

RADIATION OF THE AMPHIBIA CAUDATA: ARE WE LOOKING TOO FAR INTO THE PAST?

Bruce G. Naylor
 Departments of Geology and Zoology
 The University of Alberta
 Edmonton, Alberta, Canada
 T6G 2E9

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ABSTRACT: The radiation of salamanders into their presently known families is suggested to have been an Early Cretaceous or Late Jurassic event. This would account for the absence of salamanders from the southern continents, except as recent invaders, and is consistent with what is presently understood of phylogenetic relationships and the fossil record. North America was probably the major center of evolution for the Amphibia Caudata and it is predicted that all pre-Cretaceous salamanders will prove to be primitive or unrelated to the families presently known from the Late Cretaceous through to the Recent.

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The order Caudata probably originated in the earliest part of the Mesozoic or late in the Paleozoic (Eaton, 1959; Estes, 1965; Bolt, 1977). The only plausible ancestors for salamanders are found in the upper part of the Paleozoic, whether one considers a lepospondyl (Gregory *et al.*, 1956; Carroll and Holmes, 1980) or a labyrinthodont ancestry (Eaton, 1959; Estes, 1965; Bolt, 1977). Although there is no present consensus as to the ultimate origin of the Caudata, this lies outside the following discussion.

EARLY RADIATION: THE EVIDENCE

Owing to the long span of time between the Paleozoic "ancestors" and the first fossil occurrences of abundant derived and diversified salamanders, it is uncertain whether evolutionary radiation occurred soon after the origin of the order or somewhat later. An hypothesis of early diversification might be supported, to a greater or lesser extent, by the following:

- 1) Acceptance of salamanders as the most primitive living tetrapods that, therefore, evolved very early.
- 2) Presence of acceptable ancestral groups in the Paleozoic.
- 3) Assumption that the origin of the order and its radiation into presently known families were linked.
- 4) Inferences derived from the biochemical "clock".

There are two distinct questions involved in discussing these evidences: the time of origin of the order and the time of radiation into extant and fossil families. There must have been organisms ancestral to salamanders very long ago and it is probable that salamanders originated in the latest Paleozoic or earliest Mesozoic (see above). However, there would seem to be no reason that the diversification necessarily followed immediately upon the appearance of what would be retrospectively called the first salamander.

The first three inferences are, therefore, not really relevant to the problem of the time of radiation. In addition, the primitive nature of salamanders is questionable: they are highly derived with respect to the truly primitive (ancestral) Paleozoic lineages. Nevertheless, the primitiveness of salamanders has little relevance as to when their evolutionary radiation occurred and only the information from investigations of similarities and differences between proteins remains.

Data from the study of proteins have begun to be applied to systematic problems. The information gained from the various techniques is potentially and actually of great help in phylogenetic research (e.g., Frelin and Vuillemier, 1979). In spite of this promise, indications are that the unaided use of protein differences to

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estimate times of separation is difficult to justify. The biochemical "clock" is based on an hypothesis of neutral mutation-random drift, which is itself open to serious question (e.g., Ayala, 1976; Clarke, 1970; Johnson, 1974). In light of the poor fossil record for salamanders, this failure is unfortunate.

Utilizing micro-complement fixation to detect amino acid differences between proteins, Salthe and Kaplan (1966) suggested that radiation into modern families of salamanders began "sometime between the early Triassic [220 million years] and mid-Jurassic [160 million years]." The earlier date was provided by antisera from one rabbit, whereas the later date came from a second individual. Maxson and Wilson (1979) indicate the split between *Ambystoma* and a hypothetical amphiumid-plethodontid stock to have occurred almost 200 million years ago (latest Triassic). However, Radinski (1978) and Uzzell and Pilbeam (1971) have shown that the fossil record (the only true insight into the past) contradicts at least some of the inferences from the "clock". Critics such as Carlson *et al.* (1978) have presented rebuttals, but they have developed a potentially unfalsifiable position by rejecting the fossil record as a relevant test of times of origin.

Constancy of amino acid substitution, at least over relatively long time periods, is an assumption demanded by the biochemical "clock". Owing to the fact that almost all characters for which data are available can be demonstrated to have evolved at greatly varying rates (Simpson, 1944), it does not seem reasonable to hypothesize constancy of rate for characters for which this cannot be easily tested. In addition, there is good evidence that some proteins have not evolved at constant rates (Goodman, 1976; Jukes and Holmquist, 1972; Moore *et al.*, 1976). In what is probably as close to a direct test of the rate of protein evolution as it will be possible to develop, Lessios (1979) demonstrated marked differences in the rate of substitution in Panamanian sea urchins. Vawter *et al.* (1980) have questioned the conclusions of Lessios (1979), arguing that the clock is a "probabilistic statement" that is tested "if the predictions are correct a great majority of the time." Scientific testing does not operate in this manner (Popper, 1968) and the "clock" is simply a tool that may or may not work in any given case.

Estimates of substitution rates in protein evolution for mammals are often used in estimating times of divergence in other groups (e.g., Maxson and Wilson, 1979). This procedure is suspect, adds yet another level of uncertainty and assumption, and has been shown to be invalid for lizards (Wyles and Gorman, 1980). The primary data for estimating evolutionary events are, and will remain, derived from paleontology and geology. If a good fossil record is available, as for many mammals, it is possible to make reasoned use of biochemical evidence in the study of phylogenetic events. However, for groups as under-represented in the record as are salamanders, it is probably best to avoid such methods for timing originations. I conclude, therefore, that the biochemical "clock" does not provide evidence presently bearing directly on the time of origin of the various modern families of salamanders.

ESTIMATING THE TIME OF RADIATION

The following data are of direct and necessary importance to suggesting a time for the radiation of the Caudata:

- 1) Fossil occurrences in time and space.
- 2) First known occurrences, providing minimum times of origin.
- 3) Present familial distributions and natural history.
- 4) Continental positions during the Mesozoic and Cenozoic.
- 5) Distributions of land bridges and seaways.
- 6) Phylogenetic reconstructions.

Except for representatives of a single tribe of plethodontids, which are recent invaders into South America (Wake, 1966; Wake and Lynch, 1976), the most striking fact of the distribution of extant salamanders is their restriction to the northern continents (Fig. 1). Occurrences of fossil taxa also reflect this — a "Urodèle de

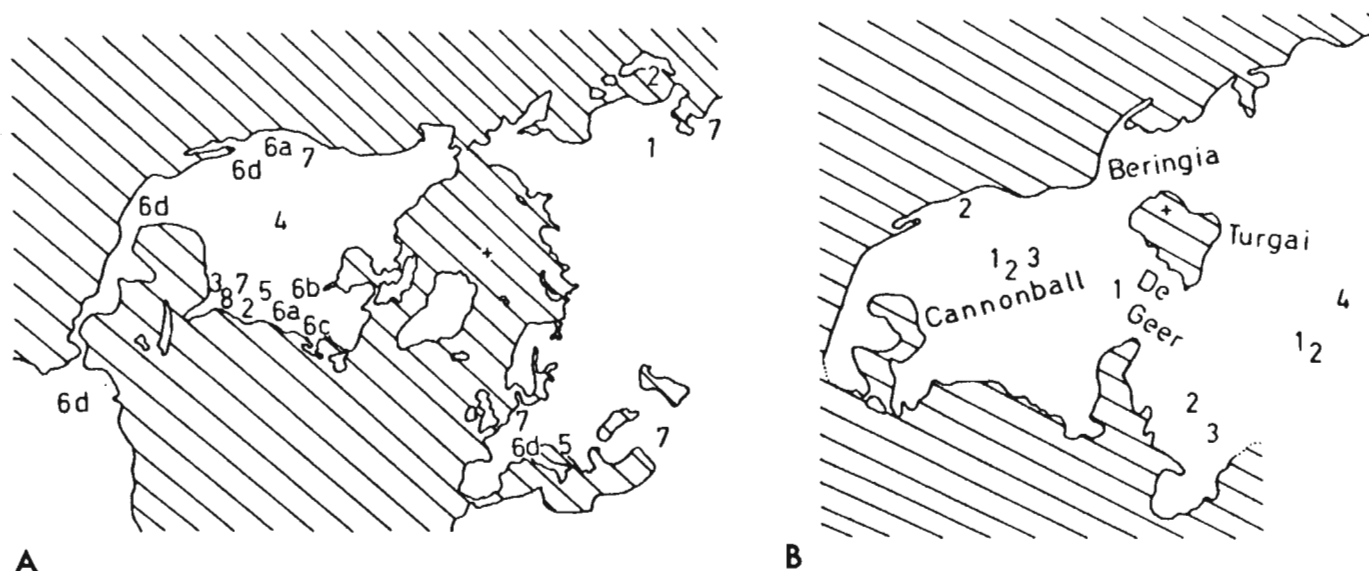


Figure 1. A. Polar projection (Smith and Briden, 1977) with distributions of extant families: 1, Hynobiidae; 2, Cryptobranchidae; 3, Amphiumidae; 4, Ambystomatidae; 5, Proteidae; 6, Plethodontidae (6a, Plethodontini; 6b, Desmoquathini; 6c, Hemidactyliini; 6d, Bolitoglossini); 7, Salamandridae; 8, Sirenidae. B. Polar projection of continental shelf margins during Late Cretaceous and Paleocene time (Smith and Briden, 1977) with major paleogeographical features labelled: 1, Scapherpetontidae; 2, Batrachosauroididae; 3, Prosirenidae; 4, Karauridae.

grande taille" is reported from the Upper Cretaceous of Niger (De Broin *et al.*, 1974), but the proper assignment and relationships of this specimen are not known (although it is procoelous and otherwise sirenid-like; R. Estes, personal communication). One hypothesis that would account for these facts is that the radiation of salamanders occurred subsequent to the time of continental separation during the Mesozoic. Salamanders are intolerant of salt water (Anderson, 1960) and any marine barrier, even if narrow, would effectively stop dispersal to the southern, Gondwanaland continents.

If a late radiation from an ancestral group isolated in the northern hemisphere is reasonable, it suggests that evolutionary diversification of caecilians (Gymnophiona) and frogs (Anura) occurred at times and conditions different from those of the Caudata. Caecilians are pan-tropical, whereas anurans are effectively of world-wide occurrence, which may indicate a radiation of these two orders significantly earlier than is the case for salamanders.

Consideration of paleocontinental reconstructions (e.g., Smith and Briden, 1977) indicates that by Late Jurassic (140 million years) or Early Cretaceous (120 million years) time connection between Laurasia and Gondwana was at least tenuous. Therefore, diversification after the Late Jurassic in the northern continents would account plausibly for the absence of salamanders from the Gondwanaland area. Drewry *et al.* (1974) have argued that it is theoretically unlikely that the world's climatic belts have shifted significantly through the Phanerozoic. They reinforce this suggestion by geological evidence. If true, this would indicate an additional barrier to the southward dispersal of salamanders, which are primarily adapted to cool, damp, climates.

In addition to inferences from palaeogeography and from fossil and Recent distributions, the scanty evidence from the fossil record of salamanders is relevant. Although earlier remains are known (Dollo, 1884; Hecht and Estes, 1960; Estes, 1969c; Ivachnenko, 1978), a diversity of taxa only appear in uppermost Cretaceous and basal Tertiary sediments. In rocks of earlier times, the rare fossils are very primitive and/or not assignable to any of the lineages known from later formations. One of these groups, the Prosirenidae, is probably an early derivative from the Caudata or

not related to salamanders (see data in Estes, 1969c; Estes and Hoffstetter, 1976; Naylor, 1979a).

Owing to the flood-plain sediments in which they occur, specimens from the Upper Cretaceous and Paleocene are almost all from derived, neotenic lineages, but they necessarily indicate the presence of allied, more "normal" salamanders from which they must have evolved (Hecht and Edwards, 1977; Naylor, 1978a). Included in this assemblage are representatives of extant paedomorphic families — the Amphiumidae (Estes, 1969b), Cryptobranchidae (Naylor, 1981a), Sirenidae (Estes, 1964, 1976), and Proteidae (Naylor, 1978b). Two extinct families, the Scapherpetontidae and Batrachosauroididae, are also common in rocks of this time (Fig. 1). Batrachosauroidids may represent the lineage that gave rise to proteids, whereas scapherpetontids are closely related to ambystomatids (Estes, 1969a, 1975; Hecht and Edwards, 1977; Naylor, 1978a, 1978b, 1979).

Members of more "typical" families begin to appear in the lower Tertiary: ambystomatids (including *Dicamptodon* and *Rhyacotriton*) from a North American Paleocene trackway (Peabody, 1954), plethodontids from the Miocene of North America (Tihen, 1968; D.B. Wake, personal communication), and salamandrids from the Paleocene of Europe (Estes et al., 1967). Although admittedly depending largely on negative evidence, the fossil record is in agreement with an hypothesis of late radiation for the Caudata. No facts necessitate suggesting that the diversification that led to any of the above families (the primitive hynobiids excluded) occurred much before the Late Cretaceous.

Except for the derived, aquatic lineages, the diet of salamanders consists largely of insects. It seems likely that the diversification of insects into their numerous taxa was, to some extent, linked with the origin and radiation of the flowering plants (see Regal, 1977). The latter event occurred during the Late Cretaceous and early Tertiary (Banks, 1972), and it is reasonable to suppose that at least some of the selective pressure leading to the radiation of salamanders would have come from the co-evolution of insects and angiosperms. Considering known diets and functional specializations of the feeding apparatus, this is probably especially true of the Plethodontidae (Dunn, 1926; Lombard and Wake, 1977) and some of the Salamandridae (Özeti and Wake, 1969). A similar argument has been advanced with respect to the origin of mammals of tribosphenic grade (Clemens, 1970).

I have suggested elsewhere (Naylor, 1981a) that congruences between fossil and Recent distributions and first occurrences in the stratigraphic column for salamandrids and cryptobranchids indicate common causal factors. These would be the canalizing influences of paleogeography (Lillegraven, 1974; McKenna, 1975; Russell, 1975) operating on evolving populations and indicating similar times for evolutionary events and dispersals. It is probable that the latter parts of the Cretaceous and early Tertiary saw the development of the main patterns of distribution that are observed today for salamanders.

CONCLUSIONS AND PREDICTIONS

There must have been a basal group of salamanders in existence throughout the Mesozoic on the northern continents, which eventually gave rise to the later families. Based on present understanding, these would probably have been hynobiid-like (Dunn, 1922; Noble, 1931; Regal, 1966; Wake, 1966; Naylor, 1978a) and, perhaps, of primitive ambystomatid-like habit and structure in North America. There would probably be ultimately sterile lineages produced during the Triassic and Jurassic, with the Prosirenidae perhaps being one such group. The model presented here merely predicts that these groups were not closely related to later salamanders. The recent discovery in Russia of a very primitive salamander named *Karaurus* by Ivachnenko (1978) perhaps samples a basal salamander lineage.

Figure 2 diagrams a phylogenetic hypothesis of the relationships of fossil and Recent salamanders, together with the known time ranges for each family. This

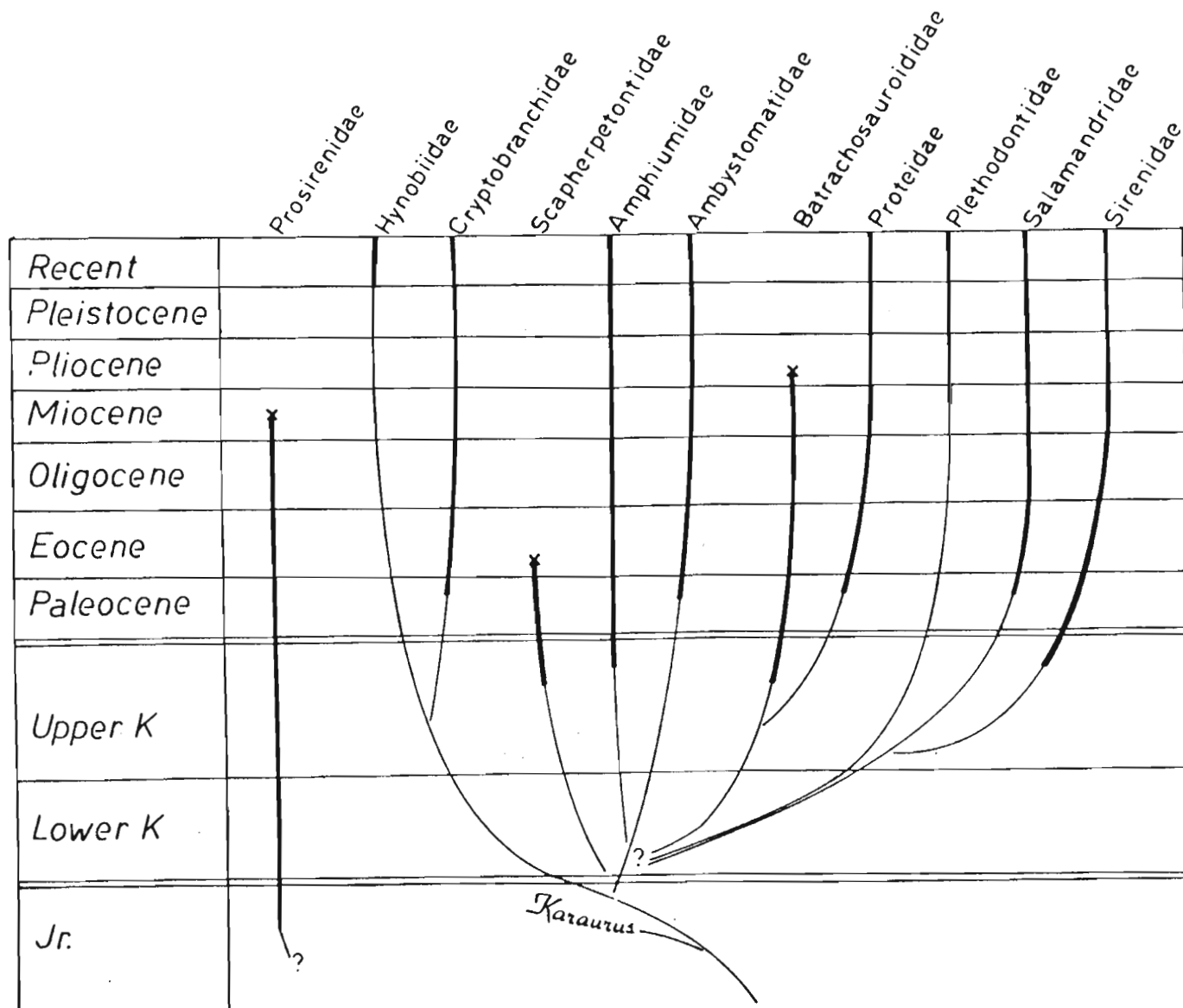


Figure 2. Phylogenetic reconstruction of the Amphibia Caudata, with known time ranges and proposed time of radiation. First occurrences from Estes (1969b, 1970, personal communication), Estes and Hoffstetter (1976), Ivachnenko (1978), Naylor (1978b, 1981a,b), Naylor and Krause (1981), Peabody (1954), Tihen (1968), and D.B. Wake (personal communication).

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phylogeny differs somewhat from that presented by Hecht and Edwards (1977) and is based on an unpublished analysis that includes new data from the trunk region (Naylor, 1978a). Differences between the two schemes are not relevant to the present discussion and the figure is presented to give known time ranges and to show the possible timing of the radiation.

Several predictions follow directly or indirectly from the above discussion:

- 1) Salamanders from pre-Cretaceous rocks will be hynobiid-like.
- 2) Representatives of living families will be found in pre-Campanian (pre-Judithian) rocks, but (except for hynobiids) not in formations significantly older than the Cretaceous.
- 3) Prosirenids will prove to be a side-branch from primitive salamander ancestry, or will prove to be unrelated to salamanders.
- 4) Much of the evolution of the Caudata occurred in North America and fossil discoveries will continue to reflect this.

Prediction four is the most tentative of these suggestions, but is nevertheless in agreement with the fossil record. It partially reflects my understanding of the phylogenetic relationships of the families of salamanders, together with the inferred paths of dispersal. Nessov (1979) reports a supposedly Turonian herpetofauna from central Asia (Besh-Toobe Mountains), which includes two unidentified genera of Scapherpetontidae and two of Batrachosauroididae. This fauna appears to be of Lancian aspect (compare Estes, 1964) and secure dating must await discovery of mammalian fossils. It is, nevertheless, of note in documenting a faunal assemblage all but identical to those found in the latest Cretaceous of central North America. All of the predictions should be easily and readily testable as future paleontological discoveries are made, although within the constraints of the lack of sediments in many areas.

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