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Partitioning of the Salamandrid Genus *Tylototriton* Anderson (Amphibia: Caudata) with a Description of a New Genus

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graueri, *P. gutterosus*, *P. keniensis*, *P. kinangopen-
sis*, *P. krefftii*, *P. latifrons*, *P. minutus*, *P. natalensis*,
P. ogoensis, *P. okingensis*, *P. perpalmatus*, *P. par-
vulus*, *P. plicatus*, *P. versicolor*, *Platymantis cor-
rugatus*, *P. dorsalis*, *Ptychadaena mascareniensis*,
P. oxyrhynchus, *Pyxicephalus adspersa*, *Rana brev-
iceps*, *R. clमितans*, *R. esculenta*, *R. sylvatica*, *Stau-
rois natator*, *Tomopterna delalandii*, *Trichobatra-
chus robustus*; RHACOPHORIDAE: *Aglyptodactylus*

madagascariensis, *Buergeria buergeri*, *Chirixalus
hanssenae*, *Gephyromantis bicalcaratus*, *G. boulen-
geri*, *Mantella betsileo*, *Mantidactylus albofrena-
tus*, *M. frenatus*, *Philautus aurifasciatus*, *P. leuco-
rhinus*, *P. nasutus*, *P. variabilis*, *Polypedates eques*,
Rhacophorus maculatus, *R. microtus*; RHINODER-
MATIDAE: *Rhinoderma darwini*, *R. rufum*; RHINO-
PHRYNIDAE: *Rhinophrynus dorsalis*.

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PARTITIONING OF THE SALAMANDRID GENUS TYLOTOTRITON ANDERSON (AMPHIBIA: CAUDATA) WITH A DESCRIPTION OF A NEW GENUS

RONALD A. NUSSBAUM AND EDMUND D. BRODIE, JR.

ABSTRACT: The salamandrid genus *Tylototriton* Anderson 1871 is partitioned. Four extant species (*asperrimus*, *kweichowensis*, *taliangensis*, *verrucosus*) are retained in *Tylototriton*. Two extant species (*andersoni*, *chinhaiensis*) are placed in *Echinotriton* gen. nov. The fossil record of salamandrids similar to *Tylototriton* is reviewed. We suggest that †*Salamandra laticeps* Goldfuss 1831, †*Tylototriton weigelti* Herre 1935, and †*Tylototriton kossuigi* Herre 1949 belong to *Tylototriton* (sensu stricto). †*Tylototriton primigenius* Noble 1928 is thought to be a synonym of †*Chelotriton paradoxus* Pomel 1853, or at least a species of †*Chelotriton*. *Echinotriton* is not represented in the fossil record.

Key words: Amphibia; Caudata; Salamandridae; *Tylototriton*; *Echinotriton* gen. nov.; Fossils; Systematics

THE salamandrid genus *Tylototriton* Anderson is presently restricted to Asia (Nepal, northeastern India, Burma, Thailand, China, Japan), although the fossil record indicates that it formerly occurred in Europe as well (Herre, 1935; Noble, 1928; Westphal, 1978). There are six extant species: *T. andersoni* Boulenger 1892, *T. asperrimus* Unterstein 1930, *T. chinhaiensis* Chang 1932, *T. kweichowensis* Fang and Chang 1932, *T. taliangensis* Liu 1950, and *T. verrucosus* Anderson 1871. *Tylototriton andersoni* and *T. verrucosus* are reasonably well represented in collections, but only a few specimens of *T. asperrimus* and *T. kweichowensis* are available. Both *T. chinhaiensis* and *T. taliangensis* are known only from their

respective holotypes, and the holotype of *T. chinhaiensis* is lost (J.-P. Risch, personal communication).

Aside from the original descriptions and repetitive summaries, very little has been published on *Tylototriton*. Thorn (1968) provided the most recent summary of the genus. Riese (1892) described and illustrated the skeleton of *T. verrucosus* in detail, and additional descriptions and figures of various parts of the skeleton of this species were presented by Bolkay (1928), M. L. Y. Chang (1936), Eber (1954), Herre (1935, 1941) and Noble (1928). Özeti and Wake (1969) described the muscles and skeletons of the hyobranchia of *T. verrucosus* and *T. andersoni*. M. L. Y. Chang (1937) described se-

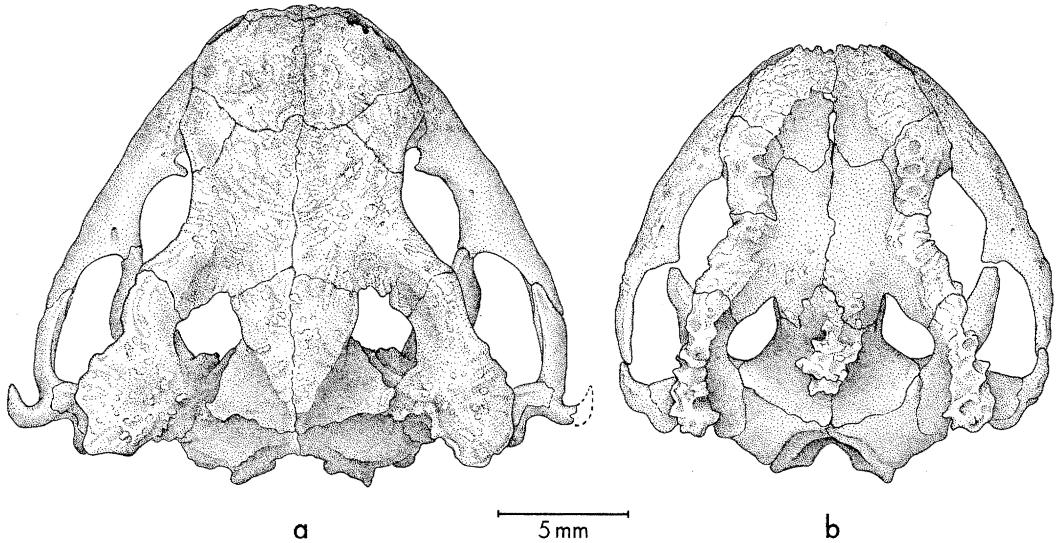


FIG. 1.—Dorsal views of the skulls of (a) *Echinotriton andersoni* (MCZ-22515) and (b) *Tylototriton verrucosus* (UMMZ-172094).

rial variation in the ribs of *T. andersoni*, and Herre (1935) briefly commented on the skull of this species based on observations from an early x-ray of poor quality. Inger (1950) noted variation in the number of metatarsals and phalanges in *T. andersoni*, and Naylor (1978) described the trunk musculature and vertebrae of this form. The skull of *T. andersoni* has not been described adequately or illustrated clearly. Fang and Chang (1932) described the external features of *T. asperrimus* and noted serial variation in the structure of the ribs of a single paratype. M. L. Y. Chang (1932, 1933) briefly characterized the skull, ribs, and external features of *T. chinhaiensis* and illustrated the quadrate region. Liu (1950) demonstrated serial and individual variation in the ribs of *T. kweichowensis*. The internal anatomy of *T. talianensis* has not been described.

There are no comparative anatomical studies of the species of *Tylototriton*, and the genus has never been revised. It is clear from our survey of the literature that the concept of *Tylototriton* virtually rests on anatomical descriptions of *T. ver-*

rucosus. Here we show that existing diagnoses of *Tylototriton* do not apply to *T. andersoni* and *T. chinhaiensis* and we erect a new genus to receive them.

Echinotriton gen. nov.

Type-species.—*Tylototriton andersoni* Boulenger 1892.

Diagnosis.—A salamandrid genus having (1) an anteriorly curved spine posterolaterally on each quadrate that is surrounded by enlarged granular glands; the spine often penetrates the skin; (2) robust anterior ribs; ribs 3–9 elongated, sharp-tipped, and distally free of trunk musculature; ribs bearing 0–3, usually one, dorsally projecting epipleural processes; (3) one lateral row of large primary warts and 0–3 medial rows of smaller secondary warts on each side of the vertebral column; primary warts supported by sharp tips of ribs, which may penetrate the thin skin at the apices of the warts, except for first primary wart, which is supported by first postscapular epipleural process; secondary warts are supported and sometimes penetrated by epipleural process-

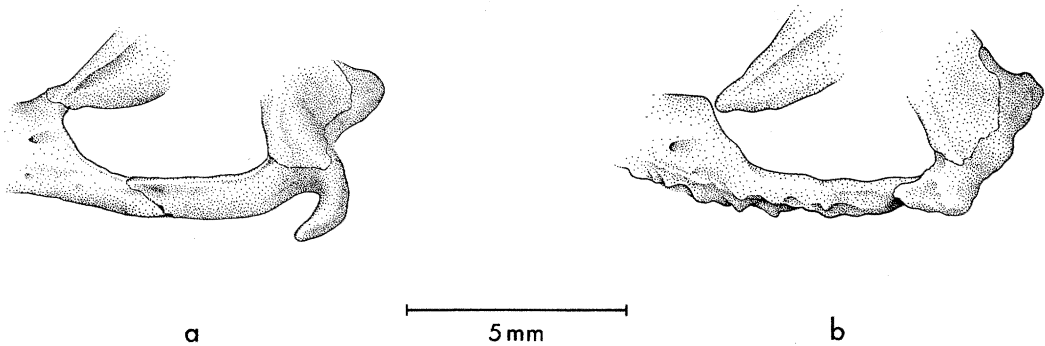


FIG. 2.—Quadrate region of (a) *Echinotriton andersoni* (MCZ-22515) and *Tylototriton verrucosus* (MCZ-22721) illustrating the presence of a quadrate spine, longer anterior process of the quadrate, and firmer articulation of the pterygoid and quadrate to the maxilla in *E. andersoni* compared to (b) *T. verrucosus*. The rugosity of the quadrate and maxilla of *T. verrucosus*, lacking in *E. andersoni*, also is shown.

es; (4) relatively large eggs (3.0–3.2 mm diameter) deposited on land.

Etymology.—*Echinos* (G.), spiny, plus *triton* (G.), a water god.

Content.—Two species: *Echinotriton andersoni* (Boulenger) and *Echinotriton chinhaiensis* (Chang).

Remarks.—*Echinotriton* is unique among amphibian genera in having an anteriorly curved spine on the posterolateral surface of each quadrate (Figs. 1, 2). Variation in the size and shape of the spine is slight. Of 60 *E. andersoni* closely examined, 58 had a single spine on each quadrate, one had four spines on the right quadrate and two spines on the left quadrate, and one had no spines on the quadrates. The latter individual may have lost the spines accidentally or during an encounter with a predator. The single known specimen of *E. chinhaiensis*, now lost, had one spine on each quadrate (M. L. Y. Chang, 1932, 1933, 1936).

Echinotriton is most similar to *Tylototriton*, but differs in a number of significant morphological and life history features. *Tylototriton* lacks spines on the quadrates (Fig. 1) and has prominent dorsolateral crests and a middorsal crest on the skull (Fig. 1), which are lacking in *Echinotriton*. The anterior processes of the quadrates do not extend as far forward in *Tylototriton* compared to *Echi-*

notriton, and the maxillae and quadrates are more solidly sutured in *Echinotriton* than in *Tylototriton*. In some individuals of *Tylototriton*, the quadrates and maxillae barely meet, and in others there is a small gap between the quadrate and maxilla (Bolkay, 1928; Herre, 1935; this study). The pterygoid is more strongly sutured to the maxilla in *Echinotriton* than in *Tylototriton*.

The size and shape of the ribs as well as their association with skin glands and trunk muscles differs markedly between *Echinotriton* and *Tylototriton* (Figs. 3, 4). In *Tylototriton*, fibers of the *M. dorsalis trunci* attach along the full length of the ribs. The ribs are not sharp-tipped and do not penetrate the warts supported by them, contrary to statements in the literature. By contrast, the ribs of *Echinotriton* are free of muscular attachment distally, sharp-tipped, and often penetrate the skin through the primary warts. *Pleurodeles waltl* is the only other salamander known to have free rib-tips that penetrate the skin, and in this case the rib-tips are not associated with concentrations of poison glands (Eber, 1954; Nowak and Brodie, 1978). Contrary to some remarks in the literature, the ribs of *Salamandrina terdigitata* do not penetrate the skin, as the ribs have muscular attachment along their entire lengths. *Ty-*

lototriton has a single row of warts on each side of the vertebral crest that runs parallel to the vertebral column (Fig. 3). *Echinotriton* has one outer row of primary warts flared out at midbody and 0–3 medial rows of secondary warts. The primary warts are supported by the first epipleural process and tips of the ribs; the secondary warts are supported by epipleural processes (Fig. 3). The ribs of *Tylototriton* also have epipleural processes, but except for the first one or two postscapular epipleural processes, which support the first one or two warts, the epipleural processes of *Tylototriton* are not associated with warts. There is only one epipleural process per rib in this genus, and the processes are smaller and usually completely bound by intercostal muscle fibers. The presence, per se, of epipleural processes in *Echinotriton* and *Tylototriton* is not evidence of close relationship. We found epipleural processes of various expressions in species of every salamandrid genus examined, including *Cynops*, *Euproctus*, *Mertensiella*, *Notophthalmus*, *Pachytriton*, *Paramesotriton*, *Pleurodeles*, *Salamandra*, *Salamandrina*, *Taricha*, and *Triturus*. Apparently, epipleural processes were present in the common ancestor of the Salamandridae. We observed epipleural processes in some species of *Hynobius* (Hynobiidae) and *Ambystoma* (Ambystomatidae) as well, and these processes occur in early developmental stages of *Necturus* (Proteidae) (Remane, 1936). It appears that of the non-paedomorphic families of salamanders, only the Plethodontidae lacks epipleural processes on the ribs. Epipleural processes that may be homologous with those of salamanders occurred in some labyrinthodonts and are present in some living frogs (Remane, 1936).

The fingers and toes of *Tylototriton* are more prominent than is the case for *Echinotriton*. The fifth toe of *Echinotriton* may be completely absent or barely expressed (Fig. 5). In some specimens of *Echinotriton*, the fifth metatarsal sup-

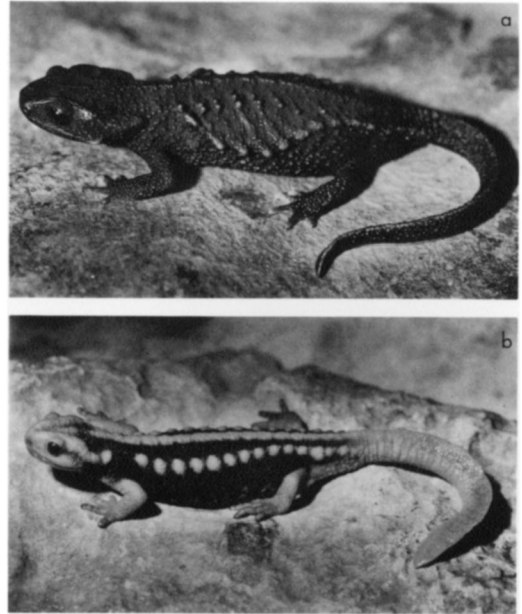


FIG. 3.—Living specimens of (a) *Echinotriton andersoni* (SVL = 65 mm) and (b) *Tylototriton verrucosus* (SVL = 75 mm).

ports a single tiny phalanx, in others the fifth toe consists only of the metatarsal, and in yet others, even the fifth metatarsal is missing (also see Inger, 1950). The hindfeet of *Tylototriton* have well-developed fifth toes with large fifth metatarsals that bear two phalanges (Fig. 5). The two genera also differ in the number and arrangement of the tarsals. The tarsals are well-calcified in both genera, and tarsals in the proximal row (tibiale, intermedium, fibulare) are similar in size, shape, and position in both genera. The intermedium of both forms supports a large centrale, and the tibiale of both supports a tarsal element in the position of the primitive first centrale. This latter element provides partial support for the first metatarsal in *Tylototriton* but is excluded from contact with the first metatarsal in *Echinotriton* by intrusion of the enlarged tarsale 1+2. The latter element provides all of the support for the first metatarsal in *Echinotriton* but only partial support (shared with first centrale) in



FIG. 4.—Cleared and stained specimens of (a) *Echinotriton andersoni* CAS-22232; SVL = 73.5 mm) and *Tylototriton verrucosus* (UMMZ-172094; SVL = 74.1 mm).

Tylototriton. The second and third metatarsals are supported solely by the second and third tarsalia, respectively, in both genera. In *Tylototriton* the fourth and fifth tarsalia are separate units, each supporting its respective metatarsal. The fourth and fifth tarsalia of *Echinotriton* are fused into a much larger element that rests upon the fibulare and supports both the fourth and fifth metatarsals, at least in specimens that have a fifth metatarsal. Thus, the ankle of *Echinotriton* normally consists of eight elements, whereas that of *Tylototriton* has nine.

Echinotriton has a stockier body with shorter limbs, digits and tail than *Tylototriton*. The tail of *Echinotriton* is almost always shorter than the combined

head and body length, whereas the tail of *Tylototriton* is almost always longer. Relative limb length will have to be checked on freshly preserved specimens when they become available. *Tylototriton verrucosus* deposits small eggs singly or in pairs in standing water (Chaudhuri, 1966; Gyi, 1969; Smith, 1924; Wolterstorff and Herre, 1935). Although the life histories of the other *Tylototriton* are unreported, they are expected to be similar to that of *T. verrucosus*, based on nearly identical morphology. *Echinotriton andersoni*, and presumably *E. chinhaiensis*, oviposit large, single eggs on land (Matayoshi et al., 1978; Utsunomiya et al., 1978). Terrestrial nesting in *E. andersoni* is confirmed by observations in the senior au-

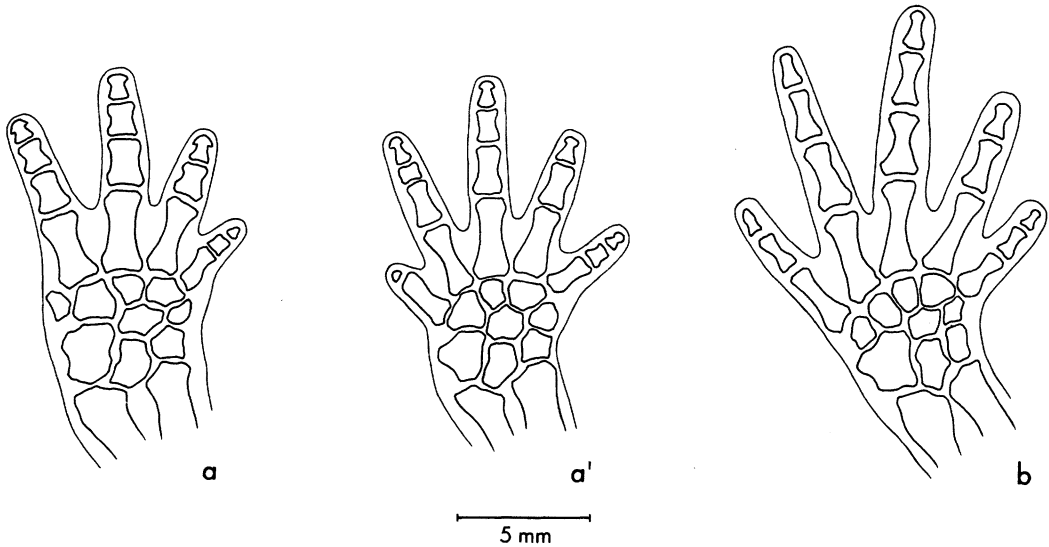


FIG. 5.—Left hindfeet of two *Echinotriton andersoni* (a, a'; CAS 22275 and 22232, respectively), illustrating eight mesopodial elements in each and variation in the length of the fifth toe; and left hindfoot of one *Tylototriton verrucosus* (b, UMMZ-172094) showing nine mesopodial elements and a long, well-developed fifth toe.

thor's laboratory. Large single eggs deposited on moist paper towels developed normally. Upon hatching, larvae of *T. verrucosus* have well-developed, functional balancers (Ferrier, 1974; Smith, 1924), while the balancers of *E. andersoni* are barely expressed and are resorbed before hatching (Utsunomiya and Utsunomiya, 1977).

Tylototriton verrucosus and *Echinotriton andersoni* have $N = 12$ chromosomes (Chatterjee and Majhi, 1974; Ferrier and Beetschen, 1973; Makino, 1951), but the karyotype of *T. verrucosus* is composed solely of metacentric and submetacentric chromosomes, whereas the centromere is nearly terminal on the 7th chromosome of *E. andersoni*. Additional cytotoxic studies are needed to determine whether or not this is a consistent generic difference.

DISCUSSION

Steiner (1950), Thorn (1968), Wolterstorff and Herre (1935), and others have summarized the diagnostic features of

salamandrid genera, but a truly critical analysis of the generic limits within this family is lacking. Despite this difficulty, we think that partitioning of *Tylototriton* (sensu lato) at this time is fully warranted for three basic reasons. Firstly, some of the characteristics that *Tylototriton* (sensu stricto) and *Echinotriton* have in common (such as separate premaxillae, frontosquamosal arches, pterygoids in contact with maxillae, two pairs of radial cartilages on the 1st basibranchial, high neural spines bearing flattened, dermal, pustular caps, ribs with epipleural processes, and ribs associated with warts) are shared with other genera. These characteristics, some of them plesiomorphic, do not constitute strong evidence for the homogeneity of *Tylototriton* and *Echinotriton*. Secondly, the traditional concept of *Tylototriton* is erroneous if applied to *E. andersoni* and *E. chinhaiensis*. For example, all published diagnoses of *Tylototriton* emphasize the well-developed bony crests on the skull. These crests are absent or weakly developed in *Echino-*

triton (Fig. 1). Thirdly, *Echinotriton* has derived features, such as rib tips free of musculature and reduced number of phalanges in the fifth toe, that are not shared with *Tylototriton* (sensu stricto) and other uniquely derived features, such as the spine on the quadrate, penetrating epipleural processes and terrestrial nest sites, that are not shared with any other salamandrid genus, including *Tylototriton*. The spine on the quadrate is a derived character not shared, to our knowledge, with any other amphibian.

Although specimens of *Tylototriton chinhaiensis* Chang were not available for study, this form is clearly assignable to *Echinotriton* based on published descriptions. M. L. Y. Chang (1932) described the holotype as having "evanescent" cranial crests and "very short" fifth toes, as in *E. andersoni*. More importantly, he described and illustrated a curved spine on the quadrate, a characteristic that he erroneously thought distinguished his new species from *E. andersoni*. In fact, M. L. Y. Chang's description of *E. chinhaiensis* so closely fits *E. andersoni* that the former may be only a junior synonym of the latter. Additional specimens of *E. chinhaiensis* will be needed to answer this question.

T. K. Chang and Boring (1934–1935) stated in three separate paragraphs that the lateral spines ("spurs") on the quadrates of *E. chinhaiensis*, as reported by M. L. Y. Chang, were undoubtedly abnormal structures or a "dislocated piece of hyoid." This may have misled later investigators and may be partly responsible for the remarkable fact that the quadrate spines of *E. andersoni* escaped detection for so many years.

The single reported specimen of *Echinotriton chinhaiensis* was collected in 1932 at Chenuan, Chinhai, Chekiang, a coastal site in eastern China. *Echinotriton andersoni* occurs in the Riu Kiu Archipelago due east of Chinhai, across the East China Sea. *Echinotriton* thus forms a cohesive geographic group that lies far to the east of the ranges of the

four species (*asperrimus*, *kweichowensis*, *taliangensis*, *verrucosus*) retained in its sister genus, *Tylototriton*.

We have examined specimens of *Tylototriton kweichowensis* and the holotype of *T. taliangensis* and confirm that they belong to *Tylototriton* in the restricted sense. We have not been able to examine specimens of *T. asperrimus*, but the redescription and illustration of this form by Fang and Chang (1932) make clear that it is properly assigned to *Tylototriton*.

Fang and Chang (1932) and Freytag (1936) recognized that the species of *Tylototriton* (sensu lato) sorted into two groups that conform to our concepts of *Tylototriton* and *Echinotriton*. At that time, however, the true extent of morphological and life history differences between the two groups was unknown. It is now clear that the differences between *Tylototriton* and *Echinotriton* are at least as great as the differences between other closely related pairs of salamandrid genera such as *Neurergus-Triturus* and *Cynops-Hypselotriton*.

Estes (1981), Estes and Hoffstetter (1976), Westphal (1980) and others have suspected that *Tylototriton* and the European fossil genera *Chelotriton* Pomel 1853, *Grippiella* Herre 1949, *Heliarchon* Meyer 1860, *Palaeosalamandrina* Herre 1949, and *Tischleriella* Herre 1949 are synonyms. If this is ever accepted, then *Chelotriton* Pomel 1853 has priority over *Tylototriton* Anderson 1871 and all of the other names listed above. Such action would not alter the conclusions of this paper unless some of the fossil material, bearing prior names, proves to be closer to *Echinotriton* than to *Tylototriton* (sensu stricto). We now consider the relationships of *Echinotriton* to the fossil salamander genera that bear resemblance.

Herre (1949) described *Grippiella*, *Palaeosalamandrina* and *Tischleriella* from isolated vertebral fragments taken from fissure fillings of Oligocene and Miocene age in Germany. These vertebrae are generally similar to vertebrae of *Tyloto-*

triton and *Echinotriton*, but they cannot be confidently allied to either of these genera because they lack diagnostic features and because they were not associated with other bones that would provide clues to their relationships.

Meyer (1863) described *Heliarchon furcillatus* (= *Chelotriton paradoxus*; Estes, 1981) from a complete but poorly preserved skeleton from the Oligocene "Braunkohle" of Germany. This salamander is similar to *Echinotriton* in having long, stout, curved ribs anteriorly, bearing large and sharp epipleural processes. The epipleural process of the fourth rib is so large that the rib appears forked, a condition that we have seen in *Echinotriton*. According to Meyer, the fourth rib is the largest, followed by the fifth and sixth, with the size of the ribs decreasing dramatically posteriorly. Meyer wrote that this arrangement of ribs gave the body an elongated oval shape with the apex of the oval towards the posterior, rather than the usual cylindrical shape of salamanders. Again, this description would apply to *Echinotriton*. The carpals and tarsals of *H. furcillatus* were cartilaginous in contrast to *Echinotriton*, but the single known specimen of *H. furcillatus* was probably a late larval stage as indicated by a trace of gills, and therefore the cartilaginous mesopodial elements may be a pedomorphic feature. The dorsal surface of the skull has "faint traces of pustular sculpture" (Estes, 1981, p. 75) reminiscent of *Echinotriton*. The dorsal arches of the anterior caudal vertebrae of *H. furcillatus* are relatively high, indicating the presence of a high tail fin. This contrasts sharply to the low arches and rounded caudal vertebrae of both *Echinotriton* and *Tylototriton*. *Heliarchon furcillatus* appears to be related to the *Echinotriton-Tylototriton* assemblage, and it has ribs that are suggestive of erectable antipredator devices that pierce the skin, more in the manner of *Echinotriton* than *Tylototriton*. However, the relatively high tail vertebrae of *H. furcillatus* indicate a more aquatic life style

than that of the two modern genera, and the lack of spines on the quadrates, if real and not due to the larval condition of the specimen, precludes *Heliarchon* from synonymy with *Echinotriton*.

Epipolysemia Brame (1973) is based on *Salamandra ogygia* described by Goldfuss (1831) and redescribed as *Polysemia ogygia* by Meyer (1860). Estes (1981) referred *E. ogygia* to *Chelotriton*. This taxon was originally based on a single, nearly complete skeleton of Miocene age from Germany, now lost. The specimen had a skull that was slightly broader than long, strong frontosquamosal arches with pustular dorsal surfaces extending anteriorly to the nasal region, posterior processes on the maxillae in contact with anterior processes on the quadrates, pterygoids in contact with maxillae, rounded otic capsules, long anterior ribs, and rounded anterior caudal vertebrae with low neural spines. These features are shared with *Echinotriton* and *Tylototriton*, but the ribs lack epipleural processes, the trunk vertebrae have low neural arches, and the mesopodial elements are cartilaginous, in contrast to these two genera. Furthermore, there was no indication of spines on the quadrates. *Epipolysemia*, with its low neural arches and long ribs, appears to be closer to *Pleurodeles* than to any other modern genus. Estes (1981) assigned two complete specimens from the Lower Miocene of Spain to *Chelotriton ogygius* (= *Epipolysemia ogygia*). However, these specimens differ from Meyer's (1860) description of the holotype by having high neural spines and epipleural processes on the third ribs.

Goldfuss (1831) described *Triton noachicus* from five skeletons from the Miocene of Germany. Meyer (1860) redescribed these specimens and removed them to a new genus named *Brachycormus*. Meyer also described two new articulated fossil specimens, apparently larvae, which he also assigned to *Brachycormus*. These are relatively small salamanders that have some skull and verte-

bral characteristics in common with *Chelotriton*, *Tylototriton*, and *Echinotriton*. *Brachycormus* has fully calcified mesopodial elements as do *Echinotriton* and *Tylototriton*. It also has long ribs that are relatively slender, and some apparently bear epipleural processes. One of the specimens assigned to *B. noachicus* by Meyer (1860) was fossilized in a manner that shows the shape of the caudal vertebrae quite clearly. The anterior-most caudals have high neural spines and elongate haemal spines, giving the tail a high rudder-like appearance. If this specimen is properly referred to *Brachycormus*, then it is highly unlikely that this fossil genus is congeneric with either *Echinotriton* or *Tylototriton*, as both of the latter have low, rounded caudal vertebrae. The apparent lack of quadrate spines is further evidence against a close association between *Brachycormus* and *Echinotriton*.

Chelotriton Pomel 1853 presently has three referred species: *C. paradoxus* Pomel 1853 from numerous Oligocene and Miocene localities in Europe, *C. robustus* Westphal 1980 from the Eocene of Germany, and *C. ogygius* (see above). *C. paradoxus* is known from numerous fragmentary and nearly complete skeletons; *C. robustus* is based on a single, articulated skeleton. *Chelotriton* is defined largely by the presence of strongly developed, flattened, dermal, bony plates or caps on the neural spines, which have a highly sculptured or pustular dorsal surface. This feature, in reduced form, also occurs in *Tylototriton* and *Echinotriton*, with the smallest caps observed in *Echinotriton*. In addition to the prominent dermal caps on the neural spines, *Chelotriton* has a highly sculptured skull dorsally, relatively short ribs with small epipleural processes as in *Tylototriton* (*sensu stricto*), pustular sculpturing on the dorsal surfaces of some of the limb bones, cartilaginous mesopodial elements, and, apparently, no quadrate spines. All of these features depart from *Echinotriton* to the extent that *Echino-*

triton cannot be merged with *Chelotriton*.

Herre (1941) described *Palaeopleurodeles hauffi* from the Miocene (Upper Oligocene according to Estes, 1981) of southern Germany as a new genus and species closely allied to *Pleurodeles* and *Tylototriton*. Herre's description was based on a single, well-preserved, articulated specimen. Westphal (1977) described a second skeleton of *P. hauffi* from the same locality as the holotype. Herre thought that the skull of *Palaeopleurodeles* more closely resembled the skull of *Tylototriton* than that of *Pleurodeles*. *Palaeopleurodeles* and *Tylototriton* share relatively broad skulls, rounded otic capsules, similarly shaped pterygoids, long posterior processes on the maxillae, and long vomeropalatine tooth rows, features by which both of these genera differ from *Pleurodeles*. However, according to Herre, *Palaeopleurodeles* lacks the prominent lyre-shaped cranial crests extending from the nasals across the frontosquamosal arches on each side, and it lacks the pustular parietal prominence. Herre believed that these features were diagnostic of *Tylototriton*, and that their absence in *Palaeopleurodeles* indicated relationship to *Pleurodeles*. Herre was not aware that "*Tylototriton*" *andersoni* also lacks the lateral and middorsal crests. The vertebrae of *Palaeopleurodeles* are, according to Herre, more like those of *Pleurodeles* than those of *Tylototriton*, in having low neural spines without pustular dermal caps. However, Estes (1981) stated that the lack of cranial crests and dermal bone on the neural spines of *Paleopleurodeles* cannot be proved because the fossils are preserved in ventral view. Herre also described the centra of both *Palaeopleurodeles* and *Pleurodeles* as weakly opisthocelous, whereas those of *Tylototriton* are strongly opisthocelous. The ribs of *Palaeopleurodeles* are quite long, strongly ossified and curved upwards distally. Herre stated that very large epipleural processes are present on some ribs, but

Westphal denied this. Herre suggested that the ribs of *Palaeopleurodeles* were associated with warts, and Westphal thought that the length and shape of the ribs indicates rib penetration as in *Pleurodeles*. The mesopodial elements of *Palaeopleurodeles* are cartilaginous, and the tail vertebrae have short neural and haemal spines, which indicate a low, rounded tail. Herre visualized *Palaeopleurodeles* as a relatively broad, flattened terrestrial salamander, with long ribs supporting warts, and with a short rounded tail. This image is closer to that of *Echinotriton* than to that of either *Tylotriton* or *Pleurodeles*. If *Palaeopleurodeles* had quadrate spines and high neural spines with pustular bony caps, then there would be no choice other than to place *Echinotriton* and *Palaeopleurodeles* together, the latter name having priority. Herre concluded that *Palaeopleurodeles* was intermediate between *Pleurodeles* and *Tylotriton*, and that the three form a distinctive clade. We would modify this only by adding *Echinotriton* to the clade.

Meyer (1860) established *Salamandra laticeps* on a single articulated skeleton (lost according to Estes, 1981) from Miocene brown coals of Czechoslovakia. Unfortunately, the skull is crushed and parts seem to be missing. The status of this fossil has been uncertain. Noble (1928) suggested that it was a species of *Tylotriton*, but Herre (1935) dismissed this idea and claimed that Meyer's original assignment to *Salamandra* was correct. Estes (1981) agreed with Herre, and synonymized *S. laticeps* with *S. sansaniensis*. However, if Meyer's description and illustration of *S. laticeps* are accurate, then this fossil is clearly much more closely related to *Tylotriton* than to *Salamandra*. The skull is broader than long and triangular in shape, much like that of *Echinotriton*. Although there is no indication of a frontosquamosal arch, it may have been destroyed. As was pointed out by Noble (1928), parts of the skull appear to have been covered by secondary bony

encrustations, as in *Chelotriton* and *Tylotriton* and unlike *Salamandra*. The ribs of *S. laticeps* are strongly reminiscent of *Echinotriton*, *Heliarchon*, and *Palaeopleurodeles* in that they are very long, sharp, decrease in length posteriorly, and they bear large epipleural processes. Meyer (1860) thought that the extraordinary length, sharpness, and direction of the ribs of *S. laticeps* indicated that the ribs penetrated through the skin as in *Pleurodeles*. Meyer stated that if this was the case, then *Salamandra laticeps* would have to be separated from *Salamandra*. It is noteworthy that none of the recent species of *Tylotriton* had been described by 1860. Had they been, we suspect that Meyer's conclusions and placement of *S. laticeps* would have been very different. The caudal vertebrae of *S. laticeps* are rounded, and the mesopodial elements are strongly calcified as in *Echinotriton* and *Tylotriton*. *S. laticeps* had nine tarsal bones as in *Tylotriton* and unlike *Echinotriton*, which has eight. The fossil has only four toes on the hindfeet, but Meyer suggested there were five. We conclude that Noble (1928) was correct in his placement of *S. laticeps* nearer to *Tylotriton*, as then conceived, than to *Salamandra*. In fact, in the size and shape of the ribs, *S. laticeps* is closer to *Echinotriton* than to our concept of *Tylotriton*. Only the absence of the quadrate spines, which could easily be artifactual, and the presence of nine tarsal elements suggests that *S. laticeps* belongs to *Tylotriton* and not to *Echinotriton*.

Having partitioned *Tylotriton*, we need to consider the statuses of the three nominate fossil species of this genus. These are *T. primigenius* Noble 1928, *T. weigelti* Herre 1935, and *T. kosswigi* Herre 1949.

Noble (1928) originally described *Tylotriton primigenius* from three fragmentary skeletons from the Miocene Öhningen beds of Switzerland. Westphal (1978) assigned five more articulated, but incomplete, fossil skeletons from the

Öhningen beds to this species. Noble showed that the fossils had the essential features of *Tylototriton*, but that they differed from living *T. verrucosus* in their larger size, heavier secondary ossifications on the skulls extending onto the quadrates, broader anterior rami on the pterygoids more extensively in contact with the maxillae, and different proportions for bones of the appendicular skeleton. Noble described the ribs as long, sharp and bifurcated (i.e., with epipleural processes). The third rib is as long as the humerus and femur, and thus relatively longer than the third rib of *T. verrucosus*. The photograph (Abb. 2A) published by Westphal (1978) of one of the paratypes shows that the ribs of *T. primigenius* are long and stoutly proportioned anteriorly, more like *Echinotriton* than restricted *Tylototriton*. But stout anterior ribs are also characteristic of some of the other early Tertiary fossils of this group, such as *Heliarchon*, *Palaeopleurodeles*, and “*Salamandra*” *laticeps*. The limbs of *T. primigenius* are relatively stout and long, and the mesopodial elements are calcified. It is clear, from Noble’s (1928) figure 2a, that the trunk vertebrae of *T. primigenius* bear large, flattened, dermal plates dorsally on the neuropophyses, which are greatly roughened on their dorsal surfaces. In this, and in the large size, long stout limbs, and extensive development of the secondary bony encrustations on the skull, *T. primigenius* is nearly identical to *Chelotriton* and probably should be referred to that genus, as suggested by Estes (1981). The ribs of *T. primigenius* are too long and stout, and the quadrate too large and pustulose for retention in *Tylototriton* (sensu stricto), and the absence of quadrate spines and the extensive secondary ossification of the skull bars it from *Echinotriton*.

Tylototriton weigelti Herre 1935 is based on fragmentary specimens from the Eocene brown coals of Germany. It is clearly related to the *Chelotriton-Echinotriton-Tylototriton* complex, and in our opinion, is properly assigned to

Tylototriton (sensu stricto), making it the oldest known fossil species of an extant salamandrid genus. Rather than repeat the detailed description of Herre (1935), which reveals *T. weigelti* to belong to this group of three genera, we will list only the features that clearly place it in *Tylototriton*. It has roughened lateral cranial crests running from the nasal region across the frontosquamosal arches. The rest of the dorsal surface of the skull is not as rough, except for the presence of a middorsal parietal boss of pustular bone. Herre (1935) described the ribs as long with epipleural processes, but from his figure (Taf. III, Abb. 21) it is clear that the ribs are not as long and as stout as in *Echinotriton*, nor are the epipleural processes as prominent and as sharp as in the latter genus. The presence of small pustular dermal caps on the trunk vertebrae and the crests on the skull exclude *T. weigelti* from *Pleurodeles*, and the relatively small size of the dermal caps on the vertebrae and the restricted nature of the pustular crests on the skull exclude this species from *Chelotriton*. The presence of lateral cranial crests and the middorsal parietal boss, the relatively short ribs, and the absence of quadrate spines excludes *T. weigelti* from *Echinotriton*.

Herre (1949) described *Tylototriton kosswigi* from the Miocene of Germany, based on a partial skeleton; Estes (1981) referred *T. kosswigi* to *Brachycormus noachicus*. We believe that this species is properly assigned to *Tylototriton*, but with less confidence than was the case with *T. weigelti*. *Tylototriton kosswigi* has the characteristics shared jointly by *Echinotriton* and *Tylototriton*, but the presence of strong cranial crests, and relatively gracile ribs that are curved down except at the tips, and the absence of quadrate spines, clearly bars the species from *Echinotriton*.

Throughout this discussion, we repeatedly noted the absence of quadrate spines on the various fossil species. We have very little confidence that the spines are, or were, truly absent. Quad-

rate spines were overlooked in *Echinotriton andersoni*, an extant species, for nearly 100 years. Herre (1935) published an x-ray image that clearly shows the spines, but he either did not notice them or mistook them for something else. T. K. Chang and Boring (1934–1935) refused to believe that the spines existed in *E. chin-haiensis*, apparently because of their extraordinary nature. It would be very easy to overlook the spines on fossil salamanders, or to remove them during preparation, as they are very small and unexpected. Palaeoherpetologists interested in salamandrid fossils are cautioned to search carefully for the quadrate spines as their presence or absence would provide valuable taxonomic information.

SPECIMENS EXAMINED

Echinotriton andersoni.—AMNH 14487, 41662; CAS 22167–72, 22203–07, 22224–27, 22229–31, 22233, 22235–47, 22260–61, 22263–67, 22273–74, 22276–82; CAS 22232 and 22275 cleared and stained; MCZ 2579(1); MCZ 2579(2), 22515–17 dried skeletons; UMMZ 70202; USNM 42464, 200041.

Tylototriton kweichowensis.—AMNH 52221; USNM 95518–26, 95557–65, 95661–63.

Tylototriton taliangensis.—FMNH 49388 holotype.

Tylototriton verrucosus.—ANSP 20558, 20597; BMNH 1901.4.26.8–9, 1923.11.10.3–8, 1933.7.3.1–2, 1949.1.8.29, 1969.8.25, 1976.286–287; FMNH 204492–3, 212344; MCZ 3569, 7362; MCZ 22721 dried skeleton; UMMZ 139791–93, 152858, 171619–27; UMMZ 172094 cleared and stained; USNM 57323.

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