

A new Ambystomatid salamander, *Dicamptodon antiquus* n.sp., from the Paleocene of Alberta, Canada

BRUCE G. NAYLOR

Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alta., Canada T0J 0Y0

AND

RICHARD C. FOX

Laboratory for Vertebrate Paleontology, Departments of Geology and Zoology, University of Alberta, Edmonton, Alta., Canada T6G 2E9

Received June 4, 1992

Revision accepted January 28, 1993

The discovery of a skull and partial postcranial skeleton of *Dicamptodon* from northern Alberta is the earliest certain record of the subfamily Dicamptodontinae. The specimen comes from Late Paleocene lake sediments, which also contain the remains of fish and plants. The close resemblance of the specimen to larvae or neotenes of extant *Dicamptodon* shows that this family exhibits the common trend of extreme conservatism known from other salamanders. The specimen is found in association with floral assemblages, confirming Nussbaum's hypothesis of the origin of the genus in northwestern North America.

La découverte d'un crâne et d'un fragment postcrânien du squelette de *Dicamptodon*, dans le nord de l'Alberta, représente le registre fossile le plus ancien et le plus authentique dans la sous-famille des Dicamptodontinae. Le spécimen a été trouvé dans des sédiments lacustres d'âge paléocène tardif, qui contenaient en outre des fragments de poissons et de plantes. La ressemblance remarquable de ce spécimen avec l'état larvaire ou néoténique du *Dicamptodon* existant actuellement indique que cette famille exhibe, elle aussi, cette tendance commune du conservatisme extrême reconnu chez les autres salamandres. Ce spécimen a été trouvé en association avec des assemblages floraux, ce qui confirme l'hypothèse de Nussbaum sur l'apparition du genre dans le nord-ouest de l'Amérique du Nord.

[Traduit par la rédaction]

Can. J. Earth Sci. 30, 814–818 (1993)

Introduction

The specimen described here (UALVP 32387) is an incomplete skeleton, including skull, lower jaws, left pectoral limb, and the anteriormost 14 vertebrae of a gilled (neotenic or larval) salamander, closely resembling unmetamorphosed individuals of the Recent *Dicamptodon* (Ambystomatidae) from the Pacific Northwest of North America. The fossil, however, comes from west-central Alberta, east of the Rocky Mountains. It was found in lacustrine silty shales of Paleocene age, in association with the skeletal remains of the earliest discovered pike, *Esox tiemani* Wilson, 1980, and undescribed osteoglossomorph and percopsid fishes (M.V.H. Wilson, personal communication). The strata containing the fossils have been referred to the continental Paskapoo Formation, approximately 62 Ma old (Christophel 1976).

UALVP 32387 is the first known articulated fossil specimen of *Dicamptodon* and is described below as the type specimen of a new species of the genus. Peabody (1959) described trackways from the Pliocene of California that he referred to *Dicamptodon* sp. Peabody (1954) also described Paleocene trackways from Montana that are very similar to those of modern *Dicamptodon*. A new genus, *Ambystomichnus*, was created for these tracks, previously called *Ammobatrachus montanensis* by Gilmore (1928) because of a perceived similarity to Permian tracks. No skeletal materials of extinct *Dicamptodon* have previously been recognized.

Discovery of a *Dicamptodon* closely similar to living species, but occurring in rocks of Paleocene age, indicates sustained morphological stasis of the genus and a taxonomic longevity comparable with what appears to characterize evolutionary rates in salamanders generally. Of salamander genera containing living species, only the neotenic *Cryptobranchus* (Cryptobranchidae), *Amphiuma* (Amphiumidae), and *Necturus* (Proteidae) accompany *Dicamptodon* in being known

from skeletal fossils as old as Paleocene (Estes 1981).

Modern *Dicamptodon ensatus* usually undergo normal metamorphosis; an adaptation that is primitive among salamanders generally, although *Dicamptodon copei* normally reaches maturity without metamorphosis (Nussbaum 1976). *Dicamptodon aterrimus* has been indicated to be a distinct species on the basis of protein variations (Daugherty et al. 1983). However, modern protein variation is not susceptible to comparison with the fossil specimen here described. All records of salamanders stratigraphically older than Paleocene are at least partially paedomorphic, and hence of derived species. Of salamanders already known from the Paleocene, adult *Cryptobranchus*, *Necturus*, and *Amphiuma*, as well as the extinct *Piceoerpeton* and *Opisthotriton*, retain some larval characteristics. Other Paleocene salamanders must have undergone complete metamorphosis, but all belong to extinct genera and are known from material too fragmentary to provide morphological evidence for metamorphosis.

Systematic paleontology

CLASS Amphibia

ORDER Caudata

SUBORDER Ambystomatoidea

FAMILY Ambystomatidae

SUBFAMILY Dicamptodontinae

Dicamptodon antiquus n.sp.

(Fig. 1)

Holotype

UALVP 32387, an incomplete skeleton, having skull, left pectoral limb, and 14 vertebrae.

Horizon and type locality

Upper Paleocene, Paskapoo Formation, NE 1/4, S 6, T 63, W6, Alberta, Canada (Location 1 of Wilson 1980).

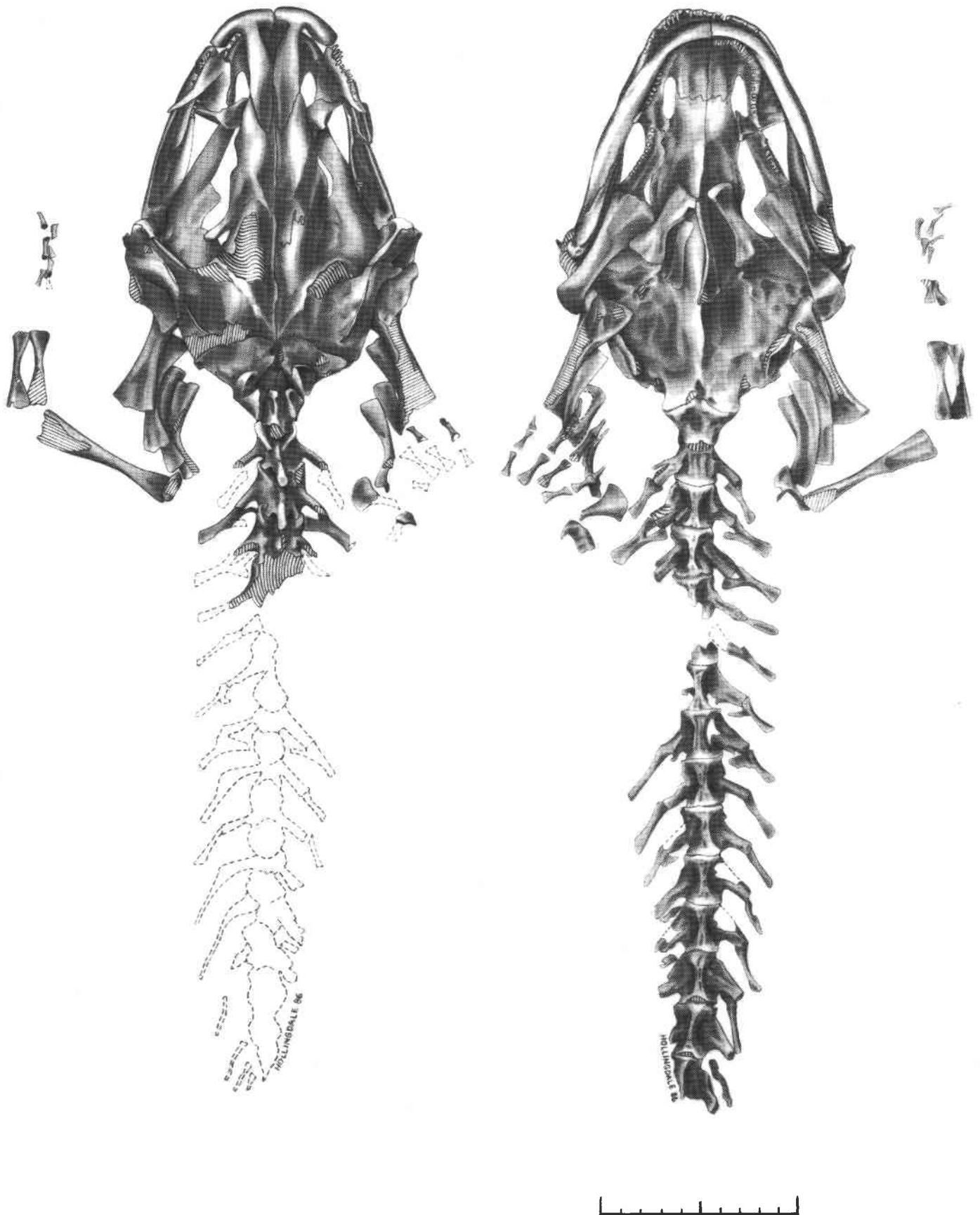


FIG. 1. Dorsal and ventral views of UALVP 32387, *Dicamptodon antiquus*, from the late Paleocene of northern Alberta. The skull bones are crushed and exact outlines of the various elements are often uncertain. Scale represents 1 cm.

Diagnosis

An extinct species of *Dicamptodon* differing from extant species in presence of palatal teeth on the anterolateral portion of the pterygoid, a more oblique orientation of the vomerine tooth row, and well-developed alar processes on the ventral arms of the rib-bearers.

Description

General features

The skull of UALVP 32387 is well preserved, but flat, having suffered postmortem dorsoventral compression from compaction of the enclosing sediments. The lower jaws and their articulation with the quadrates are also well preserved. The hyobranchial apparatus extends beyond the skull posterolaterally and is robustly developed, as in larval and nonmetamorphosing salamanders generally; the well-ossified apparatus is indicative of a paedomorphic individual. Of the left pectoral limb, the humerus, radius, and ulna are present, as are phalanges from what appear to be two digits; the carpus is missing and evidently was cartilaginous, as is the case in larval *D. ensatus*. Large paedomorphs of this species calcify the carpals, as do small adults of the neotenic *D. copei* (i.e., those with a snout-vent length of only 70 mm, Nussbaum (1976), which the fossil specimen obviously exceeds). A small piece of bone proximal to the humerus may represent the scapulo-coracoid. Of the right pectoral limb, phalanges of all four digits are present, as well as part of an indeterminate limb bone and what is probably the scapula. Parts of 14 vertebrae, including the atlas, remain with the specimen; individual vertebrae are poorly preserved, but the vertebral row is in an apparently in-life position, extending directly posteriorly from the skull. The vertebral row terminates at the edge of the slab on which the fossil was found; evidently, more posterior parts of the skeleton than these had been fossilized originally, but either were not collected or were lost thereafter. The counterpart of the specimen, which would have retained parts of the vertebrae, ribs, and perhaps the limbs, is unknown.

Skull

In dorsal view, the skull from the tip of the snout to the quadrates is approximately triangular, resembling, in these proportions, the skull in paedomorphic salamanders, such as *Necturus*, but still more closely resembling the skull in larval *D. ensatus*, which is somewhat broader. The skull of the neotenic *D. copei* is more angular and sculptured than in the larvae of the genus. The skull of UALVP 32387 is well ossified, as in *D. ensatus*, which contrasts to the weak ossification of the skull in *Rhyacotriton* (Estes 1981), the only other living dicamptodontine genus and apparently the nearest living relative of *Dicamptodon* (Estes 1981; Naylor 1978). Posterior to the quadrate condyles on UALVP 32387, the skull outline tapers gradually towards the midline and then turns in more sharply at the occiput. The occipital condyles (exoccipitals) are distinctly stalked, as in larvae of extant *Dicamptodon*.

The snout is bluntly rounded. The premaxillaries are paired, the primitive state in salamanders, and differ from the fused premaxillary in, for example, *Amphiuma*. The pars dentalis and pars facialis (premaxillary spine) are robust; they join one another lateral to the midline and enclose a central triangular fontanelle, a larval character. In adults of the neotenic *D. copei* the fontanelle is closed. The pars dentalis extends from the midline posteriorly along a broad curve to its articulation with the maxillary, rather than being restricted to the end of the

snout, as in *Amphiuma*, sirenids, or *Opisthotriton* (Batrachosauroididae). Whether more than one row of teeth is present on the premaxillary (a feature of larval *Dicamptodon*) is uncertain, but only a single row appears to have been present. The pars facialis is narrow and elongate, unlike the short, broad spine in cryptobranchids. Distal to the fontanelle, the premaxillary spines join along a midline suture beginning at about one-third of their length posteriorly and then diverge slightly from one another at their distal tips. In *Necturus*, which lacks a fontanelle, the spines are joined for a short distance proximally and then diverge from one another through their remaining distal lengths. On UALVP 32387, the premaxillary spines meet the frontals broadly, best seen on the right side where the premaxillary has been displaced slightly from its overlap with the frontal, exposing part of an extensive surface of articulation beneath.

The maxillaries are slightly displaced, having been rotated outward, exposing their teeth laterally (by contrast, the paedomorphic *Necturus*, *Proteus*, and *Siren* have lost the maxillary entirely). The pars dentalis tapers posteriorly, less so anteriorly, where it extends little if at all anteriorly of the pars facialis. The pars facialis has been crushed and its limits are not clearly seen on either side of the skull, but it appears to have been a relatively long plate, arising from much of the length of the pars dentalis. The maxillary teeth are short, slender, and conical and are probably not pedicellate, although the condition can not be clearly seen. Their shape is like that in larval *D. ensatus*, contrasting to the blade-like teeth in metamorphosed adults (Estes 1981).

The long and slender frontals, although crushed, are somewhat convex upwards across their transverse width, while being depressed along the midline suture, the latter is a post-mortem distortion. They extensively overlap the parietals posteriorly. Posteriorly on each frontal, a V-shaped ridge, with its apex directed anteriorly, probably marks the maximum encroachment on to the dermal roof of the origin of the mandibular adductor musculature. The parietals are of the normal shape in salamanders, articulating anteriorly with the frontals and sending a broad process laterally to the squamosal; although the suture with the squamosal can not be identified on the specimen. A V-shaped ridge, with its apex at the midline and directed posteriorly, probably marks the posterior extent of the origin of the mandibular adductors on the parietals.

The squamosal extends anterolaterally over the quadrate and, in life, must have extended ventrally with the quadrate, but owing to the postmortem crushing of the skull, the quadrate and squamosal together have been brought into the same horizontal plane as the remainder of the dermal skull roof. A prominent crest extends down the limb of the squamosal, marking the posterolateral limits of the origin of the mandibular adductors on the roofing bones.

The quadrate is visible on both sides of the skull in dorsal view and, like the squamosal, is directed anterolaterally; proximally, it appears to be a somewhat compressed, slender pillar, while distally it flares out into a concave cotyle, which receives the condyle of the articular.

Prefrontals are present on both sides, exposed between the frontals and the pars facialis of the maxillaries; in UALVP 32387, they appear to be overlapped by the maxillary, probably as a consequence of the crushing of the skull. The shape of the prefrontal cannot be made out in dorsal view.

Parts of the vomers and pterygoids are exposed dorsally as

a consequence of compression of the skull roof down onto the palate, but no morphologically or taxonomically significant features of these bones are evident dorsally. The vomerine tooth row extends posteriorly in a more oblique fashion than is the case for modern *Dicamptodon*. The pterygoid is a long, narrow bone extending anteromedially from the region of the suspensorium to the posterolateral border of the vomer. The vomerine tooth row extends onto the lateral margin of the pterygoid as a single line of small teeth. This contrasts with many, but not all, modern *Dicamptodon*, in which the pterygoid in larval and paedomorphic individuals remains edentulous. Neither the lacrimal, which develops as a tube in close association with the prefrontal in larval *D. ensatus* (Larson 1963), nor the nasal and septomaxillary, which only develop at metamorphosis in living *Dicamptodon* (Larson 1963), have been recognized on UALVP 32387.

Lower jaw

The lower jaws are exposed on either side posteriorly of the maxillary; the articular condyles are only slightly medial of the quadrate cotyles, implying that there has been little lateral distortion of the sides of the skull during compaction. The dentary may have been the only toothed bone of the lower jaw, although on the left, a bone with teeth in the position of a coronoid is exposed. A toothed splenial is a paedomorphic character, occurring in *Necturus*, for example, but not in larval *Dicamptodon*. However, a bone corresponding to the tooth-bearing bone is not seen on the right side of the fossil, and the bone on the left may more reasonably be interpreted as a broken part of the dentary, displaced posteriorly. The Meckelian groove is long and widely open dorsally, but is bounded medially by the prearticular, which rises high above the margin of the jaw lateral to the groove; these same features of the groove and its surrounding bones are seen in larval *Dicamptodon*, but not in *Cryptobranchus*, *Necturus*, *Amphiuma*, or the sirenids.

Hyobranchial apparatus

The hyobranchium is well ossified and robust. Ceratohyals, the first and possibly second ceratobranchials, second basibranchial, and all four epibranchials are heavily ossified. Extensive cartilaginous regions remained, as indicated by the ends of the hyobranchial elements. Ceratohyals are the largest of the hyobranchial bones, with straight shafts and ends expanded symmetrically on either side of the axis of each shaft. The more medially situated first ceratobranchials are significantly smaller. If correctly interpreted, the second ceratobranchials are smaller yet. Although no trace of the first basibranchial remains, the second basibranchial, although slender, is well ossified and elongate.

The posthyoid gill arches are less robust than the ceratohyal and less well ossified, especially at their ends. They are curved medially. Epibranchial 1 is the longest; epibranchial 2 and 3 appear to be approximately equal in length, but ossification of their ends is incomplete, and hence their possible further extent in cartilage is unknown.

Vertebral column

Although 14 vertebrae are preserved, postmortem crushing makes the analysis of features difficult. Crushing obscures the features of the atlantal neural arch, but it appears to have been fully finished in bone. The atlas appears to lack an odontoid process which, if true, stands in contrast to the robust process of modern *Dicamptodon*. Neural spines on the following vertebrae are tubular with the tips having been finished in car-

tilage. The rib-bearers are elongate and the ribs bicapital, as in modern *Dicamptodon*. The ventral rib-bearers possess well-developed alar processes, a feature differing from modern members of the genus, but often correlating with an aquatic habit in other salamanders.

Pectoral limb

The left pectoral limb is represented by the humerus, ulna and radius, and phalanges of two digits. The humerus is elongate and slender, preserved three-dimensionally, except distally where it has been somewhat crushed. In preservation, it has been rotated such that its anterodorsal surface appears to be uppermost. The proximal end appears to have been well ossified (it is partly obscured), the distal end less so, as might be expected in a larva. The ends are wider than the more central parts of the shaft, and the distal end is the more expanded in this view; normally in salamanders, the proximal end of the humerus is wider, but in UALVP 32387, the greater width of the proximal end is probably directed ventrally, into the rock matrix and is, hence, concealed. A small tubercle is located proximally on the anterior edge of the humerus, and a faint ridge is developed somewhat distal and posterior to it. The ulna and radius are side-by-side, in what must be very close to their in-life positions. Both are well ossified throughout their lengths and are expanded at either end, the ulna more so proximally and the radius distally, as is normal in salamanders.

No trace of the carpus can be seen. The phalanges that remain are arranged in two approximately parallel rows that appear not to have been displaced distally from their in-life position relative to the distal ends of the ulna and radius. There are three phalanges in each row; little detail can be seen of them, except that they appear to have been well ossified. The phalanges present on the right side reveal nothing of significance morphologically or taxonomically.

Comparisons with *D. ensatus* and *D. copei*

In its proportions, the skull of UALVP 32387 in dorsal aspect closely resembles that in larval *D. ensatus*, differing from the skull of a cleared and stained specimen (UALVP 14415) in being somewhat longer relative to its width at the quadrates. Prior to compression, the skull on UALVP 32387 was likely to have been narrower still, but the snout itself is undistorted and blunt, in contrast to the acuminate snout in *Necturus*, *Amphiuma*, or *Opisthotriton*, for example, but like that in larval *D. ensatus*.

On UALVP 14415, the elongate, separated premaxillary spines are slender and fail to meet medially, differing thereby from the spines on UALVP 32387. Larson's (1963, Pl. I) illustration of the skull of a larval *D. ensatus* shows broader premaxillary spines that still remain separate at the midline (the figured larva is presumably older than the specimen available to us), as in the fossil.

The quadrates are more robustly constructed on UALVP 32387 than on UALVP 14415, but this is probably a function of ontogenetic stage of development. Perhaps of greater significance are the different proportions of the occiput: in modern larval *D. ensatus*, the occiput is stalked, drawn out posteriorly to its termination on the condyles, which is not the case on UALVP 32387. However, the appearance of this region in the fossil may be in part owing to postmortem distortion of the bones in the area. In any case, these few differences are the only ones that clearly distinguish UALVP 32387 from the skull in unmetamorphosed *D. ensatus* in dorsal aspect.

The separated premaxillaries, with elongate spines forbid assignment to the Hynobiidae, Cryptobranchidae, Amphiumidae, Plethodontidae, Proteidae, Batrachosauroididae, Sirenidae, or Salamandridae. Within the Ambystomatidae, the separated premaxillaries, with spines converging medially towards to rear, as well as the association of the vomers and pterygoids, show clear assignment to *Dicamptodon*.

Although sometimes considered as a separate family, Dicamptodontidae (together with *Rhyacotriton*) *Dicamptodon* shares derived features with ambystomatines. These features include internal fertilization by means of a spermatophore, as well as the system of trunk musculature. It is distinguished by means of primitive features (Naylor 1978). Consequently, we prefer to retain the traditional classification within the family Ambystomatidae.

Discussion

Paleogeography and evolution

Nussbaum (1976) has presented an appealing scenario for the origin and distribution of *Dicamptodon*, linking the genus with the evolution and distribution of the Arcto-Tertiary Geoflora, starting with the Late Cretaceous. According to this hypothesis, the northern, moist Arcto-Tertiary Geoflora, dominated by redwood forests, has always been the evolutionary center of *Dicamptodon*. During the Cretaceous, with the limitation of the Arcto-Tertiary Geoflora to north of 52°N, Nussbaum envisaged the *Dicamptodon* lineage as evolving from hynobiid ancestry in arctic North America.

With the cooling trends seen during the Tertiary, the Arcto-Tertiary Geoflora and, consequently, *Dicamptodon* were ultimately restricted to the Pacific Northwest of the United States (Nussbaum 1976). The presence of the trackways, called *Ambystomichnus* in the Paleocene Fort Union Formation of Montana, in association with this flora was suggested as confirmation of this hypothesis. Finally, the redwood-dominated flora of the Oligocene John Day Formation in Oregon, together with the presence of *Palaeotaricha* (now *Taricha*, see Naylor 1979), was held to indicate the establishment of the northwest salamander fauna by late Oligocene.

Dicamptodon antiquus comes from the Paleocene Paskapoo Formation of north-central Alberta. Fossil plants from the Smoky Tower area were described by Christophel (1976), and the flora is consistent with the Nussbaum hypothesis. The sedimentology and two paleofloras described by Christophel indicate the presence of standing water, as well as the components of the plant community apparently required by modern *Dicamptodon*. The Smoky Tower floras show similarities to Fort Union floras in the United States, although they are of lesser diversity, confirming the correlation of *Dicamptodon* with the Arcto-Tertiary Geoflora.

The European genera *Bargmannia* (Miocene), *Geyeriella* (Paleocene), and *Wolterstorffiella* (Paleocene), and the Eocene genus *Chrysotriton* from North Dakota have been referred to the same subfamily as *Dicamptodon* (see Estes 1981). Although it is possible that the single North American and the three European genera are derived relatives of dicamptodontines, the discovery of a Late Paleocene member of the modern genus calls these assignments into question. It is perhaps unexpected to find dicamptodontines in Europe, which

has yet to produce any members or relatives of either the Dicamptodontinae or Ambystomatinae (although the de Geer bridge was present during Paleocene time). It perhaps is just as reasonable to consider the Paleocene and Miocene specimens currently assigned to the Dicamptodontinae as derived (in terms of hypertrophied anterior basapophyses) hynobiids. Certainly there is little in the published descriptions or figures to forbid a closer relationship to hynobiids.

Material examined

In addition to the fossil specimen, two cleared and stained skeletons of *D. ensatus* and a single cleared and stained skeleton of *Rhyacotriton* were studied. In addition, skeletons and cleared and stained specimens of *Ambystoma macrodactylum* (cleared and stained only), *Ambystoma gracile*, *Ambystoma maculatum*, *Ambystoma jeffersonianum*, *Ambystoma opacum*, *Ambystoma talpoideum*, and *Ambystoma tigrinum* provided comparative information.

Acknowledgments

We thank Dr. M.V.H. Wilson for permission to describe the specimen and for access to locality and stratigraphic information. Allan Lindoe prepared and Dianne Holingdale drew the specimen. Research support was provided by a Natural Sciences and Engineering Research Council of Canada operating grant to R.C.F. and by funds from the Department of Culture and Multiculturalism, Government of Alberta.

- Christophel, D.C. 1976. Fossil floras of the Smoky Tower locality, Alberta, Canada. *Palaeontographica Abteilung B Palaeophytologie*, **157**: 1–43.
- Dagherty, C.H., Allendorf, F.W., Dunlop, W.W., and Knudsen, K.L. 1983. Systematic implications of geographic patterns of genetic variation in the genus *Dicamptodon*. *Copeia* **1983**(3): 679–691.
- Estes, R. 1981. Gymnophiona, Caudata. *Handbuch der Palaeoherpetology*, Part 2.
- Gilmore, C.W. 1928. Fossil footprints from the Fort Union (Paleocene) of Montana. *Proceedings of the United States National Museum*, **74**(5): 1–4.
- Larson, J.H. 1963. The cranial osteology of neotenic and transformed salamanders and its bearing on interfamilial relationships. Ph.D. dissertation, University of Washington.
- Naylor, B.G. 1978. The systematics of fossil and Recent salamanders (Amphibia: Caudata), with special reference to the vertebral column and trunk musculature. Ph.D. dissertation, The University of Alberta.
- Naylor, B.G. 1979. A new species of *Taricha* (Caudata: Salamandridae), from the Oligocene John Day Formation of Oregon. *Canadian Journal of Earth Sciences*, **16**: 970–973.
- Nussbaum, R.A. 1976. Geographic variation and systematics of salamanders of the genus *Dicamptodon* Strauch (Ambystomatidae). *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, **149**: 1–94.
- Peabody, F.E. 1954. Trackways of an ambystomid salamander from Paleocene of Montana. *Journal of Paleontology*, **28**: 79–83.
- Peabody, F.E. 1959. Trackways of living and fossil salamanders. *University of California Publications in Zoology*, **63**: 1–72.
- Wilson, M.V.H. 1980. Oldest known *Esox* (Pisces: Esocidae), part of a new Paleocene teleost fauna from Western Canada. *Canadian Journal of Earth Sciences* **17**: 307–312.