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TWO NEW FOSSIL AMPHIBIA OF ZOÖGEOGRAPHIC IMPORTANCE FROM THE MIOCENE OF EUROPE

By G. K. NOBLE

While recently studying the fossil Salientia and Caudata in the British Museum, through the kindness of Dr. F. A. Bather, I had the opportunity to examine the material described by Lydekker in his Catalogue (1890). Some of the fragmentary specimens referred to *Cryptobranchus scheuchzeri* (Holl) and another to *Rana meriani* Meyer have proved upon further study to belong to very different species. This material is of considerable zoögeographic interest, for it demonstrates that a large salamandrid of the genus *Tylototriton* and a large tree frog not closely related to *Hyla arborea* were both present in Europe during the Miocene.

Salamandridæ

Tylototriton primigenius, new species

TYPE.—Brit. Mus. 42742, a fragmentary skeleton on two slabs. Paratypes, Brit. Mus. 42741, a badly preserved skeleton better articulated than the type, and Brit. Mus. 42761, skull and scapula region crushed and poorly preserved.

HORIZON AND LOCALITY.—Upper Miocene, Eningen, Switzerland.

DIAGNOSIS.—Generic characters of *Tylototriton*: vertebræ opisthocœlous, a thick bony fronto-squamosal arch, maxillary reaching quadrate, pterygoid extending forward to maxillary, ribs long and pointed, the third bifid. Differs from *Tylototriton verrucosus*, and apparently from the other species of the genus in its larger size, greater development of secondary ossification on skull (the encrustations covering squamosal and quadrate regions as well as extending forward to nasals), broader anterior ramus of the pterygoid which is in extensive contact with the maxilla, and in different proportions of limbs, girdles, and ribs.

DESCRIPTION OF TYPE SPECIMEN.—The specimen lies partly embedded in a block of limestone with its ventral side down. The plane of fracture cuts directly across the upper part of the neural arches, the left-hand slab containing the greater part of the vertebræ, the right only the upper part of these structures. Only parts of the skull, ribs and limbs are present, but certain of these exhibit diagnostic characters.

The impression of the skull and of the fragments of bone preserved are shown in Fig. 1. Although these represent a frontal section of the skull at about the level of the dorsal surface of the pterygoid, a comparison with the ventral surface of the skull of *Tylototriton verrucosus* is instructive. It is clear that the maxillaries extend to the

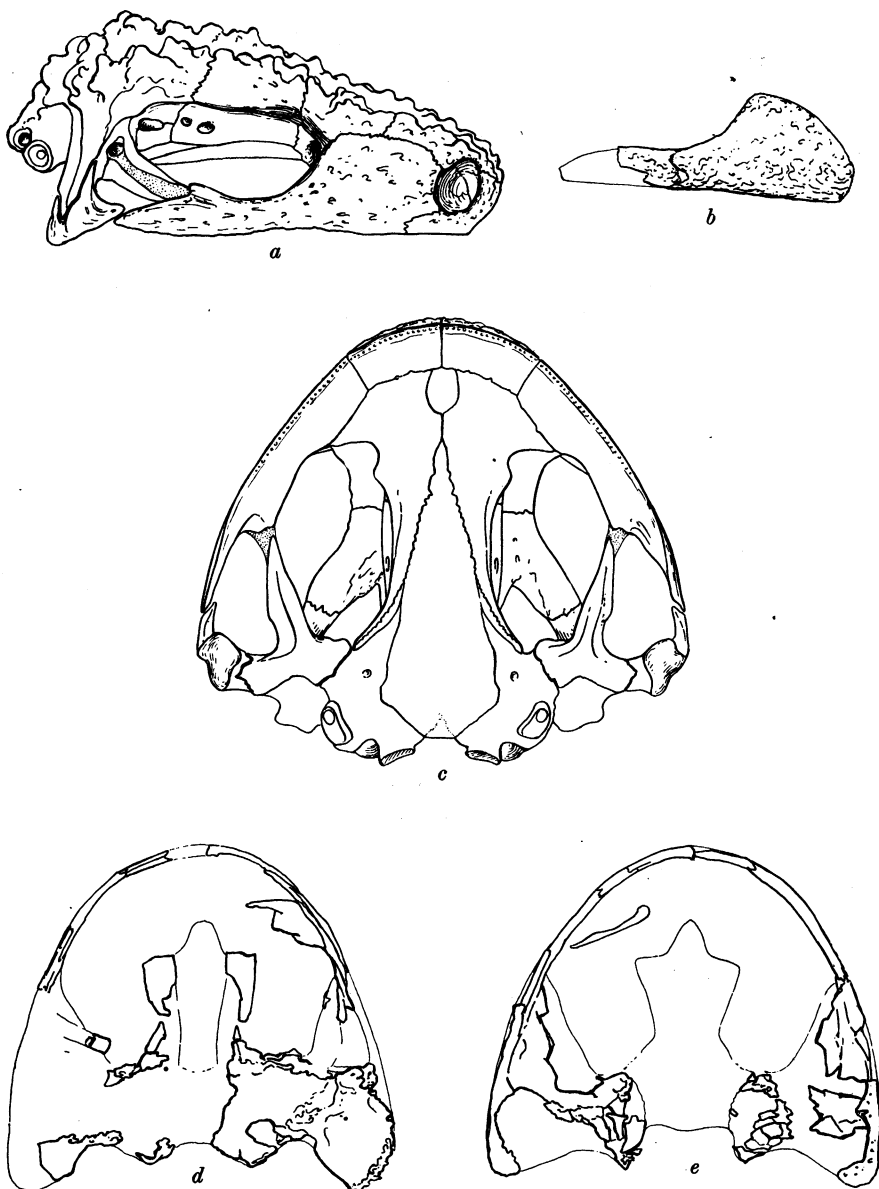


Fig. 1. Skull of *Tylotriton verrucosus* Anderson and *T. primigenius*, new species, compared.

- (a) *T. verrucosus*, lateral aspect.
- (b) *T. primigenius*, type, lateral aspect of right maxilla.
- (c) *T. verrucosus*, ventral view of skull of adult male.
- (d) *T. primigenius*, portions of skull shown on left slab of type specimen.
- (e) Same specimen, portions of skull shown on right slab.

In the fossil specimen, impressions are indicated by thin lines, bone by heavier ones.

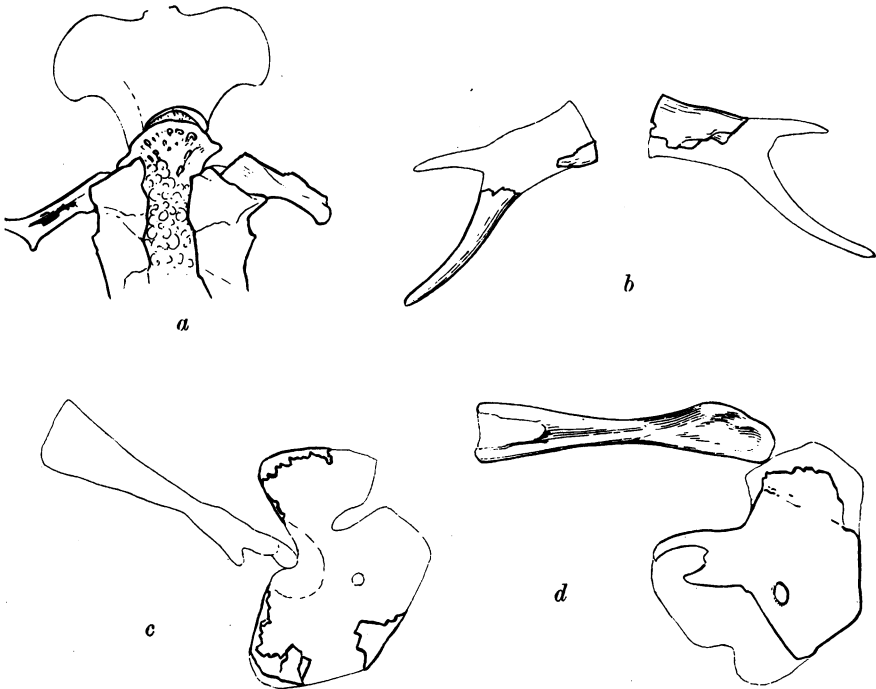


Fig. 2. *Tylotriton primigenius*, new species, type specimen.

(a) Impression of the first vertebra and remains of the greater part of the second vertebra as shown on left slab; the dorsal part of the neural arch has been broken away.

(b) Third rib of right side, impression and bone fragments shown on the left and right slabs.

(c) Impression and bone fragments of right coraco-scapula and humerus, as shown on right slab.

(d) Left coraco-scapula and humerus, left slab. The impression of the margin of the first is indicated by the narrower line.

quadrate and the pterygoids meet the maxillaries as usually described in *Tylotriton*. As a matter of fact, the pterygoids do not quite reach the maxillaries in my specimen (Fig. 1c) of *T. verrucosus*, although it is an adult male. In the fossil described here the contact is a very broad one. The fossil agrees with *T. verrucosus* in possessing extensive spenethmoids, but it differs in having broad bony encrustations covering the quadrate region. In *T. verrucosus* encrustations are found on the squamosal, but not the quadrate (Fig. 1a). The right maxilla is exposed on the right slab. It differs somewhat in form from that of *T. verrucosus* (Fig. 1b).

The vertebrae, although considerably broken, are unquestionably opisthocelous. This condition is best seen in the second vertebra on the left slab (Fig. 2a), but the first three vertebrae on the right show the same, and several fragments on the left can

be interpreted only as opisthocœlous. The plane of fracture passes through the neural arches and the opisthocœlous condition is most evident where a vertebra has fallen out leaving the ends of the adjacent ones visible.

The ribs are broken and scattered, no one being in place. It is clear from the fragments and the good impressions of ribs that they were comparatively long and sharply pointed as in *Tylotriton* and *Pleurodeles*. The bifid rib (Fig. 2b), which appears to be the third, is just as long as the humerus or the femur. Two of the mid-thoracic ribs are as long but the remainder are a trifle shorter. In *T. verrucosus* the third rib is only three fifths the length of the ossified part of the humerus and four fifths that of the femur. No rib of the fossil is longer than the third, although several project more laterally. The form of the rib is the same as in *T. verrucosus*, the head being constricted in the middle, but not divided into two heads as in various higher Caudata.

The pectoral girdle, although fragmentary, is sufficiently preserved to show diagnostic characters. On the left slab the greater part of the left coracoid plate is seen from above (inside), the scapula part of the same element being found on the right slab. The right coraco-scapula is much more fragmentary, but its outline is well indicated by an impression (Fig. 2c). Both coraco-scapulas agree with those of *T. verrucosus* in being well ossified, the coracoid element extending as an ossification farther from the glenoid than in most salamanders. In *T. verrucosus* the greatest width of the coracoid in the antero-posterior axis is about half the length of the humerus, while in the fossil described here it is two thirds the same length. Thus, in coracoid as in skull, *T. primigenius* is more bony than *T. verrucosus*. In outline the coraco-scapula of the first differs from that of the second (Fig. 3b), but this may be due partly to the fragmentary character of the first.

The limb bones of the fossil are for the most part stouter than those of *T. verrucosus*, but as these elements have been fully described in only a few salamanders, it is doubtful if the differences have any systematic value. The following characters distinguish the fossil from *T. verrucosus*: head of femur a bony condyle not cartilaginous as in the latter species; lateral (=deltoid) crest of humerus (left) pronounced (Fig. 2d), but not forming a high, sharp ridge as in the latter; fibula with a broad proximal head more than half again as wide as the middle of the shaft instead of being about the same width. The feet and part of the limb bones are missing in the fossil.

MEASUREMENTS

(1) Length of skull in median axis.....	20.5 mm.
(2) Greatest width of skull.....	27. mm.
(3) Greatest length of third rib.....	13.5 mm.
(4) Greatest width of third rib.....	3.5 mm.
(5) Greatest length of left coracoid in long axis of body.....	12. mm.
(6) Length of left humerus.....	14.5 mm.
(7) Greatest width of humerus across deltoid crest.....	3.5 mm.
(8) Length of femur.....	14.5 mm.
(9) Length of fibula.....	9.5 mm.
(10) Width of fibula.....	3.5 mm.

NOTES ON PARATYPES.—The partly articulated skeleton, although poorly preserved, shows clearly the fronto-squamosal arches (Fig. 4a), the broad triangular head, the long, pointed ribs, and the bifid third rib of *Tylotriton*, thus confirming

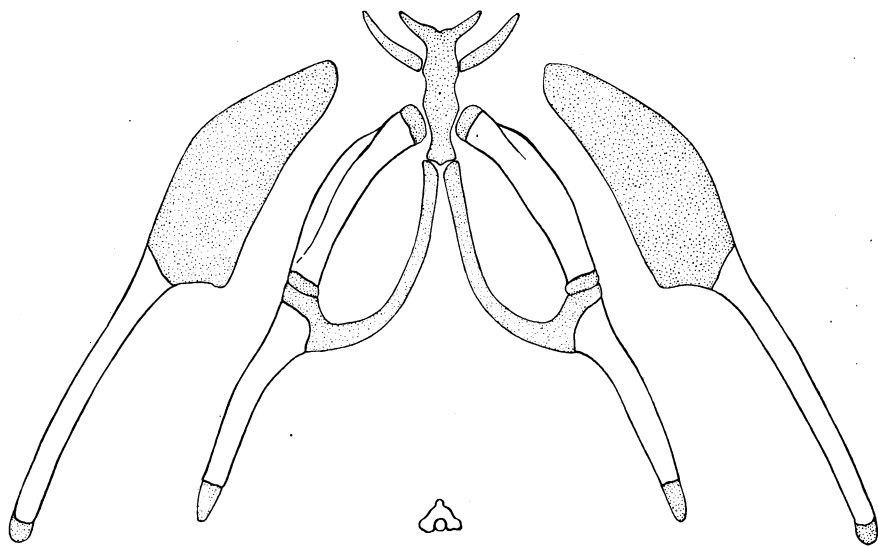
the generic identification of the type. The most important feature of this skeleton is the skull which I have compared with that of *T. verrucosus* (Fig. 4b). It is difficult to distinguish the sutures in this specimen, but it is clear that the skull was covered with rugose bone which completely covered the squamosal region (Fig. 4a). The limbs are incomplete in this specimen, but some of the phalanges, three carpal and apparently two tarsal elements are present. These are bony and as poorly preserved as the rest of the skeleton. The specimen measures 101 mm. from tip of snout to middle of the acetabulum. The skull is 24 mm. long, and 33 mm. wide. The longest rib measures 16.5 mm. in length.

The other paratype (Brit. Mus. 42761) is badly crushed and fragmentary, but the bone is not decayed. The surface texture of the secondary bone covering the quadrate and nasal regions is well shown. The left pterygoid is exposed and when compared from the same dorsal aspect with that of *T. verrucosus* is found to be much broader. The right lower jaw extends beyond the premaxillary slightly exposing a row of very small dentary teeth as in *Tylotriton*. In size and proportions this skull agrees closely with that of the other paratype.

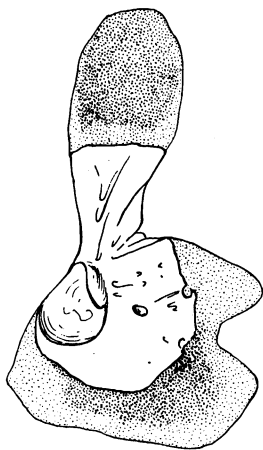
DISCUSSION.—The discovery of *Tylotriton* in the Eningen beds with *Megalobatrachus* adds another oriental genus to the Miocene fauna of southern Europe. *Megalobatrachus* and *Tylotriton*, now restricted to southeastern Asia and certain adjacent islands, must formerly have had an extensive distribution in western Europe. *Tylotriton* is a primitive salamandrid and may well represent the ancestral type from which the European newts evolved (Noble, 1927).

If *Tylotriton* was well established in western Europe during the Miocene it seems strange that the genus was not previously recorded. Further work may show that a number of the fossils already recorded under other names may be referable actually to *Tylotriton*. Thus, long ago von Meyer (1860) in describing *Salamandra laticeps* noted the long ribs and the pointed uncinatè processes in the specimen before him and discussed the possibility of the latter perforating the skin in the way the rib points do in *Pleurodeles*. There is nothing in von Meyer's description or figure which shows that his specimen is definitely a *Salamandra*, while, on the other hand, the large, triangular head and the long uncinatè processes on the anterior ribs suggest that the species is actually referable to *Tylotriton*. Further, von Meyer figures (Fig. 2) but does not discuss some bone fragments on skull and vertebræ which have the appearance of encrustations. If my interpretation of von Meyer's figure is correct his species is not a *Salamandra* but in all probability a *Tylotriton*.

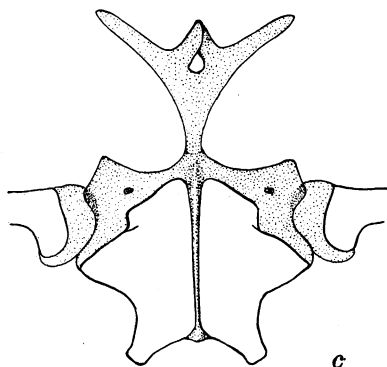
Of the many fragmentary salamandrid skeletons described from the Tertiary of Europe, only one other, to judge from the published descriptions, seems very probably referable to *Tylotriton*. Sampelayo and



a



b



c

Fig. 3. *Tylototriton verrucosus* Anderson.
 (a) Hyoid apparatus.
 (b) Right coraco-scapula, outer aspect.
 (c) Pelvic girdle, ventral aspect.

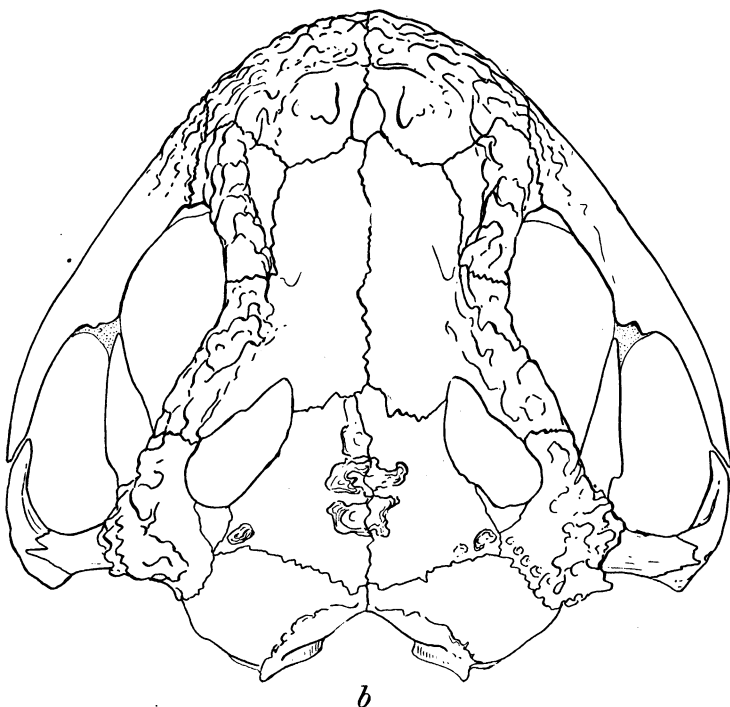
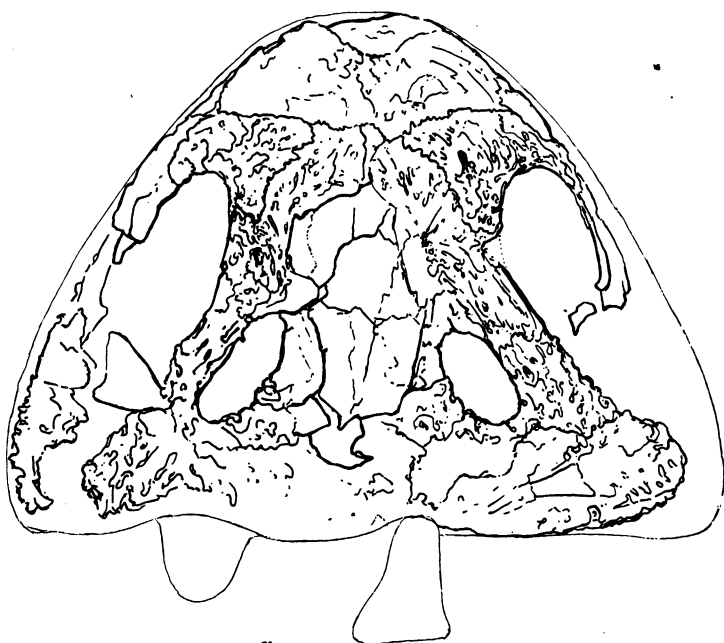


Fig. 4. Skull of *Tylototriton primigenius*, new species (a), and *T. verrucosus* Anderson (b), compared from the dorsal aspect. The first figure (a) is made from a paratype in the British Museum.

Cincúnegui have figured (1926, Fig. 63), but not identified or named, a urodele of about the same size and shape as *T. primigenius*. No details of the skull can be recognized from the figure, but the third rib is bifid and similar in shape to that of *T. primigenius*. Further, all ribs are long, curved and pointed. This unnamed salamander comes from the Oligocene of Spain (Ribesalbes formation).

These data tend to show that large salamandrids either identical or closely related to *Tylotriton* were widely spread in Europe during the Oligocene and Miocene. It seems probable that *Heliarchon furcillatus* von Meyer (1863) was the larva of one of these salamandrids, although the uncinat processes are longer than in any recent larval form.

It may be noted in passing that the only extensive account of the skeleton of *Tylotriton verrucosus*, that by Riese (1891), is not wholly accurate. My specimen of *Tylotriton verrucosus* differs from his description and figure of the skeleton of the same species in several particulars. I figure (Fig. 3) the hyoid, pectoral and pelvic girdle for comparison with his figures. An os thyroideum is present in *T. verrucosus*. The basihyal, ypsiloid apparatus, and procoracoid cartilage have a form different from his figures.

DISTRIBUTIONAL REMARKS.—Given *Tylotriton* in the Miocene of Europe it becomes unnecessary to postulate the western migrations of salamandrids, such as Boulenger (1917) has done. *Tylotriton* is primitive in the complete fronto-squamosal arch, the pterygoid in contact (or nearly so) with maxilla and the latter reaching the quadrate. The four-pronged basihyal, the long pointed ribs with long uncinat processes, and the extensive, well-ossified coracoid are also primitive features. The primitive salamandrid stock of Europe was probably rough-skinned as in *Tylotriton*, and the casque of secondary bone covering their skulls aided them in their terrestrial wanderings. From such an aggressive semi-aquatic type wide-spread in Europe, the present European newts may have been evolved by local adaptation to various ecological niches. Just as various genera of hynobiids have evolved from *Hynobius* by isolation on various mountain masses (Dunn, 1923), so we may conceive that the various mountain salamandrids of Eurasia were evolved from a *Tylotriton*-like stock. *Rhithrotriton* of the mountains of Kurdistan has the maxilla reaching the quadrate as in *Tylotriton*, but the fronto-squamosal arch is partly ligamentous (Boulenger, 1917). In *Euproctus asper* of the Pyrenees, the maxilla is reduced, while in *E. montanus* of Corsica both it and the fronto-squamosal arch are ligamentous (*loc. cit.*). The more aquatic newts have evolved by geo-

graphical isolation, and the different groups seem to have independently reduced the maxilla and pterygoid and lost or weakened the fronto-squamosal arch. The forms living today on the periphery of this original Eurasian range are in some ways more primitive than the species in the center of the area. *Pleurodeles walzl* is primitive in its long ribs, its hyoid and fronto-squamosal arch but both its maxillæ and pterygoids are reduced. The closely related *P. poireti*, however, may have more extensive maxillaries according to Boulenger (1917). *Pachytriton* is a thoroughly aquatic eastern derivative of the primitive stock. It has retained a broad pterygoid maxillary contact but greatly reduced the posterior ramus of the maxillaries. Further, its ribs and hyoid have also undergone a reduction.

Tylotriton lives today only in the eastern Himalayas, Yunnan, and the Riu Kiu Islands. But its occurrence in the Miocene of Europe shows that this stock was wide-spread in former times. It is from this stock that all other genera and subgenera of salamandrids, save *Salamandra* and *Chioglossa*, seem to have been directly or indirectly evolved.

Hylidæ

Hyla europæa, new species

TYPE.—Brit. Mus. No. 30267, the impression of a skeleton with some bone fragments adhering.

HORIZON AND LOCALITY.—Lower Miocene, Rott, near Bonn.

DIAGNOSIS.—Hylid characters: arciferal, sacrum single with greatly dilated sacral diapophyses, double condyle to coccyx, teeth in upper jaw, scapula nearly as long as procoracoid, tibiale and fibulare free, terminal phalanges claw-shaped, an intercalary present. Differs from *Hyla arborea* in larger size, more dilated sacral diapophyses and in slightly different proportions of the limb segments.

DESCRIPTION OF TYPE SPECIMEN.—The form and character of the fossil is shown in figure 5 which fails to clearly show the bone fragments adhering to the impression. The latter was made by the ventral surface of the skeleton. The greater part of the right clavicle is in place, only a small section near the midline being absent. This clavicle is strongly curved and directed forward. A proximal and a distal piece of the left clavicle are in place; these agree with homologous parts of the right. The coracoids and scapulas are represented by impressions to which a few very small pieces of bone adhere. The entire outline of neither scapula is clearly shown. Further, the glenoid cavity of the left scapula seems to be largely crushed, for the dorsal margins of both glenoids are visible as a pit on either side. That on the left side is much nearer the adjacent coracoid than the pit on the right side is near its coracoid. Each pit is about the same distance from the top of the scapula (outer edge of impression) of its own side. This distance is about two thirds the length of the clavicle measured in a straight line (while in *H. dominicensis* the same part of the scapula is three fourths the length of the clavicle). The pelvis is represented by an impression and a few bone fragments.

The ilium agrees in form with that of *H. dominicensis*, but may have been stouter. The sacrum was formed by a single vertebra, and the diapophyses were obviously dilated, as the impression of the left diapophysis is definite, except distally. The impression of the right diapophysis is not clear, but the caudal edge can be distinguished. Only scraps of the vertebræ remain in place, but these and the impressions show definitely that the column was procœlous. The posterior edge of the centra of the four vertebræ immediately preceding the sacrum is well shown. The sacrum shows a distinct impression of two condyles. The coccyx impression is without evidence of diapophyses. The diapophyses of three presacral vertebræ show as poor impressions, but it is clear that these structures were directed slightly forward. Only fragments of the skull are present, the largest piece being the middle section of the parasphenoid, which is long and narrow indicating a dagger-shaped bone. The impression of the jaws is clear. The sockets of eight teeth in the right maxilla and seven in the left are visible. The more conspicuous of these are outlined with white in the photograph. The fragments of the pterygoid, prevomers and prootic adhering to the skull impression have the same relative position as in *H. dominicensis*, but no diagnostic details can be recognized. More or less of the four limbs are indicated by impressions and bone fragments, except the left foot which is absent. The metacarpal of the second finger (left hand) is about two thirds the length of the radio-ulna which is approximately as long as the second finger. The first finger appears to be nearly as long as the second, but this may be due to a displacement, such as the impression of the proximal end vaguely suggests. The impression of the second digit of the left hand is clear-cut for its entire length. The terminal phalanx is claw-shaped (Fig. 6), and a distinct intercalary cartilage or bone is clearly indicated. The terminal phalanx of the first (inner) finger is barely indicated but under the higher binocular powers it seems clear that an intercalary was present (Fig. 6). No details of the other digits or the carpal elements can be made out. A small prehallux less than a third as long as the tibiale is indicated. The tibiale and fibulare are separate bones. The first is contained in the length of the tibio-fibula slightly less than two times. Tibio-fibula slightly shorter than the femur. Humerus slightly more than half as long as the femur.

DISCUSSION.—The specimen described above was doubtfully referred to *Rana meriani* by Lydekker (1890), who comments (p. 123), "Slab of lignite, showing the impression of the nearly entire skeleton of a somewhat smaller frog not improbably belonging to this species. The sacrum is not shown. The contour of the soft parts of the hind limbs is preserved." The specimen, although very fragmentary, is clearly of an arciferal type and hence cannot be a *Rana* or a ranid. In assigning the species to *Hyla*, I have made use of a number of characters, but as some of these are indicated merely by impressions, their validity may be questioned. It may, therefore, be well to point out why the fossil described here cannot be referred to any other arciferal group. It cannot be a species of *Palæobatrachus* because of its longer and narrower scapula, its shorter metacarpals (much shorter than the radio-ulna), its single sacral vertebra and greatly dilated sacral diapophyses. It cannot



Fig. 5. *Hyla europaea*, new species, type specimen. The diagnostic structures are outlined with white.

be a discoglossid because of its definitely procœlous vertebræ, and its longer and narrower scapula. The species has some characters in common with the pelobatids, but there is a definite double condyle to the coccyx and, although the tibiale and fibulare are free, there is no suggestion of osteoderms as in *Pelobates*, etc. If we should assume that the impressions of claw-shaped phalanges and intercalaries are both illusions,

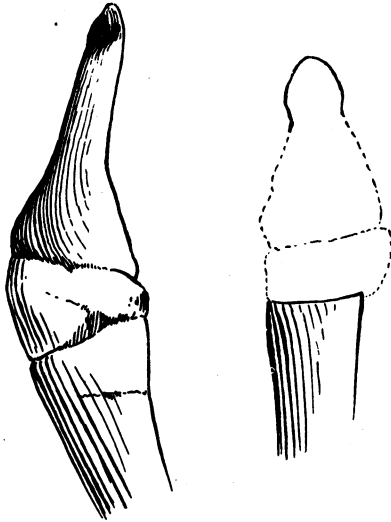


Fig. 6. *Hyla europæa*, new species. Impression of the terminal phalanges of the first and second digits of the left hand. Type specimen. The second digit is on the left.

then the species can be only a highly aberrant, toothed bufonid. As I have indicated in Fig. 6, the impression of these elements on the second finger of the left hand is perfectly clear and I do not hesitate to refer the species to *Hyla*.

Hyla europæa differs from the present tree frog of Europe, *H. arborea*, in its larger size, more dilated sacral diapophyses and slightly different limb proportions.

DISTRIBUTIONAL REMARKS.—The discovery of a tree frog in the Miocene of Europe lends considerable support to the view previously advocated (Noble, 1925) that the genus arose in the north and spread southward to its present range. Frogs and toads make few and poor fossils. In discussing the dispersal of the group, considerable allowance must be made for the scantiness of the fossil record. It is well known that a host of

mammals living in the Miocene of Europe have spread since that time to Africa, southern Asia, and some even to South America. Where the fossil record is full, as in the case of the mammals, the actual migration of such forms may be traced with some degree of confidence. The fossil described above proves that tree frogs were in Europe during the Miocene with tragulids, rhinoceros and other groups found today in Africa. Whether or not tree frogs followed the migration routes of these mammals and later died out along most of the route is unknown. But, I believe that extinctions have occurred far more often than some zoogeographers, such as Metcalf (1923), have assumed. In brief, the absence of a fossil record in the Salientia proves nothing, while the presence of even a single record may be of the greatest importance in determining the routes of dispersal.

LITERATURE CITED

- BOULENGER, G. A. 1917. 'Les batraciens urodèles rapportés au genre Euproctus, leurs rapports éthologiques et phylogéniques.' C. R. Acad. Sci. Paris, CLXIV, pp. 709-712, 801-804.
- DUNN, E. R. 1923. 'The salamanders of the family Hynobiidæ.' Proc. Amer. Acad. Arts and Sci., LVII, pp. 445-523.
- LYDEKKER, R. 1890. 'Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History), Part IV.' London.
- METCALF, MAYNARD M. 1923. 'The opalinid ciliate infusorians.' Bull. U. S. Nat. Mus. 120.
- MEYER, H. VON. 1860. 'Salamandrinen aus der Braunkohle am Rhein und in Böhmen.' Palæontographica, VII, pp. 47-73, Pls. VIII-IX.
- . 1863. 'Heliarchon furcillatus, ein Batrachier aus der Braunkohle von Rott im Sibenbirge.' Palæontographica, X, pp. 292-298, Pl. L.
- NOBLE, G. K. 1925. 'The evolution and dispersal of the frogs.' Amer. Nat., LIX, pp. 265-271.
- . 1927. 'The value of life history data in the study of the evolution of the Amphibia.' Ann. N. Y. Acad. Sci., XXX, pp. 31-128, Pl. IX.
- RIESE, H. 1891. 'Beitrag zur Anatomie des *Tylototriton verrucosus*.' Zool. Jahrb., Anat., V, pp. 99-154, Pls. IX-XI.
- SAMPELAYO, H., AND CINCÚNEGUI, M. 1926. 'Cuenca de esquistos bituminosos de Ribesalbes (Castellón).' Estudio geológico de los criaderos.' Bol. d. inst. Geol. España (3), VI, pp. 3-87.

