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PALAEOTARICHA OLIGOCENICA, NEW GENUS AND SPECIES, AN OLIGOCENE SALAMANDER FROM OREGON.

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In 1951 Mr. George R. K. Moorhead, a member of the Salem (Oregon) Geological Society, collected a fossil urodele in a small slab of shale from a locality situated about three miles southeast of Eugene, and about $\frac{1}{4}$ mile north of Goshen, Oregon. The specimen was sent by Dr. Herman Clark of Willamette University to the Museum of Comparative Zoology for study.

The strata in which the fossil was found are designated by Vokes *et al.* (1951) as post-Fisher and Eugene (Oligocene) plant-bearing tuffs. These strata are described by the authors as "a sequence of apparently water-laid coarse tuffs with interbedded thin layers of carbonaceous gray shale . . . [containing] an abundant flora . . . [of which fifteen species] were determined by Dr. Roland Brown,¹ who assigned a late Oligocene age to the containing strata." Dr. Ralph W. Chaney of the University of California has written me that he too considers the strata to be younger than Eugene or Fisher, and is terming the strata the Willamette formation. On the other hand, Dr. Clark writes that he and Dr. Ewart M. Baldwin of the University of Oregon prefer to assign them to the Eugene formation, although conclusive evidence is lacking. At any rate, all concerned seem confident of the Upper Oligocene age of the deposit. It is the gray shale just mentioned which contains the salamander.

The specimen is about 120 mm. in total length, and lacks a centimeter or so of the tail, the right mandible, most of the ribs, the left scapula and humerus, and parts of the hyoid apparatus. It is black in color, apparently highly carbonized. The skull is

¹ and listed by Vokes *et al.* (1951)

crushed dorsoventrally, and the vertebral column is twisted so that it lies on its side with respect to the skull.

The dorsal surface of the skull when first prepared seemed to be an uneven but continuous structure. Since depressions representing the orbits and the cavum internasale were visible, and the surface was much darker than the matrix, and had the outline of a skull, this dorsal material was thought to be bone in a bad state of preservation. Futile attempts to understand the skull in the light of this interpretation (the sides of the braincase, moreover, appeared to be pressed out and in contact with the maxillae), suggested that research in experimental paleontology might be useful. In this pursuit a skull of a Recent *Taricha granulosa* was decalcified with dilute hydrochloric acid, and then flattened between two glass plates and allowed to dry. The sides of the braincase were still no closer to the maxillae than before. This increased my growing suspicion that the material exposed on the dorsal surface of the fossil skull was not bone, and prompted exploratory probing through the surface. The operation revealed undeniable bone underneath. The removal of most of the matrix from the unexposed side then followed. I believe that the formerly exposed surface was mineralized skin, which had roughly followed the contours of the skull — not revealing, however, any evidence of the taxonomically important frontosquamosal arches. The same dark material is present elsewhere, as revealed by further preparation, and is separated from the bone by about 1 mm. of matrix. Additional evidence of the preservation or influence of soft parts can be seen (Pl. 1, fig. 1) in the thoracic region, where the matrix is unusually dark (and hard); and above the anterior half of the vertebral column, where a possible dorsal crest is preserved.

The specimen is recognized as a urodele by the presence of the ypsiloid cartilage, the long, broad parasphenoid reaching to the foramen magnum, the atlas with an odontoid process, and haemal arches on the caudal vertebrae. The absence of paired tooth rows, and the presence of two longitudinal vomerine tooth rows, diagnose it as a salamandrid. Paroccipital processes, frontosquamosal arches, and an unpaired premaxilla are characters of this fossil as well as, in Recent salamandrids, *Cynops* Tschudi, 1838, *Diemictylus* Rafinesque, 1820, *Euproctus* Gené, 1838, *Hypselotriton* Wolterstorff, 1934, *Pachytriton* Boulenger,

1878, *Taricha* Gray, 1845, and several species of *Triturus*¹ Rafinesque, 1815. The fossil genera *Archaeotriton* von Meyer, 1860, *Heliarchon* von Meyer, 1863, *Oligosemia* Navás, 1922, and *Polysemia* von Meyer, 1860, likewise all seem to have frontosquamosal arches and paroccipital processes, but information on the premaxillae is lacking. The phalangeal formula of the Oregon specimen is 1-2-3-2 (manus) and 1-2-3-3-2 (pes), as also in *Cynops*, *Hypselotriton*, *Pachytriton*, and *Taricha*. *Cynops*, *Hypselotriton*, and *Diemictylus* (the only Recent American salamandrid genus other than *Taricha*) can be excluded from identification with the fossil because of their relatively long, narrow skull, inconspicuous dorsal opening of the cavum internasale, and failure of the ascending processes of the premaxilla to extend beyond the anterior border of the cavum. *Diemictylus* can be further ruled out by its paired longitudinal ridges extending from the nasals to the posterior border of the parietals, and an abrupt angle in the arches posterior to the frontal-squamosal suture. *Pachytriton* is excluded by its long, narrow skull; a ridge (joining the maxillae across the premaxilla) situated between, and concentric with, the outer tooth row and the anterior border of the vomer;² and the very small dorsal cavum internasale opening. *Euproctus* is ruled out by its phalangeal formula of 2-2-3-2, 2-2-3-3-2, an elongated skull with a spatulate anterior end, concave lateral maxillary borders, and the paroccipital processes extending farther back than the occipital condyles. The five or six species of *Triturus* that have complete frontosquamosal arches are excluded by their phalangeal formula, 2-2-3-2, 2-2-3-3-2, and the elongated skull. Of all the known salamandrid genera there is no doubt that *Taricha* is the closest to the fossil. Skull, body and limb proportions are similar, and other important characters are: the frontosquamosal arches; paroccipital processes; large openings of the cavum internasale, the dorsal one bordered anteriorly and laterally by the premaxilla. All these similarities to the Recent *Taricha* species (*torosa*, *granulosa*, *rivularis*, and *sierrae*), and the fact that the fossil comes from the present geographic range of one of them (*granulosa*), may justify assigning the fossil to that genus. But some

¹ as used by Wolterstorff and Herre (1935).

² vomeropalatine or prevomer.

very important characters distinguishing the fossil from the Recent species lie in the nature of the vertebrae: characters as fundamental as some upon which several genera, known from vertebrae only, have been based. The pelvis is also peculiar, and the tarsal basale count is different, as described below. With these differences, and the belief that if the animal were alive, neoherpetologists would distinguish it generically because of the spinal column, I feel that erecting a new genus for the fossil is justified.

Class AMPHIBIA

Order CAUDATA

Family SALAMANDRIDAE

PALAEOTARICHA, new genus

Genotype: *Palaeotaricha oligocenica*, new species.

Diagnosis: Precaudal neural spines high, with laterally expanded, broad, rectangular, sculptured, flat tops, which are in contact with each other fore and aft. Fourteen presacral vertebrae. Pelvis with relatively large, knob-like, laterally directed prepubic processes. Tarsal basale formula 1, 2, 3, 4+5. Maxillae extending caudad, united by suture with quadrates.

PALAEOTARICHA OLIGOCENICA, new species

Holotype: University of Oregon Museum of Natural History no. F-5405, a nearly complete specimen.

Collector: Mr. George R. K. Moorhead, August 1, 1951.

Horizon: Upper Oligocene plant-bearing tuffs, not older than Eugene and Fisher formations, the Willamette formation of Dr. Ralph W. Chaney (*in litt.*).

Locality: About 3 miles (5 km.) southeast of Eugene, Lane County, west central Oregon; southeast $\frac{1}{4}$, sec. 14, T. 18 S, R. 3 W; "about 550 feet east of the Southern Pacific railroad tracks on the south side of a small hill in a cut made for the newly constructed highway near the east end of the overpass over the railroad. This is about 400 ft. north of lat. 44 deg. and 3000 ft. west of long. 123 deg. . . . in the Eugene quadrangle" (Dr. Herman Clark, *in litt.*).

Diagnosis: As for the genus.

Description: Total length (as preserved), 120 mm.; original length, *ca.* 135 mm.; length of skull (anterior end to foramen magnum, dorsal surface), 15 mm.; width of skull (across paroccipital processes), 13 mm.; length and also width of ischiopubis, 6 mm.; length of limb bones: humerus, 9.5 mm.; radius, 7 mm.; ulna, 7.5 mm.; digit 3, manus, 6.5? mm.; femur, 9 mm.; tibia, 5.5 mm.; fibula, 6 mm.; digit 3, pes, 6 mm.

The paroccipital processes are large and are produced laterad, abutting the squamosals from behind. The frontosquamosal arches are complete and robust. The dorsal aperture of the cavum internasale is long and wide, and is bordered anteriorly and laterally by the ascending processes of the premaxilla. The vomerine opening of the cavum internasale is large (probably in part artificially); it lies wholly within the vomer. The anterior border of the vomer is an arc of a circle (roughly), with no sharp breaks in its periphery. No teeth are preserved, but the vomerine tooth rows are evident though crushed and incomplete.

The vertebrae are relatively shorter than in *Taricha*. There are 14 presacral vertebrae (13 in *Taricha*). Even the atlas has an expanded top, which, however, narrows anteriorly. Instead of the dorsal surface of the atlas sloping downward anteroventrally as in *Taricha*, in *Palaeotaricha oligocenica* it is horizontal for most of its length, then there is a short ventrally directed slope toward the anterior end, and then a sudden vertical drop to the condylar facets (Pl. 1, figs. 2, 3). The neural spines of the caudal vertebrae lack the expanded tops.

Five¹ thoracic ribs of the left side are exposed in good condition (Pl. 1, fig. 1; Pl. 3, fig. 1). All but the caudalmost have conspicuous uncinatè processes, which, in successively posterior ribs, become shorter and more distal.

The great length of the scapula suggests that the suprascapula was ossified (or calcified). There are four digits in the manus. The phalangeal count is 1-2-3-2, which, together with the carpal basale formula (1+2, 3, 4), is the same as in *Taricha*.

The pelvic girdle has floated free and, with the limbs, is fairly well preserved as a unit. The pelvic girdle is apparently a highly ossified and coëssified structure. Zones of weakness may perhaps exist anteriorly between left and right halves, and between the

¹ Some of the things that look like ribs in Plate 1, figure 1 are phalanges of the left manus.

pubes and ypsiloid cartilage. The latter is heavily ossified (or calcified; there is no obvious difference in preservation between it and any other part of the skeleton). About 5 mm. of it are preserved, of which 2 mm. are proximal to the bifurcation. The prepubic processes are rounded and robust. They project laterally and apparently slightly posteriad in *P. oligocenica*, but anterolaterad in *Taricha*, where they are also less demarcated from the pubes. There are five digits in the pes; the phalangeal count is 1-2-3-3-2. The tarsal basale formula is 1, 2, 3, 4+5, whereas the *Taricha* specimens have 1+2, 3, 4, 5.

On the whole the skeleton gives the appearance of having great strength, with the girdles and limb elements all well ossified, and the top-heavy neural spines.

Discussion: The elongation of the maxillae seems to be a primitive character of Salamandridae. In all the fossil genera of which the skulls are known the maxillae articulate with the quadrates: *Archaeotriton*, *Brachycormus* von Meyer, 1860, *Heliarchon*, *Oligosemia*, *Palaeopleurodeles* Herre, 1941, and *Polysemia* (all Miocene; *Oligosemia* also Oligocene). In three of the more primitive Recent salamandriids, *Pleurodeles* Michahelles, 1830, *Salamandrina* Fitzinger, 1826, and *Tylototriton* Anderson, 1871, the maxillae may very nearly or actually touch the quadrates. In the *Palaeotaricha oligocenica* specimen, although the maxillae clearly articulate (fuse?) with the suspensoria, the indistinct quadrate-squamosal sutures make it difficult to see exactly which suspensorial element is involved with the maxillae. I have assumed that the quadrate is involved, because of the condition in the forms just cited. Other than the maxillae, the *P. oligocenica* skull seems to fall within the variation of the skulls of the several *Taricha* species. In *T. granulosa* the vomerine tooth rows generally diverge slightly, from the anterior to the posterior ends; in the other species they are parallel or very slightly divergent for most of their length, then suddenly they are strongly divergent for the remaining $\frac{1}{4}$ or $\frac{1}{3}$. There is, however, a good deal of individual variation and intergradation between these tooth-row patterns. The available skulls of *T. sierrae* and *T. rivularis* (three of the former, four of the latter) seem to be rather similar, and to stand apart from the skulls of the other two species. For one thing, the skull of *rivularis* and *sierrae* tends to be somewhat deep and domed, in contrast to the

more-or-less flattened and widened roof of the others. *T. rivularis* and *sierrae* tend to have the dorsal opening of the cavum internasale especially long and wide. In anterior view it is seen as a notch whose bottom lies ventral to the dorsal border of the nares, which is not the case in *torosa* or *granulosa*; nor does it extend so far forward in the latter two species. The above characters are more pronounced in *rivularis* than in *sierrae*, but the following character is equally developed in the two. The ventral (vomarine) opening of the cavum internasale is greatly elongated — roughly the size and shape of the dorsal opening — and extends beyond the anterior border of the vomer into the premaxilla. In the other species this aperture is usually circular or slightly elliptical, and is wholly situated within the vomer. In about ten alcoholic specimens each of *rivularis* and *sierrae*, and many more of *torosa* and *granulosa*, this difference is corroborated. In one skull of *granulosa*, however, there is a very small, extra, opening into the cavum internasale anterior to the vomer-premaxilla border — a feature that would be very difficult to note in an alcoholic specimen. It would be very interesting to know whether the elongated aperture is an evolutionary advance (cf. *Palaeotaricha*) or is primitive (cf. primitive extant genera of salamandrids, which have the premaxilla paired, and some have the aperture extremely large).

A full description of the skull of *T. torosa* is given by Bolkay (1928) (under the name *Diemyctylus* [*sic*] *torosus*; his specimen could be a *granulosa*, judging by the vomarine tooth rows), as well as descriptions of the skulls of most of the Recent salamandrid species.

The condition in the vertebrae — the expanded tops — of *Palaeotaricha oligocenica* is not only different from that in *Taricha*, where the neural spines are high but narrow, but quite different from any other urodele vertebrae that I can find. Among Recent salamandrids *Tylototriton* comes closest in this respect, *fide* Herre (1949) and corroborated in the specimens available to me. But in *Tylototriton* the expansion is much less prominent, and the width decreases anteriorly; the tops of the spines are, however, sculptured, and they do contact in series, as in *P. oligocenica*. The closest approach of all seems to be in the Miocene *Chelotriton* Pomel, 1853, which has a broad top on the neural spine also. But (at least in the specimen figured by Herre,

1949, p. 225, fig. 8) the anterior half of the spine comes to a rounded point, and the posterior end is bifurcated by a wedge-shaped notch. Thus it seems that the *Chelotriton* vertebra has merely a greatly expanded neural spine, and is not fundamentally different from that of most salamandrids (e.g. *Taricha*, Pl. 1, fig. 5). Now arises the question (considering the absence of visible sutures between the vertical and horizontal portions of the *P. oligocenica* neural spines) of whether we have a structural series of increasingly expanded neural spines — *Taricha*, *Tylostotriton*, *Chelotriton*, *Palaeotaricha* — or whether the latter is not in this series, the spinal expansions being dermal plates plastered on top (as suggested by the sculpturing). I favor the latter view: the expansions *look* like dermal plates; and, of course, the series just given has only descriptive validity.

The uncinata processes of the *P. oligocenica* ribs are longer than in the Recent *Taricha* specimens at hand, but these structures are quite variable in individual salamanders. In three specimens of *Taricha g. granulosa* I have seen, one has uncinata processes on ribs 2 and 3 on the right side; on rib 2 only, on the left. Another has uncinate processes on ribs 2 to 4 on both sides; the third specimen has them on 2 to 7 on both sides. One specimen of *Cynops pyrrhogaster* has uncinate processes on ribs 2 to 6 on the left side, on 2 to 7 on the right; another has no uncinate processes at all. And so it goes. In all these cases the larger and more fully ossified the individual, the greater the number of uncinata processes. In nearly every specimen I have seen there are incipient uncinate processes on the first one or two ribs distal to the last one that has a distinct uncinata process.

The tarsal basale formula in *P. oligocenica* — 1, 2, 3, 4+5 — contrasts with 1+2, 3, 4, 5 in the Recent *Taricha*, *Chioglossa* Barboza du Bocage, 1864, *Salamandra* Laurenti, 1768, *Mertensia* Wolterstorff, 1934, and *Pleurodeles* Michahelles, 1830, while *Salamandrina* with four toes on all feet apparently has 1, 2, 3, 4, and all other genera have 1+2, 3, 4+5, *fide* Bolkay (1927), and in agreement with additional material seen by me.

It is interesting to note that the carpus, as compared with the tarsus, is apparently much more nearly constant throughout the Salamandridae. As figured by Bolkay (1927) and corroborated and extended by the specimens available to me, the carpus has

basales 1+2, 3, 4, prepollex basale,¹ centrale, radiale, intermedium, and ulnare, in all genera. The latter two may or may not be fused, but usually are: in one specimen of *Triturus vulgaris* the intermedium of the right manus is separate; the left is fused with the ulnare.

While the observations of Hilton (1948) agree in general with those of Bolkay and me, Hilton illustrates various cases of fusion of carpal and tarsal elements, and extra elements (such as the non-fusion of tarsal basales 4 and 5 in a specimen of *Cynops pyrrhogaster*). In the light of Hilton's data, the difference between the *Palaeotaricha* and the *Taricha* tarsus may not be significant. Yet it must be pointed out that all of the 16 specimens of *Taricha* at hand have the same tarsal and carpal structures.

The large size and knob-like shape of the prepubic process of *P. oligocenica* also seem to be unique. When these processes exist in the Recent specimens at hand, they are always smaller, more pointed, and directed at least partly anteriad. Nor do any of these Recent pelves have the fusion of the left and right halves to the extent seen in *P. oligocenica*, where scarcely even a raphe remains of a former suture.

From all appearances *Palaeotaricha* is not ancestral to *Taricha*, but is its nearest relative. I do not feel that *Palaeotaricha* helps determine the further affinities of *Taricha*, for the one character that might seem to indicate relationship with other genera — the elongated maxillae in *Palaeotaricha* — is merely primitive and not unexpected.

Material examined: I have been fortunate in being able to examine skulls and skeletons of every genus of Recent Salamandridae, with the single exception of *Pleurodeles*, and to see alcoholic specimens of nearly every species of all genera. It must be emphasized, however, that except for 16 specimens of the three species of *Taricha*, in no case have I seen more than two skeletons. Hence I do not feel that my knowledge of intraspecific variation is sufficient for more than tentative authority on the above comparative skeletal studies.

Note on the stereophotography

The ventral view of the *P. oligocenica* skull (Pl. 2, A) was

¹ Bolkay follows another usage in calling this element carpal basale 1; and what he calls 2 is here called 1+2. Likewise he designates the prehallux basale as tarsal basale 1, and 1+2 as 2.

made by Dr. Donald Baird, of this Museum, and myself, with a binocular (stereoscopic) microscope, and a Leica 3C camera fitted with a Leitz Focaslides and Leitz Micro-Ibso. The ocular lens of the latter was inserted alternately into the two tubes of the microscope, and exposures were made in the two positions of the apparatus, at an interocular distance of $2\frac{1}{2}$ inches. The latter refers to the positions of the Focaslides, which was used because it was found that the side telescope of the Micro-Ibso was not sufficiently accurate for the depth of focus required. This method may be theoretically superior to the tilt method usually used, since it takes care of matters of interocular distance and angles more easily. But for subjects as large as the present ones considerable trial-and-error choice of microscope lenses was necessary to get the entire image into view.

All the other figures were made with a Kodak 2-D 5" x 7" view camera fitted with a 135 mm. lens, and mounted on a pivoted arm. One picture of each stereoscopic pair was taken vertically, the other at 7° from the vertical. Exposures were 20 seconds at f. 22, using panatomic film, and illuminated by two 100- and one 200-watt bulb with reflectors, each about 2 feet from the subject.

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EXPLANATION OF PLATES

PLATE 1

Figs. 1, 2, 4. *Palaeotaricha oligocenica*, holotype, University of Oregon Museum of Natural History, no. F-5405. Fig. 1. Entire specimen (except end of tail). Skull seen ventrally, spinal column from right side. Fig. 2, *A, A'*. Stereograph of vertebrae 1 to 3, left side. Fig. 4. Vertebrae 10 to 12, left side. The neural spines of all precaudal vertebrae are bent sinistrad. Figs. 3, 5. Vertebrae of a *Taricha torosa*. Fig. 3. Vertebrae 1 and 2. Fig. 5. Vertebrae 9 and 10. *od*, Odontoid process. Fig. 1 x 1; figs. 2-5 x 6.

PLATE 2

Palaeotaricha oligocenica, skull of holotype. *A, A'*, stereograph of dorsal view. *B, B'*, ventral view. *a*, Atlas; *dci*, dorsal opening of cavum internasale; *en*, external naris; *f*, frontal; *fsa*, frontosquamosal arch; *fv*, foramen vestibuli; *hy*, parts of hyoid apparatus; *in*, internal naris; *lj*, lower jaw; *m*, maxilla; *n*, nasal; *nld*, nasolacrimal duct?; *oc*, occipital condyle; *op*, occipito-petrosal; *os*, orbitosphenoid (the white dot may be the optic foramen); *p*, parietal; *pam*, palatine part of maxilla; *pm*, premaxilla; *poc*, paroccipital process; *prf*, prefrontal; *ps*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *s*, squamosal; *vei*, vomerine opening of cavum internasale; *v*, vomer. All figures x 2¼.

PLATE 3

Palaeotaricha oligocenica, holotype. Fig. 1. Right pectoral girdle and limb, and ribs 3 to 7. Forearm and manus in dorsal view, other parts in right side view. *bc 1+2*, Carpal basales 1+2; *bc ~~1+2~~ 4*, carpal basales ~~1+2~~ 4; *h*, humerus; *mc 1*, metacarpal 1; *ppb*, prepollex basale; *r*, radius; *ra*, radiale; *r6*, rib 6; *s*, scapula; *u*, ulna; *ul+i*, ulnare + intermedium.

Fig. 2. Pelvic girdle and limbs. Pelvis and left limb in ventral view, right limb (left side of photograph) in dorsal view. *bt 4+5*, Tarsal basales 4+5; *c*, centrale; *f*, femur; *fe*, fibulare; *fi*, fibula; *i*, intermedium; *phb*, prehallux basale; *prp*, prepubic process; *t*, tibia; *ti*, tibiale; *y*, ypsiloid process. Both figures x 2¼.



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