous and Wheeler, 1981; Farris, 1982; Maddison et al., 1984; Nixon and Carpenter, 1993). In our parsimony analysis of salamander relationships at the Urodela level, the stem-group caudate *Karaurus* was naturally designated as the outgroup. In many cases, character evolution was assessed by comparison with this out-group taxon, and in some cases this method was enhanced by the ontogenetic method to understand the evolution of character states. Parsimony analysis of the constructed dataset was performed by using the Macintosh version of PAUP\* 4.0 (Swofford, 2003) under the Branch-and-Bound search option. Tracing of character evolution was carried out by using MacClade 4 (Maddison and Maddison, 2003).

The initial analysis of the dataset recovered 40 most parsimonious trees (TL= 235 steps, CI= 0.506, RI= 0.727). The strict consensus shows that all the 40 MPTs have the new taxon *Beiynerpeton* placed as the basal clade of the Salamandroidea (Fig. S1). Tracing of character evolution using MacClade 4.06 (Maddison and Maddison, 2003) showed that the basal position of the new taxon within the Salamandroidea is secured by a set of shared, derived character states. To collapse this robust hypothesis requires a minimum cost of five additional steps of character evolution in the case of a forced grouping of *Beiynerpeton* with the Cryptobranchoidea (240 vs. 235 steps), or a minimum cost of four additional steps in case of moving the new taxon to a more crown-ward position in the Salamandroidea (239 vs. 235 steps). The purported salamandroid taxon *Iridotriton* was found to be a cryptobranchoid, more closely related to the Hynobiidae than to the Cryptobranchidae (Fig. S1, S2). Forced grouping of *Iridotriton* with the Salamandroidea requires a minimum cost of four additional steps (239 vs. 235 steps).

The relationships of the Cryptobranchoidea and of the several clades within the Salamandroidea, however, are poorly resolved in both the strict consensus and Adams consensus trees (Fig. S1A, B). Searching for better resolution, further analysis of the dataset after character re-weighting based on a rescaled consistency index (Farris, 1989) was carried out with the base value set at 100, and the analysis recovered ten most parsimonious trees (TL= 9131 steps, CI= 0.695, RI= 0.852). In all the ten most parsimonious trees, the new taxon *Beiynerpeton* retains the same position as the basal clade of the Salamandroidea, but improved resolution of the cryptobranchoid and salamandroid clades is obtained as shown in both the strict consensus and the Adams consensus trees (Fig. S2A, B). The Adams consensus tree is converted into a calibrated cladogram as presented in Figure 4 of the paper.

## CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS:

1. Premaxillae (Duellman and Trueb, 1986: character A): separate (0); or fused (1).

**Remarks:** The paired condition is known for salamanders in six families (Sirenidae, Cryptobranchidae, Proteidae, Ambystomatidae, Dicamptodontidae, Rhyacotritonidae), while the uniformly fused condition is only known for the Amphiumidae (Cope, 1889). Variable conditions of this character occur among hynobiids (Larson et al., 2006; contra Trueb, 1993: table 6.2A), salamandrids (Wake and Özeti, 1969), and plethodontids (Lowe, 1950; Wake, 1966; Wake and Larson, 1987).

2. Dorsal process of premaxilla (modified from Duellman and Trueb, 1986: character B): simply contacting or overlapping nasal bone (0); strong posterior extension overlapping frontal and separating nasals (1); posterior extension deeply intervening between frontals (2); posterior extension contacting frontal lateral to nasal (3).

**Remarks:** Most primitive salamanders show the state (0) condition, while most salamandriods show the derived state (1) condition. Proteids lack nasals, but have the dorsal process overlapping the frontals along the midline; thus, we coded the state (1) for the group. Highly specialized conditions are seen in amphiumids (2) and sirenids (3). Because there is no logical link between the derived states, we treat this character as unordered.

3. Maxilla (Duellman and Trueb, 1986: character C): present in adults as a normal element of maxillary arcade (0); reduced to a rudimentary element or entirely lost and functionally replaced by a modified vomer (1).

**Remarks:** The family Proteidae is the only group that shows a uniform absence of the maxilla (Larson, 1991). In both *Siren* and *Pseudobranchus* (Sirenidae), the maxilla is functionally replaced by a modified vomer, although the former genus retains a maxilla as a small knob (Rose, 2003; Gardner, 2003a). Most plethodontids retain the maxilla, while the absent condition in *Eurycea* is clearly a secondary loss within the family (Duellman and Trueb, 1986: fig. 13.4; Digimorph Staff, 2004).

4. Maxillary tooth row: extending close to the posterior extremity of maxilla (0); terminating far anterior to the posterior extremity (1).

**Remarks:** The derived state is a diagnostic feature of the Salamandridae. Variable conditions are known for the Hynobiidae (Sato, 1943; Fei et al., 2006). This character was scored as inapplicable for extant sirenids (*Siren* + *Pseudobranchus*), and as unknown for the fossil taxon *Habrosaurus* as the specimens preserved (Gardner, 2003a). Coding the character for *Liaoxitriton* is based on new specimens from the type locality and horizon.

5. Septomaxilla (Duellman and Trueb, 1986: character D): present (0); absent (1).

**Remarks:** The septomaxilla is absent in the Cryptobranchidae, Proteidae, and Sirenidae (Lapage, 1928; Wake, 1966; Hecht and Edwards, 1977; Rose, 2003). Contrary to Duellman and Trueb (1986: 503: present), a septomaxilla is also absent in the Salamandridae (Francis, 1934; Rose, 2003; Larson et al., 2006). The variable conditions observed in plethodontids are associated with paedomorphosis or asymmetrical development of the two jaws (Wake, 1966), and the septomaxilla is primitively present in the family (Larson, 1991). Although the absent condition in different groups of salamanders has been interpreted as a “paedomorphic loss” (Duellman and

Trueb, 1986), the absent condition in metamorphosed salamandrids and the presence of the element in some neotenic forms do not support this interpretation. Rose (2003) [Appendix I] refers to Lapage (1928) and Medvedeva (1986) in the report of septomaxillary bones in *Amphiuma tridactylum* and *Ambystoma mexicanum*. The former occurrence was from a more mature specimen, the latter one was based on a specimen treated with thyroid hormone. Note that the septomaxillae were described as present but coded as absent for Sirenidae in Duellman and Trueb (1986: 495, vs. table 17-1).

6. Anterodorsal fenestra: present (0); absent (1).

**Remarks:** The structure has been termed premaxillary fontanelle or internasal fenestra by other authors, but all refer to the fenestra that opens between the dorsal processes of the premaxillae and/or nasals. *Onychodactylus* (Hynobiidae), *Salamandra*, and *Taricha* (Salamandridae) are known to have such a fenestra, differing from other members of their respective families. Extant sirenids have a slit-like opening between the nasals, while the actual condition is unknown for the fossil taxon *Habrosaurus* (Gardner, 2003a).

7. Anteromedial fenestra between vomers: fenestra open (0); fenestra closed by vomers or other palatal elements (1).

**Remarks:** The anteromedial fenestra (= anterior palatal fenestra) is closed in extant cryptobranchids, amphiumids, sirenids, and the fossil taxon *Valdotriton*. The stem-group caudate *Karaurus* has a large fenestra, as in many non-caudate temnospondyls. Most salamandrids have a well-defined anteromedial fenestra, but some members of the family (e.g., *Triturus*) can have the fenestra greatly reduced or nearly closed.

8. Nasal ossification (modified from Duellman and Trueb, 1986: character E): present with midline contact (0); separate without midline contact (1); nasal absent (2).

**Remarks:** Larson (1991) combined this character with another (dorsal process of the premaxilla); we treat these as independent characters, because there is no logical overlapping between the two across the basic taxa included in our matrix. Nasals were reported as absent in *Rhyacotriton olympicus* (Dunn, 1920; Tihen, 1958; Worthington and Wake, 1971), but were rediscovered by Wake (1980; contra Vorobyeva, 2003) as small but distinctly separated bones that are the last of the cranial elements to appear in ontogeny. The derived state (1) is a synapomorphy of the Salamandroidea. The absent state (2) occurs in *Necturus* and *Proteus* (Evans, 2003; Rose, 2003; Larson et al., 2006; contra Trueb, 1993) and some but not all plethodontids as a further transformation of the character within the family.

9. Lateral expansion of nasals: same width or slightly wider than frontals (0); nasals greatly reduced and narrower than frontals (1).

**Remarks:** The derived state is coded for cryptobranchids and sirenids, with the condition unknown for fossil taxon *Habrosaurus*. Proteids are coded as unknown because they lack a nasal (Evans, 2003).

10. Lacrimal (Duellman and Trueb, 1986: character F): present (0); absent (1).

**Remarks:** Because *Karaurus* has a lacrimal (Ivachnenko, 1978; Estes, 1981), the presence of this element in urodeles is considered to be a primitive condition; however, the distribution of the (0) state among several extant groups (Hynobiidae, Rhyacotritonidae, and Dicamptodontidae)

indicates that the character is probably more complex than the simple present or absent alternatives (Worthington and Wake, 1971; Larson, 1991).

11. Quadratojugal (Duellman and Trueb, 1986: character G): present (0); absent (1).

**Remarks:** The quadratojugal is present in *Karaurus* and *Kokartus* (Skutschas and Martin, 2011), but is absent in all extant urodeles and in those fossil taxa for which this part of the skull is known. Therefore, the derived state is a urodele synapomorphy. A quadratojugal reportedly occurs in early ontogeny of some hynobiids and salamandrids (Noble, 1931; Papendieck, 1954; Trueb, 1993), but soon fuses with the quadrate or squamosal to form a mixed bone of endochondral and dermal origin (Rose, 2003). After reviewing the available evidence, we code the absent condition in the adult stage for all extant salamanders.

12. Prootic/exoccipital/opisthotic complex (modified from Duellman and Trueb, 1986: character H): three elements separate (0); exoccipital/opisthotic fused with free prootic (1); opisthotic/prootic fused with separate exoccipital (2); three elements fused into otic-occipital complex (3).

**Remarks:** Among extant families, the primitive state (0) is seen in the Proteidae (Cope, 1889; Trueb, 1993; Evans, 2003), and the derived state (1) is known in the Hynobiidae and Cryptobranchidae (see Carroll and Holmes, 1980; contra Trueb, 1993: table 6.2). Coding of this character for extant salamander groups follows Carroll and Holmes (1980) and information from Digimorph.org. Regarding sirenids, Duellman and Trueb (1986: 495) recorded that the exoccipital, prootic, and opisthotic are not fused (see also Trueb, 1993: table 6.2B). Coding of the character for *Rhyacotriton* follows AmphibiaTree (2007) (contra Trueb, 1993: table 6.2A).

13. Posterior process of vomer: poorly defined or absent (0); well-defined process contacting anterior part of parasphenoid or pterygoid (1); greatly elongated process extending along lateral border of parasphenoid (2).

**Remarks:** This is one of the characters that show a complex evolutionary pattern. Within the Hynobiidae, basal taxa such as *Onychodactylus* and *Batrachuperus* have a poorly defined posterior process while other hynobiids have an elongated process (Sato, 1943; Fei et al., 2006). Multiple independent acquisitions of the derived state (1) occur in some but not all hynobiids and dicamptodontids, and in all members of the Cryptobranchidae, Plethodontidae, Amphiumidae, Rhyacotritonidae, Proteidae, and the fossil taxon *Liaoxitriton*. The derived state (2) occurs independently in the Salamandridae and the fossil taxon *Pangerpeton* (according to Wang and Evans, 2006).

14. Posterolateral border of vomer: not notched (0); slightly concave for choana (1); deeply notched and almost embracing choana (2).

**Remarks:** The derived state (2) is seen in several families within the Salamandroidea: Plethodontidae, Salamandridae, Ambystomatidae, Rhyacotritonidae, and Dicamptodontidae.

15. Ossification of pterygoid (Duellman and Trueb, 1986: character I): present (0); absent (1).

**Remarks:** This character is anatomically related to two other characters (the shape of the pterygoid and pterygoid teeth), but we treat and code these as separate characters (see Hawkins et al., 1997 for discussion). The pterygoid is absent in all plethodontids at the adult stage, and present but small in sirenids (Larson et al., 2006).



16. Shape of pterygoid (modified from Duellman and Trueb, 1986: character I): triradiate and boomerang-shaped (0); enlarged with distinct anteromedial process suturing with parasphenoid (1); simple straight bar-shaped (2).

**Remarks:** The pterygoid is primitively triradiate and basically boomerang-shaped as seen in *Karaurus* and most urodele groups. The derived condition (1) is a unique feature for extant cryptobranchids. State (2) occurs in amphiumids and proteids; because all other neotenic salamanders but sirenids have a triradiate and boomerang-shaped pterygoid, the straight bar-shaped condition cannot be explained as a neotenic feature. In sirenids, the pterygoid is present as a slender bar in the larval stage, but is greatly reduced to a tiny bone in adults (Rose, 2003; Larson et al., 2006). The family Plethodontidae is coded as unknown owing to the absence of the element. The Sirenidae have a remnant pterygoid that is essentially straight bar-shaped (Reilly and Altig, 1996); thus, we code the derived state (2) for this group.

17. Vomer/pterygoid contact: absent (0); present (1).

**Remarks:** A vomer/pterygoid contact occurs in some neotenic species of *Dicamptodon* but such a contact is lacking in metamorphosed forms of the same taxon (Milner, 2000: fig. 8). Such a contact may occur ontogenetically in some hynobiids, but not in the fully adult stage. Contact of the two elements seen in salamandrids owing to a strong posterior extension of the vomer is clearly a derived condition, different from the ontogenetic contact in other families. Plethodontids are coded as inapplicable (also the character below) as consistent with the character above.

18. Pterygoid/maxillary contact: absent (0); present (1).

**Remarks:** Among extant salamanders, a bony pterygoid/maxillary contact is known for the hynobiid *Pachyhynobius shangchengensis* (Fei et al., 2006) and some species of the salamandrid *Tylotriton* (e.g., *T. verrucosus*; Goodrich, 1930: fig. 326). Among fossil taxa, the holotype and one referred specimen of *Valdotriton gracilis* have a short anterior process that clearly shows no pterygoid/maxillary contact (Evans and Milner, 1996: figs. 1, 3) but two other referred specimens were interpreted as having a pterygoid/maxillary contact (Evans and Milner, 1996: figs. 4, 5). Because of this uncertainty, we coded the character as unknown for this fossil taxon.

19. Palatine in adult: present as discrete element (0); absent by loss or fusion in adult (1).

**Remarks:** All extant salamanders but sirenids (Rose, 2003; Gardner, 2003a) have lost the palatine in the adult stage, but the fossil taxon *Beiyanerpeton* has a discrete palatine in adults. Because of the uncertain condition in *Karaurus* (Skutschas and Martin, 2011), this character cannot be properly polarized within Caudata, although Paleozoic temnospondyls retain a palatine (Holmes, 2000).

20. Anterior extension of parasphenoid between premaxillae (Gardner, 2003a): absent (0); present (1).

**Remarks:** The parasphenoid in most salamanders has a blunt anterior end in articulation with the vomers, but sirenids have a pointed anterior process that extends beyond the vomers to a point between the premaxillae. Gardner (2003a) recognized the derived state as a sirenid synapomorphy. While the actual condition is still unknown for the fossil sirenid *Habrosaurus*,

all other salamanders show the primitive morphology; accordingly, we coded the plesiomorphic state for salamandrids.

21. Internal carotid foramen penetrating parasphenoid (modified from Duellman and Trueb, 1986: character J): present (0); absent (1).

**Remarks:** The internal carotid foramen opens in the lateral alae of the parasphenoid in *Karaurus* and several urodele groups as coded in the data matrix. The primitive state (0) occurs in *Onychodactylus* (AmphibiaTree, 2007) and *Ranodon* (Rose, 2003), and polymorphic conditions are known for members in the genera *Hynobius* and *Batrachuperus* (Carroll and Holmes, 1980: fig. 4; Zhang, 1985; Jömann et al., 2005; Fei et al., 2006). Conflicting data occur in the literature on extant cryptobranchids (Estes, 1981; Trueb, 1993), but our examination of the comparative material in the AMNH collections shows that both *Andrias* (AMNH 58074, 104411) and *Cryptobranchus* (AMNH 55996) have well-defined internal carotid foramina penetrating the parasphenoid (see also Carroll and Holmes, 1980: fig. 5). Codings of the (0) state for *Dicamptodon* and *Rhyacotriton* are based on information from AmphibiaTree (2007: digimorph.org).

22. Prefrontal (Trueb, 1993: character 12): present (0); absent (1).

**Remarks:** The absent condition is known for proteids, sirenids, and some but not all plethodontids (Duellman and Trueb, 1986: fig. 13-4; Trueb, 1993). The fossil taxon *Liaoxitriton* was misinterpreted as having no prefrontal (Dong and Wang, 1998), but our examination of the specimens in the PKUP collection confirms the presence of the element in this taxon.

23. Nasal/prefrontal contact: present (0); or absent (1).

**Remarks:** As a prefrontal is absent in proteids (lack of nasals, see above) and sirenids, this character is coded as unknown for these two groups. The prefrontal of the fossil taxon *Valdotriton* was described as “long and slender” and “sits in a deep facet formed partly by the nasal and partly by the frontal” (Evans and Milner, 1996: 632); and we coded the character for this taxon accordingly. *Liaoxitriton* has a nasal/prefrontal contact based on specimens in the PKUP collection from the type locality and horizon.

24. Prefrontal/maxillary contact: present (0); absent (1).

**Remarks:** Both present and absent conditions are seen in species of *Onychodactylus*, *Pseudohynobius*, *Hynobius*, and *Salamandrella* (Sato, 1943; Fei et al., 2006). The contact occurs in the fossil taxon *Liaoxitriton* (unnumbered specimens in the PKUP collection). Presence of a prefrontal/maxillary contact is considered to be primitive for urodeles, because it is known for the stem-group caudate *Karaurus* (Ivachnenko, 1978; Estes, 1981). Like character 23 above, proteids and sirenids are coded as unknown for this character because of their lack of a prefrontal or maxilla.

25. Basilaris complex of inner ear (Duellman and Trueb, 1986: character N): presence of both recessus basilaris (0); loss of entire basilaris complex (1).

**Remarks:** Among extant groups, loss of the entire basilaris complex characterizes the Plethodontidae, Proteidae, and Sirenidae (Larson, 1991). All fossil taxa are coded as unknown for this character.

26. Angular/prearticular fusion (Duellman and Trueb, 1986: character Q): angular present as a separate element (0); angular fused to prearticular (1).

**Remarks:** Among extant urodeles, a separate angular bone occurs in cryptobranchids and hynobiids (contra Trueb, 1993: angular present or absent in hynobiids). Srinivasachar (1962) considered that *Rhyacotriton* retained an angular, but other authors more recently have determined that this element is absent in the genus (Good and Wake, 1992; Trueb, 1993). The diagnosis of *Karaurus* included “the angular is fused with the prearticular” but the condition was described as “the long and narrow angular is separated from the prearticular by a suture.” As the angular is clearly labeled in the line drawing of the holotype (Ivachnenko, 1978: fig. 1a), and the drawing concurs with the description, we interpret the angular is present in this taxon (see also Estes, 1981).

27. Coronoid (modified from Trueb, 1993: character 22): present in adult stage as a separate element (0); absent in adult stage (1).

**Remarks:** The coronoid is typically absent in the adult stage of most salamanders, but is retained in sirenids, proteids, and dicamptodontids (see Rose, 2003). The coronoid is toothed in sirenids and proteids at maturity, but is entirely toothless in dicamptodontids (see character 28). Although *Jeholotriton* and *Pangerpeton* are described as having a toothed/toothless coronoid-prearticular (Wang and Rose, 2005; Wang and Evans, 2006), the absent condition was coded for these taxa in accordance with the character description.

28. Coronoid teeth in adult: absent (0); present (1).

**Remarks:** A toothed coronoid (splenial of some other authors) may ontogenetically occur in some but not all salamanders, but is lost in the adult stage of most salamanders but proteids. Neotenic forms at maturity may or may not have a toothed coronoid, while metamorphosed *Dicamptodon* has a toothless coronoid in larval and adult stages (see Rose, 2003). All of the taxa that lack a coronoid in the adult stage have been coded as unknown.

29. Articular (modified from Trueb, 1993: character 23): present as separate element (0); absent by fusion with prearticular (1).

**Remarks:** The derived condition is known for the Cryptobranchidae, Amphiumidae, Proteidae, and Plethodontidae. Coding the derived state for Dicamptodontidae is based on information from Wake (2001; contra Trueb, 1993: table 6.2A). Both the primitive and derived conditions occur in the Ambystomatidae and Salamandridae, while the Rhyacotritonidae retain a separate articular (Worthington and Wake, 1971). Coding of the primitive state for *Karaurus* follows Ivachnenko (1978: described as unossified). Trueb (1993: table 6.2B) listed the absent condition for sirenids, while other authors (Reilly and Altig, 1996; Gardner, 2003a: text-fig. 2E) showed that the articular is ossified in late ontogeny in *Siren lacertina*; thus, we coded a polymorphy of this character for the genus.

30. Dentary teeth: present (0); absent (1).

**Remarks:** The dentary is toothless in extant sirenids (Cope, 1889), but is toothed in the fossil taxon *Habrosaurus* (Gardner, 2003a); thus, the derived state is a synapomorphy for crown-group sirenids (*Siren* + *Pseudobranchus*).

31. Sharp deflection of posterior part of dentary: absent (0); present (1).

**Remarks:** In both extant and fossil sirenids, the posterior part of the dentary is sharply deflected ventrally, and the derived state is recognized as a sirenid synapomorphy (Gardner, 2003a).

32. Hypobranchial I and ceratobranchial I (Duellman and Trueb, 1986: character P): two elements remain separate (0); two elements fused (1).

**Remarks:** All members of the family Amphiumidae show the derived state (Erdman and Cundall, 1984; Trueb 1993; Rose, 2003). Interspecies variations are known for some genera in the Hynobiidae (contra Trueb, 1993): the two elements are fused in *Onychodactylus fischeri*, but are separate in *O. japonicus* (Rose, 2003; Wang et al., 2004; Fei et al., 2006), and are fused in *Batrachuperus tibetanus*, but unfused in *B. londongensis* (Fei et al., 2006).

The two ossified hypobranchial elements in *Karaurus* were identified as the “first ceratobranchial and ?second basibranchial” (see Estes, 1981: 10), but we reinterpret them as hypobranchial I + II based on their relative position to the ossified basibranchial II (= copula in Ivachnenko, 1978). A similar pattern is seen in *Pangerpeton*, and in this sense we interpreted the two ossified elements in the taxon as hypobranchial I + II (contra Wang and Evans, 2006: ceratobranchial I + II). Both separate and fused conditions are known for adult *Cryptobranchus* (Jollie, 1973; Duellman and Trueb, 1986: fig. 13-7A; Cox and Tanner, 1989; Larson, 1991; Trueb, 1993; Rose, 2003; Fei et al., 2006); thus we code the polymorphic condition for the genus. Coding of this and the following characters of the hypobranchium of salamandrids is based on several sources, including Özeti and Wake (1969), Yu and Zhao (2007), and Zhao et al. (2009).

33. Ossification of hypobranchial I: present (0); absent (1).

**Remarks:** Hypobranchial I is well ossified in the primitive caudate *Karaurus* (see above) and several Jurassic salamander taxa from China, while the same element is unossified in most extant species of the Cryptobranchidae and Hynobiidae (e.g., Cope, 1889; Rose, 2003; Fei et al., 2006). The derived state is also coded for the Rhyacotritonidae (AmphibiaTree, 2007), Plethodontidae (Cope, 1889), and Ambystomatidae (Rose, 2003; Digimorph Staff, 2008). Variable conditions are seen in the Salamandridae, Dicamptodontidae, and Proteidae. Both the Sirenidae and Amphiumidae have an ossified hypobranchial I (Cope, 1889; Rose, 2003).

34. Ceratobranchial II in adults: present (0); or absent (1).

**Remarks:** Ceratobranchial II is absent in the Plethodontidae, Ambystomatidae, Salamandridae, Rhyacotritonidae, and Dicamptodontidae (Cope, 1889; Özeti and Wake, 1969)). Coding for the Amphiumidae and Proteidae is based on Cope (1889; contra Hecht and Edwards, 1977; contra Duellman and Trueb, 1986). With reinterpretation of the two ossified elements as the hypobranchials I + II (see above remarks on character 32), the ceratobranchials are coded as unknown for *Pangerpeton* (contra Wang and Evans, 2006). See Reilly and Lauder (1988) for discussion on the homology of the “epibranchials” of other authors with ceratobranchials.

35. Basibranchial II: present as ossified or cartilaginous (0); or absent (1).

**Remarks:** Basibranchial II is absent in the Cryptobranchidae, Amphiumidae, and Sirenidae (Rose, 2003). Both absent and present conditions are known among hynobiids (Parker, 1879; Rose, 2003; Fei et al., 2006), but the taxa included in the matrix all showed the derived condition, and we coded them accordingly.

36. Premaxillary teeth: present (0); absent, replaced by horny beaks (1).

**Remarks:** The derived state is only known for extant sirenids (Cope, 1889; Duellman and Trueb, 1986), while *Habrosaurus* as a stem-group member of the family has toothed premaxillae (Gardner, 2003a). Thus, the derived state is a synapomorphy of crown-group sirenids.

37. Vomerine teeth: forming simple anterior arcade parallel to maxillary tooth row (0); forming simple tooth row or patch close to vomerine-parasphenoid suture (1); curved longitudinal tooth row extending to the base of parasphenoid (2); forming complex tooth batteries covering entire surface of the bone (3).

**Remarks:** Coding of state (1) for *Rhyacotriton* is based on the adult condition in *Rhyacotriton variegatus* (AmphibiaTree, 2007), although state (0) is known in the larval stage of *R. olympicus* (Worthington and Wake, 1971). The derived state (2) is characteristic of salamandrids, and state (3), of sirenids.

38. Multiple and parallel rows of palatine teeth in adult: absent (0); present (1).

**Remarks:** Palatine teeth, where present ontogenetically or in the adult, form a single row in most salamanders. In sirenids palatine teeth form multiple and parallel rows in both extant and fossil forms (e.g., Gardner, 2003a). Multiple rows of palatine teeth may ontogenetically occur in other salamander families (Ambystomatidae, Plethodontidae, Hynobiidae, Salamandridae; see Rose, 2003: fig. 4), and thus the polarity of this character is uncertain. All taxa that lack a discrete palatine in adults are coded as inapplicable.

39. Pterygoid teeth: absent (0); present (1).

**Remarks:** A toothed pterygoid is known for *Kokartus*, but the actual condition in *Karaurus* remains unknown (Skutschas and Martin, 2011). Most crown-group salamanders have a toothless pterygoid, but the toothed condition is known for proteids (e.g., Carroll and Holmes, 1980; Evans, 2003; Rose, 2003). Sirenids have a small and toothless pterygoid (Rose, 2003; Larson et al., 2006). *Dicamptodon* is coded as polymorphic based on information from Milner (2000) and AmphibiaTree (2007: digimorph.org). Plethodontids lack a pterygoid, and thus this character was coded as inapplicable.

40. Parasphenoid tooth shagreen: absent (0); present (1).

**Remarks:** The derived state seems to be characteristic of the Plethodontidae, as most members of the family have a parasphenoid tooth shagreen (Cope, 1889; Wake, 1966). *Pseudobranchius* was described as having parasphenoid tooth rows (Cope, 1889), but these are actually vomerine and palatine teeth (e.g., Gardner, 2003a).

41. Marginal teeth (Parsons and Williams, 1962): nonpedicellate (0); pedicellate (1).

**Remarks:** Most salamanders have pedicellate teeth, but the nonpedicellate condition is known in some proteids and some sirenids (Gardner, 2003a). Although having nonpedicellate palatal teeth, *Siren* is coded as unknown because of a lack of marginal teeth. The stem-group caudate *Karaurus* is coded as having nonpedicellate teeth based on the information from its sister taxon *Kokartus* (Skutschas and Martin, 2011).

42. Tooth crown: monocuspid (0); bicuspid (1).

**Remarks:** The common ontogenetic pattern is that pedicellate and bicuspid teeth replace nonpedicellate and monocuspid teeth at metamorphosis (Wistuba et al., 2002; Davit-Béal et al.,

2006 and references cited therein). However, teeth in neotenic salamanders at adult stage may or may not be pedicellate and may or may not be bicuspid. For example, *Necturus* has monocuspid teeth that can be either pedicellate or nonpedicellate (Means, 1972; Larsen and Guthrie, 1974; see also Beneski and Larsen, 1989 for similar conditions in neotenic forms of *Ambystoma*), indicating no direct correlation of pedicellularity with bicuspidation. There is evidence that at least in some salamanders pedicellularity is ontogenetically established before bicuspidation (Beneski and Larsen, 1989). Neotenic forms may express positional variation (e.g., monocuspid teeth interspersed with incipient bicuspid teeth), or regional variation (e.g., premaxillary teeth are bicuspid, while dentary teeth are monocuspid) in the same individual at the same developmental stage (Beneski and Larsen, 1989). In such cases, we coded the bicuspid condition for the taxon.

Marginal teeth are absent and replaced by a horny beak in extant sirenids, but are present as nonpedicellate and monocuspid teeth in the fossil taxon *Habrosaurus* (Gardner, 2003a). The teeth in proteids are essentially monocuspid, and absence of the pedicellate condition is “more apparent than real as indicated by SEM for *N. maculosus*” (Larsen and Guthrie, 1974: 638). Although lacking premaxillary and maxillary teeth, the palatal teeth in extant sirenids are monocuspid and nonpedicellate (e.g., Gardner, 2003a). The tooth structure is uncertain for most of the fossil taxa known from China, but the new taxon *Beiyanerpeton* from Upper Jurassic beds in western Liaoning unequivocally shows that the teeth are nonpedicellate and monocuspid as in the stem salamander *Kokartus* (Skutschas and Martin, 2011). The marginal teeth in the Early Cretaceous *Valdotriton* from Spain were described as “pointed and pedicellate, but it is unclear whether they are unicuspid or bicuspid” (Evans and Milner, 1996: 634).

43. Sphenethmoid as a discrete bone: present (0); absent (1).

**Remarks:** Sphenethmoid (= orbitosphenoid) is normally ossified as a discrete element of the lateral wall of the braincase in most salamanders, but the derived condition is a unique feature of proteids (e.g., Rose, 2003; Evans, 2003). Coding of the character for *Liaoxitriton* is based on information from the specimens in the PKUP collection.

44. Parasphenoid/pterygoid contact: contact at the base of parasphenoid (0); contact along anterior extension of parasphenoid (1); contact absent (2).

**Remarks:** The stem caudates *Kokartus* and *Karaurus* as reconstructed have a parasphenoid/pterygoid contact at the base of the parasphenoid (Skutschas and Martin, 2011). This is recognized as the primitive condition for salamanders. The derived state (1) occurs in extant cryptobranchids, amphiumids, proteids, and *Pseudobranchius*. The derived state (2) occurs in rhyacotritonids, ambystomatids, salamandrids, and some hynobiids.

45. Y-shaped dorsal crest in trunk vertebrae: absent (0); present (1).

**Remarks:** Gardner (2003a) recognized the derived state as a unique feature of sirenids, including the Cretaceous fossil taxon *Habrosaurus*. The Eocene *Paleoamphiuma* also shows the Y-shaped dorsal crest in trunk vertebrae, a strong indication of its sirenid affinity (Gardner, 2003b).

46. Vertebral centrum: amphicoelous (0); opisthocoelous (1).

**Remarks:** Most salamanders have amphicoelous vertebrae, but the derived state is known in Salamandridae and Plethodontidae. The opisthocoelous condition was considered as independently derived in the Salamandridae and Plethodontidae (Wake and Lawson, 1973); however, our previous analysis of morphological data (Gao and Shubin, 2001) hinted at a

possible homology in congruence with other characters, and our analysis of the expanded dataset in this study enhances our previous hypothesis in this regard.

47. Tuberculum interglenoideum of atlas: absent (0); present (1).

**Remarks:** The presence of the tuberculum interglenoideum of the atlas for a four-faceted articulation with the exoccipital was considered as a unique feature of urodeles (Trueb, 1993). Since both *Karaurus* and *Kokartus* have a tuberculum interglenoideum of the atlas (Estes, 1981; Averianov et al., 2008), the derived state (1) is apparently a feature for all caudates generally. Although this character is uninformative in this analysis, it could be informative when undertaking a more global analysis with inclusion of caecilians (see Wake, 2003: absent in extant caecilians; but Jenkins et al., 2007: present in *Eocaecilia*). Among the fossil taxa included in the dataset, an interglenoid prominence was described for the atlas in *Pangerpeton* (Wang and Evans, 2006); we coded the (1) state for the taxon accordingly.

48. Head of postatlantal ribs (Duellman and Trueb, 1986: character W): bicapitate (0); unicapitate (1).

**Remarks:** Most urodeles have double-headed ribs as seen in the stem-group caudate *Karaurus*. The single-headed condition as a derived state occurs in hynobiids, cryptobranchids, and their closely related fossil taxa from China. Fossil and extant amphiumids may have both bicapitate and unicapitate ribs in the same individual because of rib reduction (see Gardner, 2003b), but we coded the normal bicapitate condition in these taxa.

49. Postatlantal ribs in association with vertebrae (Rose, 2003): ribs present in association with all trunk and sacral vertebrae (0); ribs only present in association with no more than eight anterior trunk vertebrae (1).

**Remarks:** Most caudates have postatlantal ribs in association with all trunk vertebrae, but the derived state is independently acquired in sirenids and amphiumids (Noble, 1931; Rose, 2003).

50. Atlantal spinal nerve foramen: absent (0); present (1).

**Remarks:** The derived condition is known for all extant urodeles (Edwards, 1976) and those fossil taxa for which the condition can be determined (e.g., Gardner, 2003a), but the primitive state is coded for *Karaurus* following Duellman and Trueb (1986). The atlantal spinal nerve foramen is also absent in *Kokartus* (Averianov et al., 2008).

51. Postatlantal spinal nerve foramina (modified from Hecht and Edwards, 1977): all postatlantal spinal nerves exit intervertebrally (0); spinal nerve foramina present on posterior caudal vertebrae (1); foramina present on all caudal vertebrae (2); foramina occur in trunk, sacral and caudal series (3).

**Remarks:** All extant urodeles have atlantal spinal nerve foramina, but foramina on postatlantal vertebrae extend from the caudal to trunk series (Edwards, 1976). The primitive state (0) is known for all cryptobranchoids and proteids; the derived condition (1) is unique for amphiumids; the derived state (2) is known for dicamptodontids and rhyacotritonids, and the fossil taxon *Valdotriton*. All other salamandroids in which this character is known show the derived state (3). The fossil taxon *Habrosaurus* is coded based on information from Gardner (2003a).

52. Ossified stapes (Duellman and Trueb, 1986: character K): present in adults (0); absent in adults (1).

**Remarks:** The absent condition occurs in all salamandrids (see Rose, 2003) and in neotenic species of plethodontids (Wake, 1966). Among sirenids, *Siren* has an ossified stapes, while *Pseudobranchius* does not (Edwards, 1976; Rose, 2003).

53. Operculum (Duellman and Trueb, 1986: character K): ossified and free (0); free operculum absent (1).

**Remarks:** Although the family Karauridae is coded as having (0) state in Duellman and Trueb (1986), the actual condition remains unknown for both *Karaurus* and *Kokartus* (Estes, 1981; Skutschas and Martin, 2011). Data in the literature on the presence/absence of the operculum in extant groups of salamanders are extremely confusing. For example, Trueb (1993: table 2B) listed the operculum as “free with ossified stapes” for both the Proteidae and Sirenidae, while Rose (2003: 1728) clearly stated that “the operculum is missing in rhyacotritonids, plethodontids, some hynobiids (*Salamandrella* and *Onychodactylus*), cryptobranchids, sirenids, proteids, and amphiumids.” Regarding the same structure, the operculum is described for the Salamandridae as fused to the columella (Duellman and Trueb, 1986), “bony or cartilaginous, filling fenestra ovalis” (Trueb, 1993: table 6.2B), and as a free element by Larson et al. (2006). After reviewing the evidence from different sources, we coded the primitive state for salamandrids, and the derived state for proteids and sirenids. Coding of this character for several other taxa in the matrix is based on the information from Rose (2003) and Larson et al. (2006). In addition, we coded the present/absent alternatives, but were unable to code the fused condition as a separate state without unambiguous evidence regarding the developmental nature of the structure in different taxa.

54. Lateral wall of nasal capsule (Trueb, 1993: character 4): complete (0); incomplete (1).

**Remarks:** According to Trueb (1993: table 6.2), the primitive condition occurs in extant hynobiids and cryptobranchids, and the derived state occurs in all other extant urodeles, including sirenids. All fossil taxa are coded as unknown because the cartilaginous capsule is not preserved in any fossil taxa.

55. Lateral narial fenestra (Trueb, 1993: character 5): absent (0); present (1).

**Remarks:** The lateral narial fenestra in Trueb (1993) is the structure termed lateral fenestra (fenestra retronarina) in Rose (2003). The lateral fenestra is absent in cryptobranchids, hynobiids, amphiumids, proteids, and sirenids (Trueb, 1993: table 6.2). The presence of the fenestra in several families within the Salamandroidea (Plethodontidae, Rhyacotritonidae, Salamandridae, Dicamptodontidae, and Ambystomatidae) can be interpreted as a derived morphology.

56. Posterior wall of nasal capsule (Trueb, 1993: character 6): complete (0); incomplete (1).

**Remarks:** The incomplete condition is known for proteids, amphiumids, and sirenids (Trueb, 1993). Since the distribution of this character within the urodele taxa does not overlap with the character concerning the lateral wall of same anatomical structure (nasal capsule), these are treated as separate characters.

57. Nasolacrimal duct (Trueb, 1993: character 8): present (0); absent (1).



**Remarks:** According to Trueb (1993: table 6.2), the absent condition is seen in all of the four neotenic groups (cryptobranchids, amphiumids, proteids, sirenids), but contrary to Trueb (1993: table 6.2: absent), a nasolacrimal duct is present in salamandrids (Francis, 1934; Rose, 2003). This soft anatomical character is coded as unknown for all fossil taxa.

58. Sculptured dermal skull roof: present as heavily sculptured surface covering (0); weakly sculptured or absent (1).

**Remarks:** The primitive condition is known for *Karaurus* and *Kokartus* (Estes, 1981; Skutschas and Martin, 2011). The derived state is coded for most urodeles, but variable conditions occur in salamandrids, amphiumids, and plethodontids. The holotype skull of *Pangerpeton* is known from ventral view, but the lateral surface of the maxillae shows no sculpture (Wang and Evans, 2006: fig. 1), and we coded the character for this taxon accordingly.

59. Frontal anterior extension: frontal does not extend lateral to nasal bone (0); frontal does extend to lateral border of nasal (1).

**Remarks:** The derived condition is independently acquired in cryptobranchids and sirenids. Proteids are coded as inapplicable because of the lack of a nasal. All other fossil and extant taxa included in the analysis show the primitive state.

60. Anterolateral process of parietal: poorly defined or absent (0); well-developed process extending to or surpassing midlevel of orbit (1).

**Remarks:** The derived state (1) is independently achieved in the Cryptobranchidae and in all salamandroids but the Plethodontidae and Salamandridae.

61. Parietal/prefrontal contact above orbit: contact absent (0); contact present to embrace frontals (1).

**Remarks:** The derived condition has been recognized as a diagnostic feature for extant cryptobranchids (Cope, 1889), and it is also known in amphiumids and ambystomatids (Cope, 1889; Digimorph staff, 2008). Most *Hynobius* species show no contact, but the derived state is seen in *Hynobius yunanicus* (Fei et al., 2006: fig. 53). Since *Hynobius yunanicus* has been recognized as the synonym of *Pachyhynobius shangchengensis* (Xiong, 2007), we simply coded the primitive condition for the genus *Hynobius*. The parietal in proteids and sirenids has an extension reaching the anterior border of the orbit, but we coded the inapplicable condition for the two groups because of the absence of the prefrontal.

62. Frontal/maxillary contact: contact absent (0); contacts present (1).

**Remarks:** A frontal/maxillary contact occurs in extant cryptobranchids and in some but not all plethodontids (see Duellman and Trueb, 1986: fig. 13-4). Proteids and sirenids are coded as inapplicable because of the lack of a maxilla.

63. Squamosal orientation in dorsal view: squamosal present as simple transverse bar (0); squamosal strongly slanting anteriorly or parallel to skull midline (1).

**Remarks:** The derived condition is seen in sirenids, salamandrids, proteids, amphiumids, and some plethodontids. Coding of this character for *Rhyacotriton* could be ambiguous (see Cloete, 1961; Srinivasachar, 1962; Worthington and Wake, 1971), but we coded the character for the genus based on the information from AmphibiaTree (2007: *Rhyacotriton variegatus*).

64. Exposure of otic-occipital complex in dorsolateral view: otic-occipital complex largely concealed by parietal (0); mainly exposed posterior to parietal (1); large exposure extends lateral to parietal bone (2).

**Remarks:** The derived state (2) is seen in ambystomatids, rhyacotritonids, plethodontids, dicamptodontids, some salamandrids, and the fossil taxon *Valdotriton*. *Amphiuma* shows the derived state (2), despite a small process of the squamosal nearly contacting the parietal (see Carroll and Holmes, 1980: fig. 10). Coding of the derived state (2) for *Siren* is based on Cope (1889: pl. IX), Carroll and Holmes (1980: fig. 24), and AmphibiaTree (2008).

65. Midline contact of otic-occipital complex over foramen magnum: contact absent (0); contact present (1).

**Remarks:** Among extant families, the derived state (1) occurs in most salamandroids but proteids. The primitive state (0) occurs in cryptobranchids, and in some but not all hynobiids (*Ranodon* shows no contact—Jömann et al., 2005; *Onychodactylus* shows a contact—AmphibiaTree, 2007).

66. Medial contact of squamosal with parietal or other roofing element: contact present (0); contact absent (1).

**Remarks:** The derived state (1) occurs in most salamandroids, but exceptions occur in amphiumids, proteids, and some salamandrids. Coding of *Onychodactylus* is based on information from AmphibiaTree (2007). The fossil taxon *Valdotriton* is coded with the derived state according to Evans and Milner (1996).

67. Origin of *M. adductor mandibulae internus superficialis* (Duellman and Trueb, 1986: character Z): on dorsolateral surface of parietal (0); origin on side of skull (1); origin extends to exoccipital or to cervical vertebra (2).

**Remarks:** Estes (1981) recognized the association of an adductor groove on the squamosal with this character, and considered the dorsal origin of the muscle as the primitive state in salamanders. Coding of the character for extant family groups is based on Duellman and Trueb (1986). See also the illustration and discussion of this character in Carroll and Holmes (1980).

68. Ypsiloid cartilage (Duellman and Trueb, 1986: character Y): present (0); absent (1).

**Remarks:** The ypsiloid cartilage is a Y-shaped structure that lies anterior to the pelvis (Whipple, 1906b). According to Duellman and Trueb (1986), the pelvis lacks a well-defined ypsiloid cartilage in sirenids, proteids, plethodontids, amphiumids, and rhyacotritonids. Thus, the absent condition occurs in both neotenic and metamorphosed salamanders (see also Edwards, 1976).

69. Dorsal and ventral crests of humerus: poorly defined (0); well developed (1).

**Remarks:** A dorsal crest (crista dorsalis humeri) and a ventral crest (crista ventralis humeri) are well developed in most metamorphosed salamanders in relation to their terrestrial life, but both *Rhyacotriton* and *Ambystoma* show the primitive state (AmphibiaTree, 2007). Coding of the character for salamandrids and hynobiids is based on information from several publications (Francis, 1934; Zhang, 1985; Wang et al., 2004; Zhang et al., 2009; Zhao et al., 2009).

70. Radial and ulnar condyles of humerus: not well separated from one another (0); well-defined condyles separate from one another (1).

**Remarks:** This character is largely correlated with the aquatic or terrestrial life-style of salamanders. Coding of this character for sirenids and salamandrids is based on information from AmphibiaTree (2008) and Digimorph Staff (2008).

71. Femoral trochanter forming a twig-like projection: absent (0); well developed as a twig-like process branching off from shaft (1).

**Remarks:** *Karaurus* shows the primitive condition (see Estes, 1981). Hynobiids, with the exception of *Batrachuperus* (Zhang et al., 2009), have a very small process, while most salamandrids (e.g., *Salamandra*, Francis, 1934: pl. V) have a prominent femoral trochanter that forms a twig-like projection branching off from the shaft. The femur has a small trochanter in *Necturus* (Cope, 1889). Sirenids are coded as inapplicable because they lack hind limbs.

72. Fusion of distal carpal 1+2 into a single basale commune in the carpus (Shubin and Wake, 1996): fusion absent (0); or fusion present (1).

**Remarks:** The derived state has been recognized as a unique synapomorphy of urodeles (Shubin and Wake, 1996, 2003). Pending on the actual condition in the stem-group caudates Karauridae, the derived state may be a synapomorphy of the Caudata. This and the following character are uninformative for this analysis, but are useful when performing a molecular-morphology combined analysis with Anura and Gymnophiona designated as outgroups.

73. Fusion of distal tarsal 1+2 into a basale commune in the tarsus (Shubin and Wake, 1996): fusion absent (0); fusion present (1).

**Remarks:** Sirenids are coded as inapplicable because of the loss of the hind limb. The distribution of this character parallels the above character, and both characters are excluded from the actual analysis because of their uninformative status.

74. Number of centralia in manus and pes (Shubin and Wake, 1996): more than one central element (0); or one central element (1); or no central element (2).

**Remarks:** Polymorphic conditions (0/1) are seen in both the Cryptobranchidae and Hynobiidae. Most salamandroid families show the derived state (1), with a further derived condition (2) known for the Proteidae and Amphiumidae. Sirenids are coded based on the forelimb, although the hind limb is lost. Coding of the character for *Tylotriton* is based on Yu and Zhao (2007: *T. kweichowensis*) and Zhao et al. (2009: *T. taliangensis*). The fossil taxon *Liaoxitriton* is figured as having two centralia (Dong and Wang, 1998), but several specimens in PKUP collection seem to show a single central element; this character cannot be confidently scored for the taxon before the actual condition is determined.

75. Intermedium and ulnare: separate intermedium (0); fused to ulnare (1).

**Remarks:** The fused condition as a derived state occurs in sirenids, proteids, rhyacotritonids, some but not all salamandrids and amphiumids (Cope, 1889). The fossil taxon *Iridotriton* was described as having a fused condition, but this was inferred in the type and only known specimen from a splayed series of carpals completely out of articulation; thus, we have coded the uncertain condition on this character for the fossil taxon.

76. Distal carpal 4 and distal carpal 5: two elements remain separate (0); two elements fused (1).  
**Remarks:** The derived state uniformly occurs in the Amphiumidae, Proteidae, and Sirenidae; and also in some but not all members of the Cryptobranchidae, Hynobiidae, Plethodontidae, and Salamandridae (Shubin and Wake, 1996). Because of its distribution in several metamorphosed and terrestrial groups, the fused condition apparently cannot be interpreted as a neotenic feature.

77. Haploid chromosome number (modified from Duellman and Trueb, 1986: character DD): ranging from 20 to 32 (0); reduced to 19 (1); further reduced to 14 or less (2).

**Remarks:** All urodeles have the haploid chromosome number of no more than 32; all salamandroid families including the Sirenidae are characterized by a reduction to 14 or fewer, but the Proteidae have 19 (see Morescalchi, 1975; Milner, 1988 for discussion; see also Duellman and Trueb, 1986: table 16-2).

78. Diploid chromosome number (modified from Duellman and Trueb, 1986: character DD): 56 or more (0); 40-55 (1); lower than 40 (2).

**Remarks:** Sirenids show the derived condition (1), while all salamandroids show the (2) condition. In view of the distribution patterns, the derived (2) condition is apparently a salamandriod synapomorphy, regardless of the phylogenetic position of sirenids.

79. Microchromosome (Duellman and Trueb, 1986: table 16-2): present (0); absent (1).

**Remarks:** Absence of a microchromosome is known for all salamandriod families, while the Hynobiidae and Cryptobranchidae show the primitive state of this character (Morescalchi, 1975; Milner, 1988). Surprisingly, the supposed basal clade Sirenidae shows the derived condition.

80. Ciliated epithelium of cloaca (modified from Sever, 1991: characters C and D): present in both sexes (0); present in male but absent in female (1); or absent in both sexes (2).

**Remarks:** Because Sever's characters C and D refer to the same structure in different sexes, we have combined the two binary characters into a single multi-state character. Sever (1991) considered the presence of ciliated epithelium in both sexes to be the ancestral condition for salamanders, and absence of cilia to be a derived condition. According to Sever (1991: table 2), the family Sirenidae is the only group showing the (2) condition.

81. Extent of epidermis in female cloacal chamber (Sever, 1991: character E): epidermal lining does not extend to anterior one-half of the cloacal chamber (0); or does extend into anterior one-half of the chamber (1).

**Remarks:** According to Sever (1991), the derived state occurs in the Plethodontidae, Rhyacotritonidae, Proteidae, Sirenidae, and some but not all hynobiids. Hynobiids are found to have polymorphic conditions at the familial level, but we are unable to code the character for the two genera (*Hynobius* and *Onychodactylus*) sampled in our data matrix because of uncertainty.

82. Primary and secondary folds in male cloacal tube and associated glands (Sever, 1991: characters H): both primary and secondary folds absent (0); or both folds present (1).

**Remarks:** According to Sever (1991), the derived state (1) is known for three familial groups, Ambystomatidae, Rhyacotritonidae, and Dicamptodontidae. All other extant families show the primitive state (0).

83. Anteroventral cloacal glands (modified from Sever, 1991: characters L and Q): absent in both sexes (0); present in male but not in female (1); or present in both sexes (2).

**Remarks:** Because both characters L and Q in Sever (1991) refer to the same structure but in different sexes, we have combined the two binary characters into a single multi-state character. According to Sever (1991), the family Sirenidae is the only group that shows the primitive (0) condition; the derived state (1) occurs in the Amphiumidae and Rhyacotritonidae, while the further derived state (2) is known for all other extant families but the Sirenidae. Since both the Hynobiidae and Cryptobranchidae show the derived state (2), this character obviously cannot be correlated with internal fertilization.

84. Spermathecae in cloaca (Sever, 1991: character M): absent (0); or present (1).

**Remarks:** According to Sever (1991), this is one of the characters that are well corroborated with the mode of fertilization. Those salamander families that perform external fertilization lack spermathecae in the cloaca, while all those families that practice internal fertilization show the derived state (1).

85. Dorsal cloacal glands (modified from Sever, 1991, characters O and W): absent in both sexes (0); present in male only (1); or present in both sexes (2).

**Remarks:** Since the characters O and W in Sever (1991) refer to the same anatomical structure in different sexes, we combined the two characters into a multi-state character. The primitive state (0) occurs in three families that practice external fertilization (Hynobiidae + Cryptobranchidae + Sirenidae), while in those that undertake internal fertilization at least the males possess dorsal cloacal glands (Sever, 1991: table 2).

86. Posteroventral cloacal glands (Sever, 1991: character R): absent (0); or present (1).

**Remarks:** According to Sever (1991), posteroventral cloacal glands are present in all salamander families but the Hynobiidae and Cryptobranchidae. The Salamandridae and Plethodontidae are coded as polymorphic following Sever (1991).

87. Kingsbury's glands and dorsal pelvic glands in male cloaca (modified from Sever, 1991: characters S and T): both Kingsbury's and dorsal pelvic glands absent (0); or both groups of glands present (1).

**Remarks:** Sever's (1991) character S and T refer to the Kingsbury's glands and the dorsal pelvic glands, respectively. Since the two characters show a fully compatible distribution among the extant salamander families, we chose to combine the two characters in this analysis. The primitive state (0) is seen in all salamander families that practice external fertilization (Hynobiidae, Cryptobranchidae, and Sirenidae), while all families that practice internal fertilization show the derived state (1).

88. Lateral pelvic glands in male cloaca (Sever, 1991: character U): absent (0); or present (1).

**Remarks:** Sever's (1991) character U at the family level shows a pattern of distribution that is incompatible with the characters S+T; thus, we treat this as a separate character from the above. Following Sever (1991), the derived state (1) is coded for all salamandroid families but the Amphiumidae and Salamandridae.

89. Pubotibialis and puboischiotibialis muscles (Duellman and Trueb, 1986: character AA): separate (0); or fused (1).

**Remarks:** The fused condition is known for extant hynobiids and cryptobranchids. The primitive (0) state was coded for the fossil taxon *Karaurus* in Duellman and Trueb (1986: table 17-1), but we found no indication in the literature (Ivachnenko, 1978; Estes, 1981) regarding the morphology of the muscles in this taxon; thus, we coded the character as unknown for this stem caudate.

90. Kidney (Duellman and Trueb, 1986: character BB): glomeruli normally well developed (0); or anterior glomeruli reduced or absent (1).

**Remarks:** This is one of the characters that were used to support the placement of the Sirenidae as a basal clade of urodeles (Duellman and Trueb, 1986: figure 17-1). However, because the soft anatomy of the kidney is unknown in stem caudate *Karaurus* and all fossil salamanders, this character must be treated as unpolarized at the Urodela level.

91. Number of free ribs on anterior caudal vertebrae: more than three pairs (0); two to three pairs (1); or free ribs absent (2).

**Remarks:** The stem-group caudate *Karaurus* has more than three pairs of caudal ribs, and other salamanders except salamandroids have no more than three pairs of caudal ribs. The derived state (2) is characteristic for the crown-group salamandroids.

92. Ectopterygoid: present (0); or absent (1).

**Remarks:** This character is uninformative at the caudate level, but is kept in the data matrix for performing more global analysis in the future.

93. Postfrontal: present (0); or absent (1).

**Remarks:** Like the above character regarding the ectopterygoid, this character is uninformative for this phylogenetic analysis, but will be useful when undertaking a more global analysis in the future.

94. Scapula-coracoid ossification (Duellman and Trueb, 1986: character U): ossified as separate elements (0); co-ossified as a single element (1).

**Remarks:** This is one of the characters used to support the placement of the Sirenidae as a basal urodele clade (Duellman and Trueb, 1986: figure 17-1). The Sirenidae have a separate coracoid (Noble, 1931), while all other salamander families have a single ossification of the scapulocoracoid. Moreover, because the stem-group caudate *Karaurus* had a co-ossified scapulocoracoid (Estes, 1981), the separate ossifications of the scapula and coracoid in sirenids provide no support of the purported basal position of sirenids.

95. Movable eyelids (Duellman and Trueb, 1986): absent (0); present (1).

**Remarks:** This character is both ontogenetically and ecologically significant: movable eyelids are developed at metamorphosis for an adult life on land, but are lacking in all larvae and adult neotenic forms. Consequently, the absent state is coded for the Cryptobranchidae, Amphiumidae, Proteidae, and Sirenidae.

96. Nasolabial groove (Duellman and Trueb (1986: character LL): absent (0); or present (1).

**Remarks:** Paired nasolabial grooves (sulcus nasolabialis) are only present in the Plethodontidae (Whipple, 1906a; Edwards, 1976; Duellman and Trueb, 1986) and the grooves have a primary function in respiration and a secondary function in olfaction (Jorgensen, 2000).

97. Mode of fertilization (Duellman and Trueb, 1986: character CC): external (0); or internal (1).

**Remarks:** Cryptobranchoids (Cryptobranchidae + Hynobiidae) and probably sirenids perform external fertilization, while all other salamanders are known to practice internal fertilization as a derived reproductive behavior. The actual mode of fertilization is unknown in sirenids, but has been inferred to be external based on the lack of cloacal glands that function in the production of spermatophores in males and the storage of sperm in females (Sever, 1991; Sever et al., 1996; see discussion in Zhang and Wake, 2009).

98. Lungs (Duellman and Trueb, 1986: character MM): normally developed (0); or reduced (1); or entirely lost (2).

**Remarks:** Besides the typically lungless plethodontids, the genus *Onychodactylus* (Hynobiidae) also lacks lungs; a reduced condition is known in *Rhyacotriton* and *Ranodon* (Duellman and Trueb, 1986). Independent reduction or losses of lungs also occur in several unsampled taxa (*Chioglossa*, *Salamandrina*, *Euproctus*; Wake, 1969) in the Salamandridae (Larson et al., 2006).

99. Number of presacral vertebrae: ranging from 14-30 (0); exceeding 30 (1).

**Remarks:** Most salamanders have 14-16 presacral vertebrae (atlas + trunk vertebrae), but quite variable counts are known in different groups of salamanders. Litvinchuk and Borkin (2003) compiled the data on presacral vertebral counts in extant families, which can be summarized as follows: Hynobiidae (15-22), Cryptobranchidae (19-23), Plethodontidae (14-24), Proteidae (17-37), Amphiumidae (61-65), Rhyacotritonidae (15-18), Dicamptodontidae (15-16), Ambystomatidae (14-16), Salamandridae (12-19), Sirenidae (33-43).

The Mesozoic taxa known from China have the number of presacral vertebrae ranging from 14-16. Among these, different specimens of *Chunerpeton* consistently show 15 presacrals, while those of *Liaoxitriton* show slight variations of having 14-15 presacrals (Dong and Wang, 1998; Chen and Gao, in prep.).

100. Pattern of vertebral development (Boisvert, 2009): neural arch developed before centrum (0); centrum developed before neural arch (1).

**Remarks:** Vertebral development pattern is a robust character for understanding the phylogeny of amphibians (Boisvert, 2009). Because all dissorophoid temnospondyls (Amphibamidae, Micromelerpetontidae, Branchiosauridae) show the “arch-first” developmental pattern, this has been recognized as the plesiomorphic condition for amphibians. Among modern amphibians, frogs show the “arch-first” pattern (Carroll et al., 1999), while caecilians show the “centrum-first” pattern (Wake and Wake, 1986, 2000). All salamanders but some hynobiids show the centrum first pattern. Among hynobiids, the primitive developmental pattern (0) is known for *Hynobius* and *Ranodon*, while *Salamandrella* shows the derived state (Boisvert, 2009); the ossification pattern is unknown for the basal hynobiid *Onychodactylus*. Contrary to Boisvert (2009), the presence of both plesiomorphic and derived states of this character among hynobiids provides no evidence for the family being possibly paraphyletic; by contrast, there has been strong molecular support for the monophyly of the family (e.g., Wiens et al., 2005; Zhang et al., 2006; Roelants et al., 2007; Zhang and Wake, 2009; Zheng et al., 2011; Pyron and Wiens, 2011).

101. Quadrate: present (0); absent (1).

**Remarks:** All extant salamanders but sirenids have a quadrate that may represent an amalgamation of quadratojugal and quadrate (Rose, 2003). A quadrate is absent in extant sirenids (Rose, 2003), while the actual condition is unknown for the fossil taxon *Habrosaurus* (Gardner, 2003a). The out-group condition is scored based on information from Estes (1981).

102. Frontosquamosal arch: absent (0); present (1).

**Remarks:** The frontosquamosal arch is a bony bridge over the temporal fenestra, formed by an anterior extension of the squamosal contacting the posterior process of the frontal. Presence of the frontosquamosal arch in newts has been recognized as a derived condition within the Salamandridae, functioning as a defensive structure against predators (Naylor, 1978b).

103. Maxillary arcade: incomplete (0); complete (1).

**Remarks:** All salamanders, including the stem-group caudate *Karaurus*, have an incomplete maxillary arcade resulting from the abbreviation of the maxilla and loss of the quadratojugal. Secondary completion of the maxillary arcade by both the posterior extension of the maxilla and fusion of the quadratojugal with the quadrate is seen in two salamandrids (*Echinotriton* and *Tylotriton*) (Sato, 1943; Nussbaum and Brodie, 1982; Fei et al., 2006).

104. Columellar process of squamosal: absent (0); present (1).

**Remarks:** The columellar process of the squamosal is a hooked bony projection from the squamosal attached to the stylus of the stapes (columella) by the squamoso-columellar ligament. The derived condition is recognized as a unique feature of proteids with great phylogenetic significance (Larsen and Guthrie, 1974). As the actual conditions in many extant and fossil taxa are still unknown, the phylogenetic significance of this character is obviously worth future investigation. Coding of the character for *Amphiura* is based on the specimen UA 14364 (University of Alberta Paleontological Collection), and for *Ambystoma* on UA 14338 and UA 14339.

105. Facial nerve in relation to ligamentum squamoso-columellare (Kingsbury and Reed, 1908): facial nerve passes below columellar-squamosal connection (0); facial nerve passes above columellar-squamosal connection (1).

**Remarks:** According to Kingsbury and Reed (1908: 83), *Necturus* and *Proteus* have the facial nerve passing above the squamoso-columellar ligament. The primitive state (0) is coded for several other taxa, with available information from Kingsbury and Reed (1908). Although the actual condition is still unknown for many salamanders, this is a potentially significant character that needs to be investigated in future studies.

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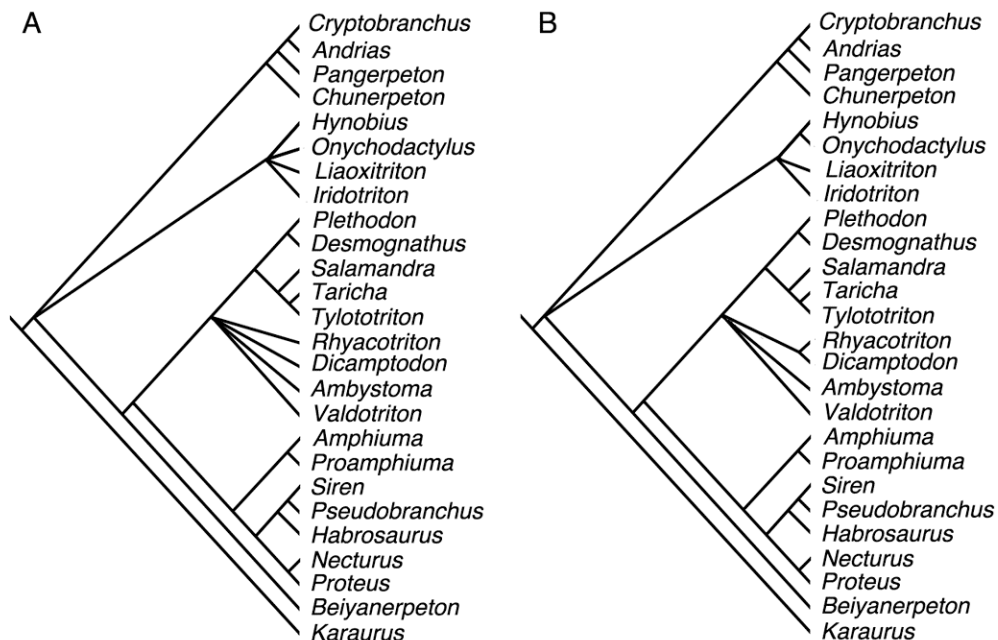
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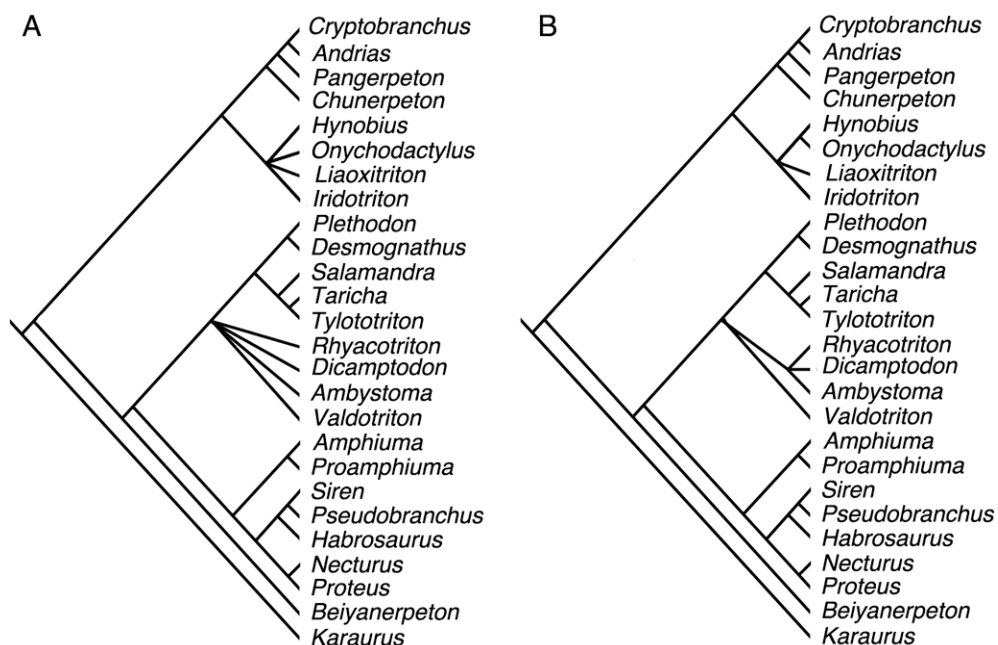
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**Figure S1.** Strict consensus (A) and Adams consensus (B) of 40 most parsimonious trees (TL= 235 steps, CI= 0.506, RI= 0.727). See SI text for explanation.



**Figure S2.** Strict consensus (A) and Adams consensus (B) of ten most parsimonious trees (TL= 9131 steps, CI= 0.695, RI= 0.852) based on analysis of reweighted characters. For detailed information on the phylogenetic analysis, see SI text for explanation.



<i>Liaoxitriton</i>	0 0 0 0 ? 0 0 0 0 0	0 ? ? 0 0 0 ? 1 0 ?	? 0 ? ? ? ? ? 1 0 0
<i>Pangerpeton</i>	0 ? 1 0 1 0 1 0 0 0	? ? 0 ? 0 0 1 1 0 1	? ? ? ? ? ? ? ? ? ?
<i>Chunerpeton</i>	0 0 0 ? 0 0 0 0 0 0	? ? 0 ? 0 0 ? 1 0 ?	? 0 ? ? ? ? ? 1 1 1
<i>Beiyanerpeton</i>	0 ? 0 ? 0 0 0 0 1 0	1 0 0 0 0 0 ? 0 0 1	? 0 0 ? ? ? ? 1 0 1
<i>Iridotriton</i>	? ? ? ? ? 0 ? ? ? ?	1 ? ? ? 0 0 ? 1 0 ?	? ? ? ? ? ? ? 1 ? 0

	65	70	75	80	85	90
<i>Karaurus</i>	0 0 0 0 ? 0 0 ? 0 0	0 ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?			
<i>Cryptobranchus</i>	1 1 0 1 0 0 2 0 0 0	0 1 1 0 0 A 0 0 0 0	0 0 2 0 0 0 0 0 1 1			
<i>Andrias</i>	1 1 0 1 0 0 2 0 0 0	0 1 1 A 0 1 0 0 0 0	0 0 2 0 0 0 0 0 1 1			
<i>Hynobius</i>	0 0 0 1 A A 2 0 1 1	0 1 1 A 1 0 0 0 0 0	? 0 2 0 0 0 0 0 1 1			
<i>Onychodactylus</i>	0 0 0 1 1 1 2 0 1 1	0 1 1 1 0 1 0 0 0 0	? 0 2 0 0 0 0 0 1 1			
<i>Plethodon</i>	0 0 A 2 1 1 2 1 1 ?	? 1 1 1 0 1 2 2 1 1	1 0 2 1 2 1 1 1 0 1			
<i>Desmognathus</i>	0 1 0 2 1 1 2 1 1 ?	? 1 1 1 0 ? 2 2 1 1	1 0 2 A 2 1 1 1 0 1			
<i>Amphiuma</i>	1 0 1 2 1 0 2 1 0 0	0 1 1 2 A 1 2 2 1 0	A 0 1 1 1 0 1 0 0 1			
<i>Proamphiuma</i>	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?			
<i>Rhyacotriton</i>	0 0 0 2 A 1 2 1 0 0	0 1 1 1 1 0 2 2 1 1	1 1 1 1 1 1 1 1 0 1			
<i>Siren</i>	? 0 1 2 1 1 1 1 0 0	? 1 ? 1 1 1 2 1 1 2	1 0 0 0 0 0 0 0 ? 0			
<i>Pseudobranchus</i>	? 0 1 1 1 1 1 1 0 0	? 1 ? 1 1 1 2 1 1 2	1 0 0 0 0 0 0 0 ? 0			
<i>Habrosaurus</i>	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?			
<i>Necturus</i>	? ? 1 2 0 0 2 1 0 0	0 1 1 2 1 ? 1 2 1 1	1 0 2 1 1 1 1 1 0 1			
<i>Proteus</i>	? ? 1 1 0 0 2 1 0 0	0 1 1 2 1 ? 1 2 1 1	1 0 2 1 1 1 1 1 0 1			
<i>Salamandra</i>	0 0 0 2 1 1 2 0 1 1	1 1 1 1 1 1 2 2 1 0	0 0 2 1 1 1 1 0 0 1			
<i>Taricha</i>	0 0 1 2 1 1 2 0 1 1	1 1 1 1 1 1 2 2 1 0	0 0 2 1 1 1 1 0 0 1			
<i>Tylototriton</i>	0 0 1 1 1 0 2 0 1 1	1 1 1 0 1 1 2 2 1 0	0 0 2 1 1 0 1 0 0 1			
<i>Dicamptodon</i>	1 0 0 2 1 1 2 0 1 1	0 1 1 1 0 0 2 2 1 0	0 1 2 1 1 1 1 1 0 1			
<i>Ambystoma</i>	1 0 0 2 1 1 2 0 0 0	0 1 1 1 0 0 2 2 1 0	0 1 2 1 2 1 1 1 0 1			
<i>Valdotriton</i>	? 0 0 2 1 1 ? ? 1 ?	0 ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?			
<i>Jeholotriton</i>	0 0 0 1 1 0 ? ? 0 ?	0 ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?			
<i>Liaoxitriton</i>	0 0 0 ? ? 0 ? ? 1 ?	0 1 1 0 0 ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?			
<i>Pangerpeton</i>	? ? ? ? ? ? ? ? 0 0	0 ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?			
<i>Chunerpeton</i>	0 0 0 1 1 0 ? ? 0 0	0 ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?			
<i>Beiyanerpeton</i>	1 0 0 ? ? 0 ? ? ? 0	0 ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?			
<i>Iridotriton</i>	? ? ? ? ? ? ? ? 1 1	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?			

	95	100	105
<i>Karaurus</i>	0 1 1 1 ? ? ? ? 0 ?	? 0 0 ? ?	
<i>Cryptobranchus</i>	1 1 1 1 0 0 0 0 0 1	0 0 0 0 0	
<i>Andrias</i>	1 1 1 1 0 0 0 0 0 1	0 0 0 0 ?	
<i>Hynobius</i>	1 1 1 1 1 0 0 0 0 0	0 0 0 0 ?	
<i>Onychodactylus</i>	1 1 1 1 1 0 0 2 0 ?	0 0 0 0 ?	
<i>Plethodon</i>	2 1 1 1 1 1 1 2 0 1	0 0 0 ? 0	
<i>Desmognathus</i>	2 1 1 1 1 1 1 2 0 1	0 0 0 ? 0	
<i>Amphiuma</i>	2 1 1 1 0 0 1 0 1 1	0 0 0 ? 0	
<i>Proamphiuma</i>	2 ? ? ? ? ? ? ? ? ?	? ? ? ? ?	
<i>Rhyacotriton</i>	2 1 1 1 1 0 1 1 0 1	0 0 0 ? ?	
<i>Siren</i>	2 1 1 0 0 0 0 0 1 1	1 0 0 0 0	
<i>Pseudobranchus</i>	2 1 1 0 0 0 0 0 1 1	1 0 0 ? ?	
<i>Habrosaurus</i>	? ? ? ? ? ? ? ? ? ?	? ? ? ? ?	
<i>Necturus</i>	2 1 1 1 0 0 1 0 0 1	0 0 0 1 1	
<i>Proteus</i>	2 1 1 1 0 0 1 0 1 1	0 0 0 1 1	
<i>Salamandra</i>	2 1 1 1 1 0 1 0 0 1	0 0 0 ? 0	
<i>Taricha</i>	2 1 1 1 1 0 1 0 0 1	0 1 0 ? ?	
<i>Tylototriton</i>	2 1 1 1 1 0 1 0 0 1	0 1 1 ? ?	
<i>Dicamptodon</i>	2 1 1 1 1 0 1 0 0 1	0 0 0 0 ?	
<i>Ambystoma</i>	2 1 1 1 A 0 1 0 0 1	0 0 0 ? 0	

<i>Valdotriton</i>	2	1	1	1	?	?	?	?	0	?	?	0	0	?	?
<i>Jeholotriton</i>	?	1	1	1	?	?	?	?	0	?	?	0	0	?	?
<i>Liaoxitriton</i>	?	1	1	1	?	?	?	?	0	?	0	0	0	0	?
<i>Pangerpeton</i>	?	1	1	1	?	?	?	?	0	?	?	0	0	?	?
<i>Chunerpeton</i>	1	1	1	1	?	?	?	?	0	?	0	0	?	?	?
<i>Beiyanerpeton</i>	1	1	1	1	?	0	?	?	0	?	0	0	?	0	?
<i>Iridotriton</i>	?	?	?	1	?	?	?	?	0	?	0	?	?	?	?