

A redescription and phylogenetic analysis based on new material of the fossil newts *Taricha oligocenica* Van Frank, 1955 and *Taricha lindoei* Naylor, 1979 (Amphibia, Salamandridae) from the Oligocene of Oregon

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Abstract.—Complete body fossils of salamanders are relatively rare, but provide critical information on the evolutionary roots of extant urodele clades. We describe new specimens of the fossil salamandrids *Taricha oligocenica* Van Frank, 1955, and *Taricha lindoei* Naylor, 1979, from the Oligocene Mehama and John Day formations of Oregon that illustrate aspects of skeletal morphology previously unseen in these taxa, and contribute to our understanding of population-level variation. Morphological analysis of these specimens supports the classification of *T. oligocenica* and *T. lindoei* as two different species, distinct from extant *Taricha*. Parsimony-based, heuristic analysis of phylogeny using 108 morphological characters for 40 taxa yields different results from a phylogenetic analysis that excludes four taxa known only via vertebrae. Our smaller analysis generally agrees with molecular phylogenies of the family Salamandridae, but with poorer resolution for molgin newts, especially between *Taricha* and *Notophthalmus*. The analysis including all taxa produced polytomies mostly related to complications from several fossil taxa. The presence or absence of dorsally expanded, sculptured neural spine tables on trunk vertebrae, an important character in past descriptions of fossil salamandrids, appears to be either homoplastic within the Salamandridae, or requires an expansion of characters or character states. *Taricha oligocenica* and *T. lindoei* are separate species of an at least 33 million-year-old clade, but their relationships with each other and extant North American salamandrids remain unclear with current levels of morphological data. Salamandrid research requires additional morphological data, particularly for the vertebrae and ribs, to better resolve salamandrid evolutionary history through morphological characters.

Introduction

The pre-Pliocene fossil record of North American newts (Salamandridae, Tarichina) is sparse, especially west of the Rocky Mountains, yet it extends far back into the Oligocene (32–33 Ma). Previous morphological comparisons with extinct and extant North American salamanders recognized at least two species of fossil salamanders from Oregon's early Oligocene deposits: *Taricha oligocenica* of the Mehama Formation in western Oregon (Van Frank, 1955), and *Taricha lindoei* of the John Day Formation in eastern Oregon (Naylor, 1979). Van Frank's *T. oligocenica* and Naylor's *T. lindoei* are found in beds assigned to the Rupelian Stage (30–33 Ma; early Oligocene; dates by Retallack et al., 2000, 2004), suggesting correspondence with the Orellan NALMA of the early Oligocene for *T. oligocenica* and *T. lindoei* (Albright et al., 2008). Naylor (1982) described another *Taricha* specimen from the early Oligocene (32–33 Ma) Gumboot Mountain strata in Washington, but to genus only. Farther east, vertebrae from a third species, *Taricha miocenica*, have been uncovered in Montana's late Oligocene (Arikarean; 24–26 Ma) Middle Cabbage Patch Beds (Tihen, 1974; Rasmussen, 1977; Rasmussen and Prothero,

2003), while fossil trackways from the late Miocene of California and the late Miocene of Kansas have also been identified as *Taricha* (Peabody, 1959; Holman, 2006). Although we did not examine any fossils of *T. miocenica* in this study, Tihen (1974) proposed the grouping of *T. oligocenica* and *T. miocenica* into the subgenus *Palaeotaricha* (not recognized in the latest classifications; Estes, 1981; Holman, 2006; Dubois and Raffaëlli, 2009). If the latest classifications are correct, then *T. miocenica* would represent one of the two occurrences of *Taricha* (along with the Kansas Miocene trackways) east of the Rocky Mountains.

Several previously described, partial to nearly complete skeletons from Oligocene localities in the John Day and Mehama formations of Oregon represent excellently preserved, post-metamorphic individuals of the genus *Taricha*, also known as Pacific (or Western) newts (Van Frank, 1955; Naylor, 1979; Holman, 2006; Fremd, 2010; McCloughry et al., 2010). Additional undescribed specimens include fossils from new localities near Gray Butte, Oregon and Lyons, Oregon, and a large individual from Goshen, Oregon. This study examines the new specimens and redescribes previously examined material. We also investigate the evolutionary relationships of the family Salamandridae in North America, because the migration of salamandrids to North America and their subsequent divergence into the genera *Taricha* and

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Notophthalmus is poorly understood (Tihen, 1974; Naylor, 1979; Naylor and Fox, 1993).

We identify Oregon's fossil salamanders and examine diagnostic skeletal characters for use in future phylogenetic analyses with extinct and extant North American salamandrids. Furthermore, we examine previously described fossil *Taricha* to determine whether these specimens are truly separate species, morphological variations within a single species, or if they represent a distinct genus from extant Pacific newts. We incorporate new, previously undescribed specimens from various Oregon localities, along with the previously described specimens of *T. oligocenica* (Van Frank, 1955) and *T. lindoei* (Naylor, 1979). By pursuing these goals, we aim to answer the following questions: Are previous identifications and descriptions of the Oligocene fossil salamanders of Oregon adequate? How do these fossil salamanders relate to each other and to extant taxa? Can we gain any insight on the functional morphology of these newts? Finally, what can the paleoecology and distribution of these salamanders tell us about the distribution and evolution of North American salamandrids?

Geologic setting

The southern Willamette Valley of Oregon is an alluvial basin bordered to the west by the Coast Range and to the east by the Western Cascades physiographic provinces. The basin is within the seismically active Puget–Willamette Lowland, and is situated along the Cascadia subduction zone, where the Juan de Fuca plate has been subducting obliquely beneath the North American continental plate for much of the Cenozoic (McCloughry et al., 2010). This has resulted in a complicated forearc basin that has locally accumulated >7,000 m of sedimentary and volcanic strata since the Paleocene (Retallack et al., 2004; McCloughry et al., 2010). The exposed rocks of the southern Willamette Valley include a diverse series of Paleogene marine sedimentary rocks with submarine lavas, Paleogene and Neogene terrestrial volcanic and sedimentary rocks and intrusions, and Quaternary surficial deposits (Retallack et al., 2004; McCloughry et al., 2010). The Mehama Formation of the Little Butte Volcanics, within which the Willamette and Lyons floras and all Western Oregon salamander fossils are preserved, is locally fossiliferous and represents generally nondescript volcanoclastic sedimentary rocks that occur between the more distinctive features of the Little Butte Volcanics, such as mapped formations, marker beds, and volcanic centers (McCloughry et al., 2010).

Along with the latest Eocene–earliest Oligocene Goshen flora (34.85–32.8 Ma, $^{40}\text{Ar}/^{39}\text{Ar}$ dates), the early Oligocene Willamette flora (>30.64 Ma) is regarded as a critical indicator of climatic and vegetational shift across the Eocene–Oligocene transition (Retallack et al., 2004; Retallack, 2008). Thick lahars separate the dated ash from the lake beds of the Willamette flora, which is found between Spores Point tuff (31.3 ± 0.6 Ma) and a Little Butte Volcanics tuff (30.6 ± 0.5 Ma; Myers et al., 2002; Retallack et al., 2004; McCloughry et al., 2010). The presence of thick andesitic debris-flow deposits suggests that the Willamette Flora (and the salamanders found within it) grew in an unstable environment adjacent to the increasingly active Western Cascades (Myers et al., 2002).

The dark gray to whitish-tan shales of the Mehama Formation produce vertebrate specimens alongside numerous plant fossils. The presence of fossil *Taricha* agrees with the interpretation of the bedded shales as lake-margin deposits because this genus and the majority of this family feed in a freshwater environment; species of the genus *Taricha* prefer slow-moving or still water conditions (Wake and Özeti, 1969; Goin et al., 1978; Naylor, 1978a, 1978b, 1979; Retallack et al., 2004; Pollett et al., 2010).

The Lyons flora, located in northwestern Oregon (southeast of the town of Lyons, Oregon in the upper Thomas Creek area), is comprised of at least 24 plant taxa, 12 of which are identifiable to species, while the other 12 are identifiable to genus. The rocks within which the leaves are preserved are composed of thinly laminated, tuffaceous material that has been silicified (Meyer, 1973). The stratification of the beds, abundance of fossil leaves, and the presence of a water plant (*Nymphoides*) in the fossil record suggest a shallow, quiet lacustrine environment (Meyer, 1973). Retallack et al. (2004) have listed the Lyons flora among the forested Oligocene lacustrine floras. The Lyons flora has produced one definite salamander fossil, consisting of part and counterpart, thus far.

The John Day Formation is a complex series of strata with a unique record of the long-term change (~20 Myr) of climate and biotas for the Pacific Northwest of North America (Fremd, 2010). The John Day Formation occurs within a number of basins in north-central and central Oregon, all within the Blue Mountains physiographic province (Fremd, 2010).

The Big Basin Member of the lower John Day Formation has distinctive red and tan claystones and contains excellent paleobotanical localities, which also produce the vast majority of caudate fossils from eastern Oregon. Radiometric dates indicate that the Big Basin Member preserves ~9 Myr of deposition, from ~30–39 Ma (Bestland and Retallack, 1994; Retallack et al., 2000). The Bridge Creek Flora type localities, which are near the Eocene–Oligocene boundary, are within the lacustrine shales of the Big Basin Member in the Painted Hills Unit of John Day Fossil Beds National Monument, where fish and amphibian fossils have also been recovered (Meyer and Manchester, 1997; Retallack et al., 2000; Dillhoff et al., 2009; Fremd, 2010). The Bridge Creek flora's age is well dated (Bestland and Retallack, 1994; Retallack et al., 2000) because it is sandwiched between the underlying Biotite Tuff (32.99 ± 0.11 Ma) and the overlying Overlook Tuff (32.66 ± 0.03 Ma).

The fossil salamanders found in the Big Basin Member of the John Day Formation have been unearthed at the Wheeler County High School exposures in the town of Fossil, Wheeler County, Oregon (Naylor, 1979). Plant, vertebrate, and invertebrate fossils preserved in these rocks are consistent with a cooler temperate climate than found in the Willamette flora, with fewer Eocene subtropical holdovers present (Meyer and Manchester, 1997; Retallack, 2008; Dillhoff et al., 2009). Salamander fossil-bearing beds are between 32.66 Ma and 32.99 Ma, placing these fossils solidly in the Orellan NALMA (Bestland and Retallack, 1994; Retallack et al., 2000; Albright et al., 2008).

The smallest fossil salamander, and most recent acquisition for this study, is from a new locality for vertebrate fossils. The area, near Gray Butte and the town of Prineville in central Oregon, has produced a limited fossil flora in the past. Based on

the work of Thormahlen (1984) and Smith et al. (1998), the location of this specimen coincides with the Trail Crossing flora, which to date has produced *Acer*, *Alnus*, *Fagus*, and *Quercus* fossils from ashy, tan to yellow, massive to stratified, highly silicified lacustrine siltstone and sandstone beds. These beds are consistent with the temperate, hardwood-dominated Bridge Creek flora of the Oligocene. The fossils from Gray Butte are between 32–33 Ma because the overlying alkali-olivine basalt is $^{40}\text{Ar}/^{39}\text{Ar}$ -dated at 32.49 ± 0.30 Ma, and the lithology of the Gray Butte area aligns with the middle Big Basin Member of the western facies of the John Day Formation.

Materials and methods

Systematic paleontology and comparative morphology.—For this study, we re-examined all the previously described specimens of fossil salamanders from the Oligocene of Oregon, as well as a number of previously undescribed specimens and the skeletons of several extant salamandrids. This included comparing them to modern salamander taxa in order to understand caudate evolutionary relationships during a period of climatic cooling, floral transition, and perhaps increased seasonality during the early Oligocene in the Pacific Northwest of North America. The specimens are in collections at the University of Oregon Museum of Natural and Cultural History (UOMNH), University of California-Berkeley Museum of Paleontology (UCMP), and John Day Fossil Beds National Monument (JODA).

Table 1 contains a list of the specimens examined. We examined skeletons and isolated bones of eight *Taricha granulosa*, a single *Taricha sierrae*, seven *Taricha torosa*, 12 *Taricha rivularis*, and four *Notophthalmus viridescens*, in addition to the fossils of five *T. oligocenica*, 12 *T. lindoei*, and one fossil identified to genus *Taricha*. For all examined specimens, we recorded morphologic details of the scapulocoracoid, phalangeal count, and vertebral column, especially the atlas and trunk vertebrae, since these features have been noted as useful for diagnosing fossil salamanders in the past (Estes, 1981; Holman, 2006). We paid special attention to details of the skull when possible because it is rare to find a complete or mostly complete salamander skull in the fossil record, where skull fragments and postcrania (particularly trunk vertebrae) are much more common than articulated specimens. The systematic descriptions provide details of the morphology of these structures. We coded several of these details into the phylogenetic analysis as characters.

Because each fossil preserves different areas of the skeleton, establishing useful measurements is a complex task. For example, the vertebral measurements used in Tihen (1974) are difficult to apply to fossils that are articulated skeletons, impressions, or flat (as are so many of the relatively complete salamander fossils). Instead, this study uses a variety of measurements, as applied by Good and Wake (1992) to the morphometrics of the genus *Rhyacotriton* and by Kuchta (2007) to the morphometrics of *T. torosa* and *T. sierra*, whenever possible. While the small sample size and limited variety of age classes for fossils make it unlikely that we can perform a morphometric analysis in the manner of Good and Wake (1992) and Kuchta (2007), these measurements are still useful for determining body proportions and predicting the size of

Table 1. List of specimens with collection numbers. Dagger symbol (†) indicates extinct taxa.

Taxon	Specimen #
<i>Taricha oligocenica</i> †	UOMNH F-5405, UOMNH F-30648, UOMNH F-36412, UOMNH F-55196, UOMNH F-59812 A-B,
<i>T. lindoei</i> †	UOMNH F-35553, UOMNH F-59813, UOMNH F-30616, UOMNH F-109709, UOMNH F-109710, UOMNH F-110577, UOMNH F-111395 A-B, UOMNH F-37883 A-B, JODA 10429 A-B, JODA 1230, UCMP 137464, UCMP 137466
<i>Taricha</i> sp.†	UCMP 137465
<i>T. granulosa</i>	UCMP 118876, UCMVZ 67956, UCMVZ 67969, UCMVZ 218168, UCMVZ 218169, UCMVZ 218170, UCMVZ 218171, UCMVZ 218172
<i>T. rivularis</i>	UCMP 81746, UCMVZ 78190, UCMVZ 111544, UCMVZ 111546, UCMVZ 111548, UCMVZ 68232, UCMVZ 68233, UCMVZ 68234, UCMVZ 68235, UCMVZ 68236, UCMVZ 68237, UCMVZ 78191
<i>T. torosa</i>	UCMP 81747, UCMVZ 4480, UCMVZ 68179, UCMVZ 68180, UCMVZ 68181, UCMVZ 68182, UCMVZ 129891
<i>T. sierrae</i>	UCMP 129892
<i>Notophthalmus viridescens</i>	UCMP 117050, UCMP 118873, UCMP 118874, UCMVZ 185290

individual specimens. These measurements include snout-vent length (SVL), tail length (TL), snout-gular length (SG), head width (HW), eye width (EW), distance between the eyes (E-E), distance from eye to nostril (E-N), axilla-groin length (AG), trunk width (TW), forelimb length (FLL), hind limb length (HLL), and foot length (FL). We used digital calipers or a metric ruler at the millimeter scale for all attainable measurements for each fossil. Some of these measurements (SVL, SG, and AG) use soft-tissue reference points (Good and Wake, 1992; Kuchta, 2007), and we adjust these to use osteological landmarks that represent corresponding measurements for fossil taxa. Here, the anterior edge of the premaxilla to the posterior edge of the pelvic girdle is SVL, the anterior edge of the premaxilla to the anterior portion of the atlas is SG, and the length of the trunk between the forelimb and the hind limb is AG.

We took all University of Oregon (UO) and John Day Fossil Beds National Monument (JODA) fossil salamander photos with a Nikon D-90 at a focal length of 90 mm. We photographed all University of California–Berkeley specimens using either a Nikon optiphot2-pol with a Nikon digital sight ds-fi2 attachment, or a Nikon Coolpix L24 digital camera.

Phylogenetic analysis.—Our matrix expands upon the matrix of Marjanović and Witzmann (2015), with the addition and/or adjustment of a few characters (Supplementary Data Sets 1, 2). Many of the characters in our matrix also use characters (Supplementary Data Set 1) first established in Wake and Özeti (1969), Titus and Larson (1995), Venczel (2008), and Schoch and Rasser (2013). Naylor (1978b) made a few adjustments to the morphology-based phylogeny of Wake and Özeti (1969), some of which are adopted in this analysis. We also added a few characters of our own to test their usefulness for analyzing North American taxa specifically (specimen availability did not allow us to make clear observations on taxa outside of North America for the purpose of coding these characters). We coded other characters relating to non-North American taxa according to the observations of Wake and Özeti (1969), Titus and Larson

(1995), Venczel (2008), Schoch and Rasser (2013), Naylor (1978b), and Marjanović and Witzmann (2015). We included a variety of characters, comprising skeletal, behavioral (including reproductive), soft-tissue, and geographic characters in this matrix, and we coded soft-tissue and behavioral characters as unknown for fossil taxa.

We assembled the matrix of this study in Mesquite 2.75 (Maddison and Maddison, 2011), then ran a heuristic analysis using the Phylogenetic Analysis Using Parsimony program Version 4.0a152 (PAUP; Swofford, 2002) to produce simple parsimony trees. We elected to use simple parsimony for our analyses because they contained multistate, ordered, and unordered characters. We analyzed a total of 108 characters and a total of 40 taxa in a matrix using all characters, including both unconstrained and molecularly constrained (via consensus data assembled in Marjanović and Witzmann, 2015) from Zhang et al. (2008) and Pyron (2014) analyses. With 108 characters (33 ordered), this analysis is the largest morphological matrix used for analyzing salamandrid evolutionary relationships to date. In another round of heuristic analyses, we removed fossil new taxa known only from vertebrae (*Koalliella*, *Taricha miocenica*, *Notophthalmus crassus* [in this case, including the fossils sometimes assigned to *Notophthalmus slaughteri*; Holman, 2006], and *Notophthalmus robustus*) prior to running unconstrained and molecularly constrained analyses. We coded characters inapplicable or unknown for a taxon (e.g., soft tissue characters when coding fossil taxa) with question marks. Bracketed numbers indicate a character's original number from its referenced source (Supplementary Data Sets 1, 2). We performed a heuristic search with 1000 repetitions of stepwise addition with random addition sequence using the sectorial search algorithm setting, and TBR (tree bisection and reconnection), with all characters weighted equally. We calculated the Consistency Index, Retention Index, and Homoplasy index, as well as strict consensus trees, in PAUP.

Ambystoma and *Dicamptodon* are outgroups for our analyses. Within *Taricha*, *T. sierrae* was combined with *T. torosa* because there was not enough morphological character data available, and few positively identified skeletal specimens available to distinguish the species from *T. torosa*. As such, *T. sierra* as presently understood scores identically to *T. torosa* in our morphological phylogenies. Because of our lack of data, we did not include *Notophthalmus slaughteri* because it may be synonymous with *Notophthalmus crassus*, and we have no direct observations of either potential species (Holman, 2006).

We modified the assigned character states for taxa in a few cases for previously used characters based on personal observations and/or previously published literature; this is particularly true for *Tylotriton* in character 71, and character 61 for extant species of *Taricha*. Character 71 refers to the presence of ribs either as short rods (0) or as long as three vertebral centra (1), yet in at least *Tylotriton verrucosus*, the ribs do not quite exhibit character state 1 (based on Nussbaum and Brodie, 1982) because they are closer to the length of two vertebral centra, while *Tylotriton asperrimus* was initially assigned to *Echinotriton* partially because their trunk ribs fit character state 1 (Nussbaum et al., 1995). We assigned both

states 0 and 1 to *Tylotriton* as a genus. The length of the ribs in *Taricha oligocenica*, and to a lesser extent, *Taricha lindoei*, are visually similar to those of *Tylotriton verrucosus*, both in terms of length and in the number, structure, and orientation of the epipleural processes, which we discuss briefly later. We therefore assigned a character state of 0 to these taxa, but recommend further investigation of this character as a whole, because the ribs of *Tylotriton verrucosus* and *Taricha oligocenica* do not quite fit either character state (longer than simple, short rods, but shorter than described in state 1).

Repositories and institutional abbreviations.—JODA, John Day Fossil Beds National Monument; UALVP, University of Alberta Laboratory for Vertebrate Paleontology; UCMP, University of California – Berkeley Museum of Paleontology; UCMP, University of California – Berkeley Museum of Vertebrate Zoology; UOMNH, University of Oregon Museum of Natural History.

Systematic paleontology

Class Amphibia Gray, 1825
 Subclass Lissamphibia Haeckel, 1866
 Order Caudata Scopoli, 1777
 Suborder Salamandroidea Fitzinger, 1826
 Family Salamandridae Goldfuss, 1820
 Genus *Taricha* Gray, 1850

Type species.—*Taricha torosa* (Rathke, 1833).

Diagnosis.—Osteologic characters of extant *Taricha* include a low to moderately high neural spine without an extensive pitted dermal cap (Wake and Özeti, 1969; Naylor, 1978b). The genus *Taricha* also possesses concave inter-prezygapophyseal neural arch margins (Boardman and Schubert, 2011). The premaxillae are fused, nasals are separated, the rib processes do not extend past the body wall (no costal grooves), anterior caudal ribs (caudosacral ribs of Estes, 1981) are absent, and the cotyles of the vertebrae appear horizontally oval (Estes, 1981). The hyobranchium possesses a cartilaginous, mineralized first basibranchial and second ceratobranchial, but lacks the second basibranchial and anterior radii. *Taricha* also has a reduced interradial cartilage (Estes, 1981).

Remarks.—*Taricha*'s closest relative is *Notophthalmus*, the only other North American newt genus. It is important to note that extinct species *Taricha oligocenica* (Van Frank, 1955) and *Taricha miocenica* (Tihen, 1974) possess pitted spine tables on the dorsal side of their vertebrae, leading to questions about the ancestral state of North American newts. Weaver (1963) determined that the shape of the vomerine (then incorrectly thought to be “prevomerine”; Atkins and Franz-Odenaal, 2015; Marjanović and Witzmann, 2015) tooth row of extant *Taricha* is distinguishably different between *Taricha granulosa*, which displays the plesiomorphic V-shaped arrangement, and *Taricha torosa*, *Taricha sierra*, and *Taricha rivularis*, which all display a Y-shaped pattern.

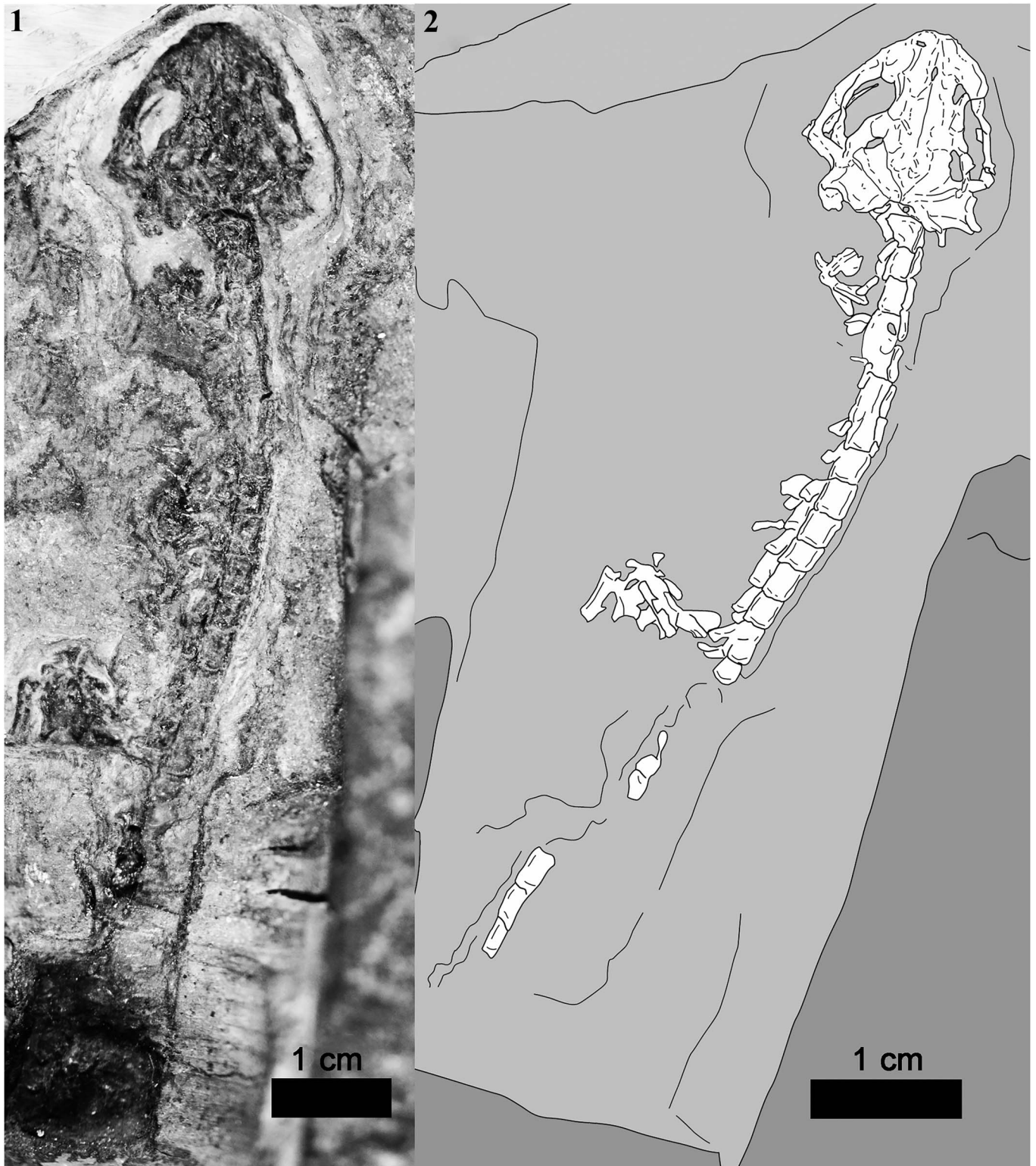


Figure 1. Dorsal view of UOMNH F-5405, type specimen of *T. oligocenica* as a photograph (1) and a line drawing (2).

Taricha oligocenica Van Frank, 1955
 Figures 1–4, 5.1, 5.3

1955 *Palaeotaricha oligocenica* Van Frank in Van Frank,
 p. 4, pl. 1–3.

1974 *Taricha (Palaeotaricha) oligocenica* Van Frank in
 Tihen, p. 215.

1981 *Taricha oligocenica* Van Frank in Estes, p. 85.

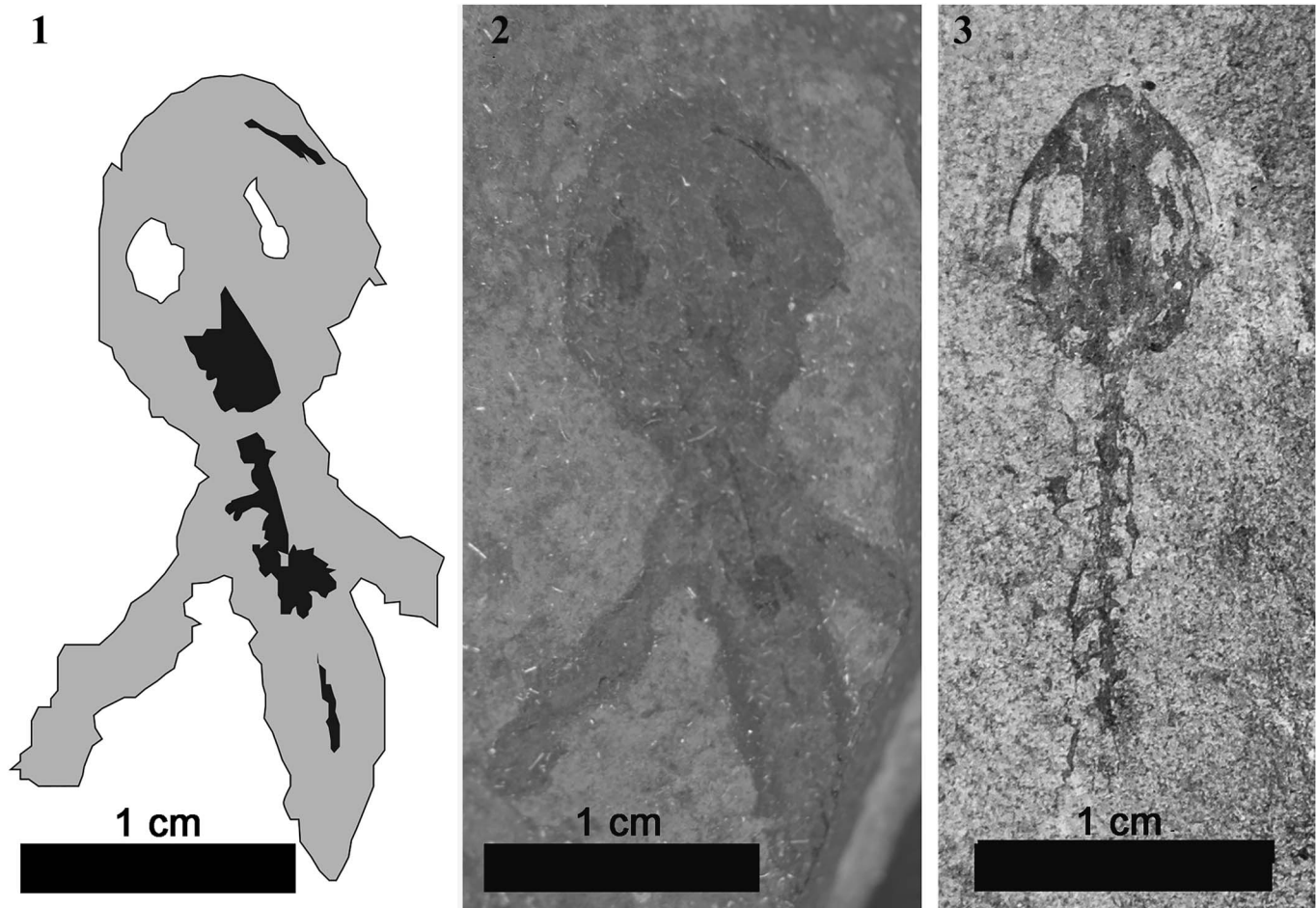


Figure 2. Possible juveniles of *T. oligocena*. UOMNH F-36412: (1) line drawing and (2) photograph; (3) photograph of UOMNH F-30648.

Holotype.—UOMNH F-5405, a mostly complete skeleton, early Oligocene, Mehama Formation, Lane County, Oregon, UO 11026 Goshen.

Diagnosis.—Possesses a broad, rectangular, expansive dorsal spine table on the neural spines of the vertebrae (Fig. 5.1, 5.2; Tihen, 1974; Estes, 1981; Holman, 2006). *Taricha oligocena* exhibits three apparently unique characteristics for the genus: (1) the atlantal neural crest of *T. oligocena* is tall and extends laterally on the dorsal side of the vertebra towards the anterior end of the atlas, before forming a short anteroventral slope, followed by an abrupt ventral drop to the condylar facets (Fig. 5.3, 5.4); (2) *T. oligocena* has an anteriorly narrowing, dorsal expansion on the top of the atlas (Fig. 5.3); and (3) *T. oligocena* exhibits a narrow scapular portion of the scapulocoracoid (Van Frank, 1955; Naylor, 1979, 1982; Holman, 2006). *Taricha oligocena* also possesses sculpturing in the dermal bones of the skull roof, particularly the frontals, parietals, squamosals, and frontosquamosal arch. *Taricha oligocena* possesses elongate, distinct epipleural rib processes.

Occurrence.—Early Oligocene, Oregon

Description.—The posterior extension of the maxillae of UOMNH F-5405 and UOMNH F-30648 project nearly to the

quadrate, similar to extant *Taricha* and much farther than in extant *Notophthalmus*. Preparation performed on the type specimen (UOMNH F-5405) after its initial publication revealed that the maxillary and quadrate elements do not fuse or suture in *T. oligocena*. The premaxillae are fused and the paroccipital processes project strongly, abutting the posterior side of the squamosals. The bony frontosquamosal arches in all specimens appear to be more robust than in modern *Taricha* of similar size, and are complete; the skull and the frontosquamosal arches (best preserved in the type; Fig. 1) are also more sculptured than typically seen in extant *Taricha*. As in all Western newts, the opening of the cavum internasale is large (Van Frank, 1955; Wake and Özeti, 1969).

The vertebral features are also listed in the diagnosis. The vertebrae are opisthocoelous with laterally extensive rectangular dorsal expansions that are broad, flat, and somewhat sculptured (Fig. 5.1). These spine tables extend over the entire dorsal surface of the trunk vertebrae, including the atlas, and abut each other both anteriorly and posteriorly (Figs. 4, 5). While previously only the type specimen preserved these spine tables, this character appears to be similarly expansive and identical in shape in the newer UOMNH F-59812 A-B (Fig. 4) specimen. The neural spines are high and elongate, and there are 14 presacral vertebrae. The atlas differs significantly from that of recent *Taricha*.

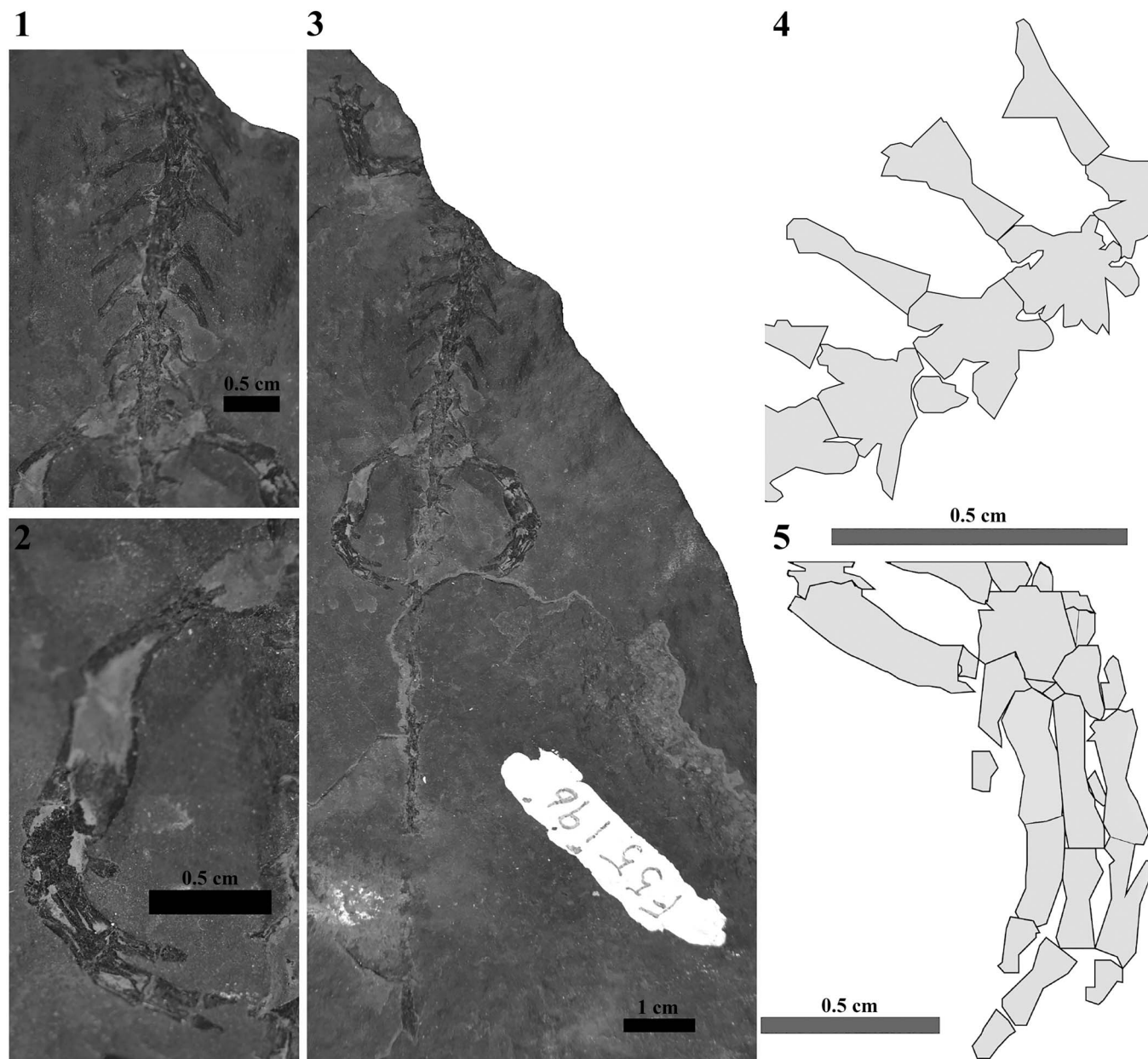


Figure 3. Ventral view of UOMNH F-55196, the largest individual of *T. oligocenica*. (1) Close-up of the trunk, showing the diagnostic epipleural rib processes; (2) right pes (left side), which is fully ossified, a condition not commonly seen in extant *Taricha*; (3) full ventral view of UOMNH F-55196; (4) line drawing of right ribs, ventral view, with epipleural processes clearly visible; (5) line drawing of fully ossified left pes.

The ribs of *T. oligocenica* possess long epipleural processes that decrease in size towards the tail (Figs. 3.1, 3.4, 4.1, 4.2). Van Frank (1955) noted that the number of these epipleural rib processes varied in number by individual, but that these processes were consistently much shorter and less robust in extant *Taricha* than in the type of *T. oligocenica* (UOMNH F-5405); Naylor (1979) noted that *T. lindoei* shares these long processes with *T. oligocenica*. These long processes are easily distinguishable in UOMNH F-55196 and UOMNH F-59812 A–B (Figs. 3.1, 3.4, 4.1, 4.2), more so than in F-5405, which was embedded in epoxy during preparation, obscuring the view of this character. There is no variation in this character in the sample examined.

Comparison of the forelimbs and hind limbs of *T. oligocenica* to extant taxa reveals little difference morphologically, and Van Frank (1955) asserted that limb proportions were the same between the type specimen and extant skeletons. However, the degree of ossification apparent in the specimens with limbs preserved (UOMNH F-5405, F-55196, and F-59812 A–B) is different than seen in extant *Taricha*, especially in the previously undescribed specimens. Specifically, *T. oligocenica* preserves fully ossified tarsals (Figs. 3.2, 3.5, 4.3, 4.4), which differs from extant *Taricha*, where the tarsals fully ossify only rarely, even in older individuals (Shubin et al., 1995). This difference in tarsal ossification may indicate that UOMNH F-5405, F-55196, and F-59812 A–B are old individuals, or may

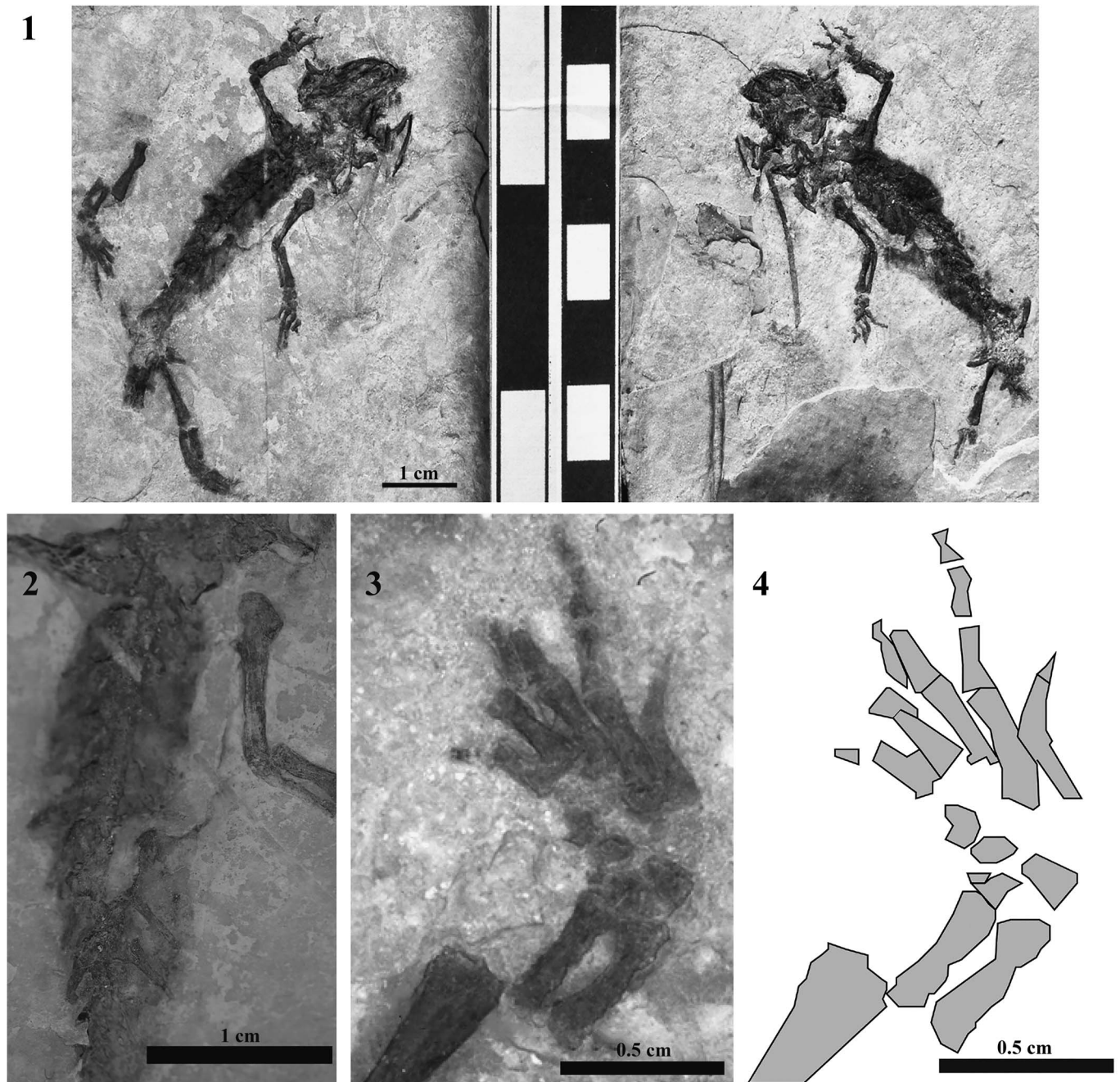


Figure 4. Nearly complete skeleton of UOMNH F-59812 A–B, found in association with the Lyons flora. (1) Full view of part and counterpart; (2) view of the trunk of F-59812 showing soft-tissue preservation and preservation of rib processes; (3) fully ossified right pes of F-59812 A; (4) line drawing of right pes of F-59812 A.

represent a legitimate character differentiation in *T. oligocenica*. It seems unlikely that all specimens preserving the tarsals (UOMNH F-5405, F-55196, and F-59812 A–B) would be as old as extant *Taricha* individuals would have to be to preserve this pattern, which suggests that *T. oligocenica* ossifies this region differently than modern members of the genus. It can be alternatively argued that the lack of tarsal preservation in the smaller individuals (UOMNH F-36412 and F-30648; Fig. 2.2, 2.3) suggests a lack of ossified tarsals. The phalangeal count of extant *Taricha* is 1-2-3-2 (manus) and 1-2-3-3-2 (pes). This holds true in the fossils as well, as exhibited in F-5405, F-55196 (pes only; Fig. 3.2, 3.5), and F-59812 A–B (Fig. 4.3, 4.4).

Van Frank (1955) described the pattern of bones in the tarsus (tarsal formula) in the type specimen of *T. oligocenica* as having an arrangement of 1, 2, 3, 4 + 5. We are unsure of his meaning on this, but we find that there appears to be a union of adjacent distal carpals four and five (dt 4 + 5); however, epoxy covering the ventral side of the specimen has yellowed with age and obscures that side, making it difficult to confirm if this is an original arrangement or a result of taphonomy. If Van Frank's (1955) assessment is taken to portray our observations, and if neither are a result of taphonomy, this tarsus arrangement contrasts with the pattern typically seen in extant *Taricha*, which possesses a basale commune, with distal tarsal three, four,

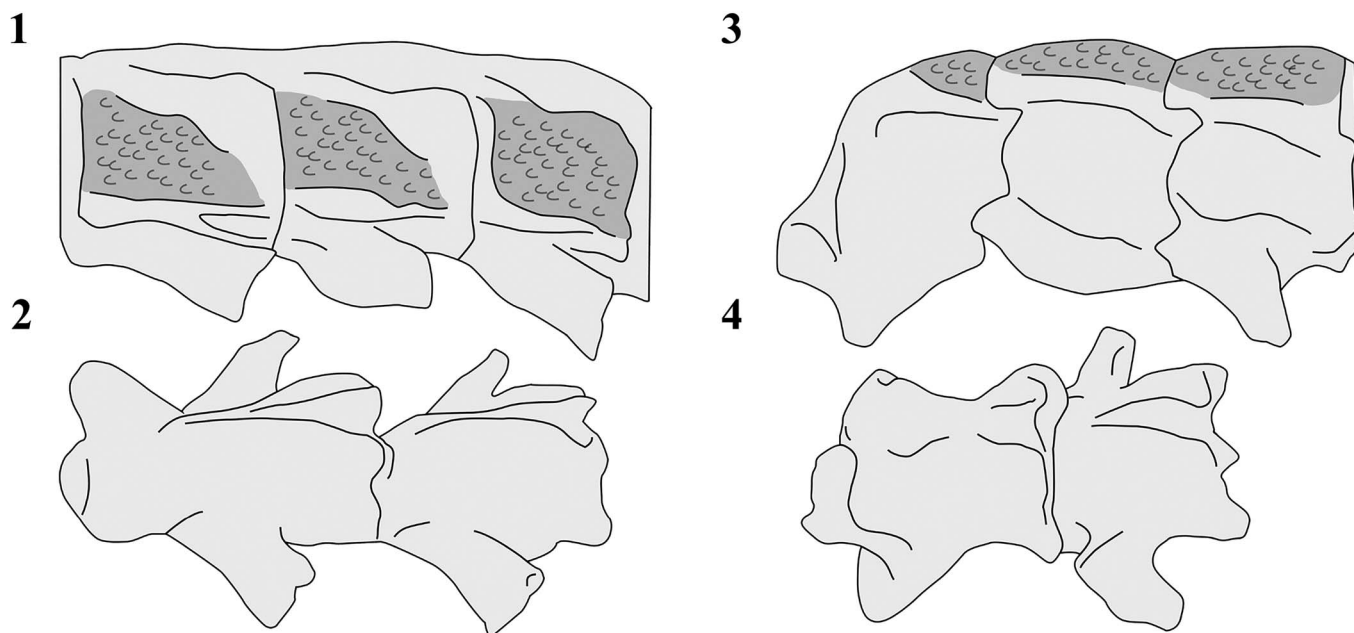


Figure 5. Line drawings for comparison of trunk (1, 2) and atlas (3, 4) morphology between *T. oligocenica* and *T. torosa* in lateral view, anterior to the left. (1) *Taricha oligocenica* trunk vertebra; (2) *T. torosa* trunk vertebra; (3) atlas of *T. oligocenica*; (4) atlas of *T. torosa*.

Table 2. Measurements of extinct *Taricha*. Some specimens are too poorly preserved to perform accurate measurements. Approximate length calculated as between 10x skull width and 10x snout-gular length. Instances in which only partial measurements were available, such as when part of the tail is missing, are listed in the table with a > symbol to denote that the structure is partial and therefore larger than the available measurement. Abbreviations: head width (HW), snout-gular length (SG), snout-vent length (SVL), axilla-groin length (AG), tail length (TL), hind limb length (HLL), foot length (FL), forelimb length (FLL), trunk width (TW), distance between the eyes (E-E), eye width (EW), and distance from eye to nostril (E-N). All measurements in millimeters.

Specimen #	I.D.	HW	SG	SVL	AG	TL	HLL	FL	FLL	TW	E-E	EW	E-N	Approximate Length
F-5405	<i>T. oligocenica</i>	13	14	60	34	>60	23	11	23	10	?	?	?	130–135
F-36412	<i>T. oligocenica</i>	8	8	?	?	?	?	?	?	?	3	2	2	85–90
F-30648	<i>T. oligocenica</i>	8	7.5	?	?	?	?	?	?	?	3	2	2	85–90
F-55196	<i>T. oligocenica</i>	?	?	?	40	>85	32	13.5	32	14	?	?	?	165–170
F-59812 A-B	<i>T. oligocenica</i>	13	15	62	35	?	24	12.5	24	10	?	?	?	130–135
F-35553	<i>T. lindoei</i>	9.5	10.5	43	28	>25	>6	?	>5	?	3.5	2	?	100–105
F-59813	<i>T. lindoei</i>	6	8	33	18	>13	>12	?	16	6	?	?	?	60–65
F-30616	<i>T. lindoei</i>	9.5	11	45	30	?	?	?	?	?	3.5	2	?	95–100
F-110577	<i>T. lindoei</i>	9.5	11	?	?	?	?	?	?	?	3.5	2	3	95–100
F-38883 A-B	<i>T. lindoei</i>	11	11	54	30	>40	?	?	?	?	?	?	?	100–105
JODA 10429 A-B	<i>T. lindoei</i>	9	10	?	?	?	?	?	?	?	?	?	?	90–95
JODA 1230	<i>T. lindoei</i>	7	9	?	?	?	?	?	?	?	?	?	?	70–75
UCMP 137466	<i>T. lindoei</i>	7	9	?	?	?	?	?	?	?	?	?	?	70–75

and five as separate elements. Our observation is, however, within variation for at least extant *Taricha granulosa*, even within a single population (Shubin et al., 1995). While there is a preferred arrangement within a species (Shubin et al., 1995), a large sample size is required to describe variation and determine a most common arrangement. With only two other specimens of *T. oligocenica* partially preserving bones of the tarsus (UOMNH F-55196 and F-59812 A–B), the sample size is not nearly large enough to undertake such a study at this time, and even within this sample, UOMNH F-59812 appears to have the formula seen in extant *Taricha* (Fig. 4.3). Given the variation found in extant populations and the small sample size of fossil specimens, this study does not use the tarsus bone arrangement as a character for use in phylogenetic analyses. The arrangement of the carpus bones is the same in both extant *Taricha* and specimens UOMNH F-5405, F-55196, and F-59812 A–B of *T. oligocenica*. The scapular portion of the scapulocoracoid is long and narrow compared to extant *Taricha*, as noted by

Van Frank (1955), Naylor (1979), Estes (1981), and Holman (2006).

In *T. oligocenica*, the total body lengths of the more complete fossils (F-5405, F-59812 A–B) appear to be between ten times the skull width and ten times the snout-gular length (Table 2). The type for *T. oligocenica*, which measures 120 mm, but is missing a little over a centimeter of the tail, is between 130–135 mm in total length. For this same specimen, the skull width is 13 mm, while the snout-gular length is 14 mm. Naylor (1979) made similar calculations, determining that the total body length in extant *Taricha* was ~12 times the skull width, but these calculations were done with specimens that still possessed soft tissues, and therefore appear to over-predict the total body length of specimens with only skeletal material remaining.

Materials.—Mehama Formation, Lane County, Oregon, UO 11026 Goshen: UOMNH F-5405, a nearly complete skeleton

(Fig. 1); UOMNH F-36412, a carbonized imprint preserving a few highly carbonized vertebrae representing a young, but metamorphosed individual (Fig. 2.1, 2.2); UOMNH F-30648, a partial skeleton preserving the dorsal side of the skull and anterior vertebral column representing a young adult (Fig. 2.3); UOMNH F-55196, partial skeleton preserving the ventral side of the salamander, but missing the skull, atlas, and left forelimb (Fig. 3). Mehama Formation, Linn County, Oregon, UO 4356 Thomas Creek Drive: UOMNH F-59812 A-B, a nearly complete but crushed skeleton in part and counterpart (Fig. 4).

Remarks.—Van Frank (1955) originally described the type specimen of *Taricha oligocenica* (Fig. 1) as a new genus and species, *Palaeotaricha oligocenica*, citing several differences he observed from extant *Taricha*, including: (1) a maxilla/quadrates suture or fusion; (2) a slightly different arrangement of tarsal bones; (3) extensive, expanded and sculptured spine tables on the neural arches, (4) long epipleural rib processes, (5) an unusually large, knob-like prepubic process in the pelvis; and (6) one additional trunk vertebra (14 as opposed to 13). The latter of these traits is highly variable within species (Holman, 2006). It should be noted that Van Frank (1955) was unclear on whether he believed the maxilla and quadrates to be truly fused, or simply sutured, because the terms may have been used interchangeably. This practice is no longer recommended, since fusion should indicate a lack of a detectable suture (Irmis, 2007). Later, additional preparation of the type led to elimination of some differences (maxilla-quadrates suture/fusion, prepubic process morphology), therefore Tihen (1974) reclassified the type, relegating *Palaeotaricha* to the subgeneric level within *Taricha*, and assigned *Taricha miocenica* to the *Palaeotaricha* subgenus.

Naylor (1979), in his description of the *Taricha lindoei* type, saw no reason to eliminate the subgeneric separation of *Palaeotaricha* and modern *Taricha*, even noting differences (atlas shape, height of the trunk vertebrae) that Tihen (1974) and later, Estes (1981) apparently did not take into account. Estes (1981) did not recognize the *Palaeotaricha* subgenus because he was unconvinced that there was enough evidence to differentiate any of the fossils from extant taxa at a subgeneric level. Curiously, the long epipleural rib processes are not something seen in extant *Taricha*, as recognized by Van Frank (1955), not discussed in Tihen (1974), and reestablished by Naylor (1979). These features were not discussed when the status of the *Palaeotaricha* was first changed by Tihen (1974), then later, when the subgenus was not recognized at all (Estes, 1981; Dubois and Raffaëlli, 2009). Holman (2006) provided only a summary of the previous work done on the type specimen (UOMNH F-5405), and used the diagnosis and classification of Estes (1981). Unlike Estes (1981), Holman (2006) noted the presence of elongate epipleural rib processes. The most recent taxonomy of family Salamandridae in Dubois and Raffaëlli (2009) listed all fossil *Taricha* species as “incertae sedis” at the subgeneric level, likely intended to indicate the uncertainty of their position in the absence of a study subsequent to the original descriptions of these species (in which *T. oligocenica* and *T. lindoei* are described from one specimen each).



Figure 6. UOMNH F-59813, the only specimen of *T. lindoei* from Gray Butte. This specimen is not only the smallest articulated individual of *Taricha* in the fossil record, but also preserves a soft-tissue outline for much of the specimen's body.

Taricha lindoei Naylor, 1979
Figures 6, 7

Holotype.—UALVP 13870, partial skeleton impression, Oligocene, Big Basin Member, John Day Formation, Wheeler County, Oregon.

Diagnosis.—*Taricha lindoei* lacks sculptured spine tables on the neural spines of the vertebrae, but has a very slight expansion of the posterior neural crest. The skull of *T. lindoei* is elongate and narrows anteriorly; however, the posterior region of the skull remains wide and possesses minor sculpturing. *Taricha lindoei* also possesses a broad scapular region of the scapulocoracoid, prominent epipleural pectoral rib processes, and concave inter-prezygapophyseal margins.

Occurrence.—Early Oligocene, Oregon.

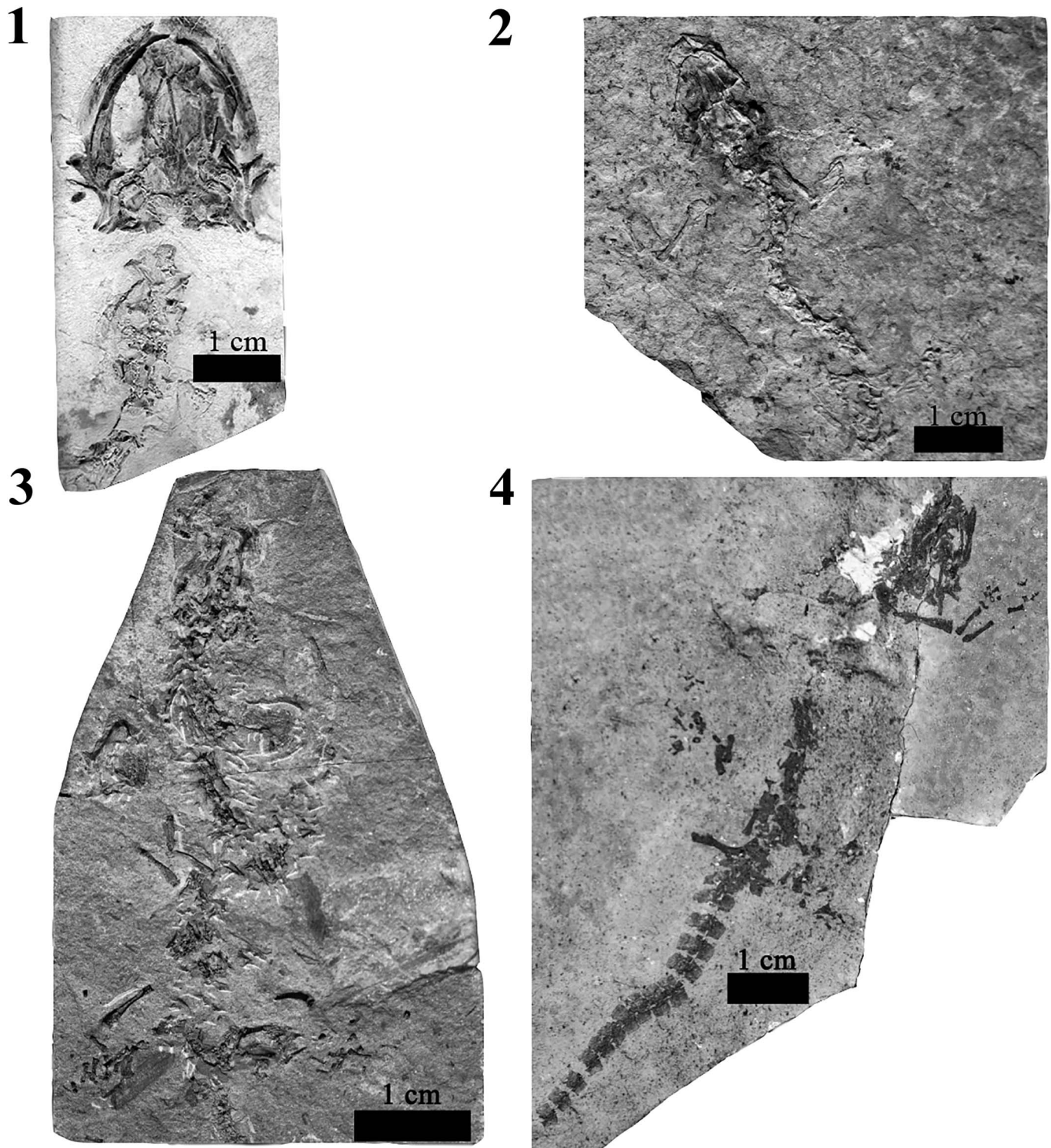


Figure 7. *Taricha lindoei*: (1) UOMNH F-110577, (2) UOMNH F-30616, (3) UOMNH F-37883A, and (4) JODA 1230. All specimens were found associated with the early Oligocene Bridge Creek Flora in Wheeler County, Oregon.

Description.—The vertebrae of *Taricha lindoei* are opisthocelous, as in all salamandrids, with long, thin, low neural crests that do not possess expansive, sculptured spine tables, and concave inter-prezygapophyseal neural arch margins. The type specimen (UALVP 13870), UOMNH F-35553, and UOMNH F-59813 (Fig. 6) all possess 14 trunk vertebrae, as also seen in *T. oligocenica* (Van Frank, 1955; Naylor, 1979); extant *Taricha*

typically possess 13 trunk vertebrae (Van Frank, 1955; Naylor, 1978b, 1979). However, the number of trunk vertebrae is variable within the genus, and therefore ineffective in differentiating species of *Taricha* without a larger sample size of the fossil taxa (*T. oligocenica* and *T. lindoei*) and an analysis of intraspecific variation (Naylor, 1978b, 1979). The type specimen of *T. lindoei* exhibits the general proportions of

modern *Taricha* in the neural arches and zygapophyses (Naylor 1979), but differ from the proportions of *T. oligocenica* and *Notophthalmus* (Naylor, 1978b, 1979). Furthermore, *T. lindoei* has a similar vertebral length and width to *Taricha miocenica* described in Tihen (1974), although the neural spine is much higher in the latter (Naylor, 1979; Estes, 1981). The atlas of *T. lindoei* is robust and slopes anteriorly, and the scapular part of scapulocoracoid is broad, both characters as in extant *Taricha* and unlike in *T. oligocenica* (Naylor, 1979; Holman, 2006). The epipleural processes of the pectoral ribs are longer than those of extant *Taricha* species, as best seen in UOMNH F-59813 (Fig. 6; Naylor, 1979; Estes, 1981; Holman, 2006). As in all members of the genus *Taricha*, the skull of *T. lindoei* is broad posteriorly; however, the snout of *T. lindoei* narrows anteriorly, and the frontosquamosal arch is bony and complete. The premaxilla is fused (Figs. 6, 7). Dermal sculpturing of the skull and frontosquamosal arch is greater than in extant *Taricha*, but less than in *T. oligocenica* and *Notophthalmus*; the overall amount of sculpturing is minor. The preservation of the vomerine tooth row reveals a V-shape, similar to the shape exhibited in *T. granulosa*.

Materials.—UO 2783 Gray Butte, John Day Formation, Crook County, Oregon: UOMNH F-59813, an imprint/compression of a near complete skeleton and body impression of a young adult, except the distal limbs and girdles (Fig. 6). UO 10744 Fossil locality, John Day Formation, Wheeler County, Oregon: UOMNH F-35553, an impression of a nearly complete skeleton, except for the distal parts of limbs, posterior portion of the tail, most of the ribs, and the pectoral and pelvic girdles; UOMNH F-30616, a partial skeleton impression lacking girdles, distal ends of limbs, and posterior end of tail (Fig. 7.2); UOMNH F-109709, a partial skeleton imprint; UOMNH F-109710, part and counterpart of a flattened partial skeleton; UOMNH F-110577, impression of partial skeleton including skull and several vertebrae (Fig. 7.1); UOMNH F-111395 A–B, flattened partial skeleton in part and counterpart; UOMNH F-37883 A–B, part and counterpart of a flattened skeleton, and additional flattened partial skull, and a flattened vertebra (Fig. 7.4); JODA 10429 A–B, flattened skull and first several vertebrae compressed onto block; JODA 1230, a block with skeletal impressions (Fig. 7.3). UCMP John Day Formation locality V5636, Fossil, Wheeler County, Oregon: UCMP 137466, an anterior salamander impression/compression; UCMP 137464, partial skeleton compression.

Remarks.—Naylor (1979) first described *Taricha lindoei* as the earliest representative of the subgenus *Taricha*, which at the time contained all extant members of the genus *Taricha*. The new taxonomy of Dubois and Raffaelli (2009) has since placed *T. rivularis* as the lone member of the subgenus *Twittya* based on iris color, ventral coloration, egg deposition, and habitat (flowing water as opposed to standing or mildly flowing water), while maintaining the earlier caution of Estes (1981) by labeling all Oligocene salamanders assigned to the genus *Taricha* as *Incertae sedis*. Estes (1981) stated that *T. lindoei* may very well represent the earliest member of the subgenus *Taricha*, but did not find the characterization of multiple subgenera of *Taricha* in the fossil record to be adequate, given one described individual

each for *T. lindoei* and *T. oligocenica*, and fewer than 40 individual skeletal elements in *T. miocenica*. Without further evidence, it was not possible for Naylor (1979) or Estes (1981) to determine if the combination of smaller size, narrower skull, and absence of sculptured spine tables represented ontogenetic features of one taxon or a taxonomic difference; however, the existence of *T. miocenica*, which was similar in size to *T. lindoei*, but possessed less extensive expansion of the spine table than *T. oligocenica*, was enough for Estes to maintain them as separate species. With the additional specimens now available, we can confirm that even the largest individual assigned to this species (UOMNH F-37883 A–B) bears no dermal cap on the vertebra, as in modern *Taricha*, while also possessing the broad scapular region of the living group and a narrower rostrum. Additionally, none of the specimens representing this species appears to be larval or juvenile in age; they instead represent young to mature adults. The possibility of *T. lindoei* and *T. oligocenica* belonging to the same species and differing in only age at death and preservation is therefore unlikely.

The long epipleural rib processes resemble those seen in *T. oligocenica*, best seen in (Naylor, 1979). Interestingly, the shape of the vomerine tooth row revealed in *T. lindoei* bears a V-shape similar to that seen in extant *Taricha granulosa*. *Taricha lindoei* consistently presents an anterior narrowing the skull not seen in other members of the genus.

It is possible that the body size of *T. lindoei* is smaller than *T. oligocenica*, given that even the most mature specimens do not reach the same size as mature *T. oligocenica* (Table 2). Notably, the vertebrae of fully adult *T. miocenica* are also smaller than those of *T. oligocenica*, and are around the same size as adult *T. lindoei* (Estes, 1981). The fact that salamandrids are known to be variable in size (Estes, 1981; Duellman and Trueb, 1986; Holman, 2006), combined with the small sample sizes of *T. lindoei* and *T. oligocenica*, does not currently permit accurate assessment of these differences, and therefore cannot be used as a diagnostic tool for species identification. Nonetheless, it is worth noting that, while salamanders possess the potential for indeterminate growth, in reality, body size is limited by a number of factors, especially age of first reproduction (Bruce, 2010) and climatic conditions such as temperature and precipitation (Reading, 2007; Caruso et al., 2014). Hence, the difference in stresses between the cooler, drier, seasonal environment preserved in the Big Basin Member versus the wetter, milder environment preserved in the Mehama Formation (due to proximity to the Pacific Coast) may also explain the apparent segregation of species and the difference in body sizes for two fossil newts of similar age.

Phylogenetic analyses

Results.—Because our focus is on the North American newts, specifically the extant genus *Taricha* and the fossil species attributed to that genus, most of our discussion of these results will focus specifically on the North American taxa. Marjanović and Witzmann (2015) produced a detailed and authoritative discussion of the taxa outside of North America, and with few specimens available, we have little to add to their discussion of those taxa beyond a few additional details and an adjustment to

character 71 for *Tylotriton*, in which the length of the trunk ribs differs between species.

The unconstrained analysis with all 40 taxa produced 420 most parsimonious trees, with a length of 635 steps, a consistency index of 0.501, a retention index of 0.633, and a homoplasy index of 0.753. The strict consensus (Fig. 8) is not exceptionally well resolved, although the outgroups (*Ambystoma* and *Dicamptodon*), Salamandrinae (*Salamandra* and *Chioglossa*), Pleurodelini (*Tylotriton*, *Echinotriton*, and *Pleurodeles*), and Molgini (including a European and North American clade) form monophyletic groups as in molecular studies (Zhang et al., 2008; Pyron, 2014). Unfortunately, the Molgini, along with *Salamandrina*, form a massive polytomy in the strict consensus tree as presently coded. This polytomy includes uncertain placements of *Notophthalmus viridescens* and the fossil *Notophthalmus crassus*, as well as several European fossil taxa, *Cynops*, and *Paramesotriton*. We also retain a stepped relationship of *Lissotriton* species (along with *Carpathotriton*) and a clade including *Neurergus*, *Ommatotriton*, *Triturus*, and *Ichthyosaura*. Finally, we recovered a clade including all living and extinct species of *Taricha*, along with fossil species *Notophthalmus robustus* in our analysis.

The constrained analysis of all 40 taxa produced 760 most parsimonious trees, with a length of 667 steps, a consistency index of 0.4768, a retention index of 0.5956, and a homoplasy index of 0.7646. The strict consensus of these trees (Fig. 9) forms a large polytomy within the Salamandrinae. Within this polytomy, the strict consensus retains the entirety of the North American clade, but retains only minor parts of the Pleurodelini and European newts. Within the North American clade, the fossil species (except for *N. crassus*) form a polytomy alongside the group of extant *Taricha* species, while living *N. viridescens* and extinct *N. crassus* form a polytomy with the larger North American newt group.

Our unconstrained analysis without the “vertebrae-only” fossil taxa produced 32 most parsimonious trees, with a length of 630 steps, a consistency index of 0.503, a retention index of 0.629, and a homoplasy index of 0.751. The strict consensus tree of this analysis (Fig. 10) retains the outgroup, the Salamandrinae, and the Pleurodelini-Molgini sister groups. Within the Molgini, we have a trichotomy of extinct and extant *Taricha*, *Notophthalmus viridescens*, and all other newts within Molgini, including the fossil taxa. Within *Taricha*, the fossil taxa *T. oligocenica* and *T. lindoei* form a separate branch from extant species of *Taricha*, which have additional soft tissue and reproductive character data available.

Finally, our constrained analysis without the “vertebrae-only” fossil taxa produced 16 most parsimonious trees, with a tree length of 662 steps, a consistency index of 0.4789, a retention index of 0.5907, and a homoplasy index of 0.7628. The strict consensus tree (Fig. 11) portrays the outgroup, *Salamandrina*, the Salamandrinae, and a North American clade of *Taricha* and *Notophthalmus* well, but overall reduces the newts into a large polytomy, removes *Pleurodeles* and several fossil taxa to one step outside of the Pleurodelini, and struggles to separate the taxa into a distinct Pleurodelini-Molgini sister-group relationship. *Notophthalmus viridescens* forms a sister group to living and fossil species of *Taricha*, while the non-North American Molgini also form a single large clade with fair similarity to molecular trees.

Discussion.—This paper focuses on North American taxa, although our analysis enables us to make a few observations about non-North American taxa in addition to those found in Marjanović and Witzmann (2015). Both of our constrained analyses (Figs. 9, 11) form a large polytomy including the newt taxa while not recovering a monophyletic Pleurodelini, fossil *Chelotriton* (both the Enspel/Randeck and MB.Am.45 specimens), and *Pleurodeles*. The analysis reflects a North American clade including all living and fossil North American species. Removal of the “vertebrae-only” taxa before analysis greatly reduced the number of trees (from 760 to 16), suggesting that the current status of vertebral characters in Salamandridae as a whole is insufficient to properly understand several of the taxa, perhaps because of a lack of data and/or low samples sizes, homoplasy in vertebral characters, poor description of character states, or some combination of the above. One possible example of this issue pertains to the width and dorsal sculpture of the neural crest of the vertebrae (character 61; character 61 in Marjanović and Witzmann, 2015; characters 2 and 3 in Buckley and Sanchiz, 2012). Using *Taricha* as an example, Venczel (2008) assigned state 0 (neural crest not expanded into spine table), whereas Buckley and Sanchiz (2012) and Marjanović and Witzmann (2015) assigned *Taricha* state 2 (dorsal surface of broadened spine table sculptured). Examination of extant species of *Taricha* (Table 1) reveals a mix of character states even within a single vertebral column. Fully mature individual skeletons typically exhibit both state 1 (unsculptured expansion of the neuropophysis into spine table) and the previously mentioned state 2, apparently across all living species in our analysis. We have coded the extant species as such. *Taricha oligocenica* and *Taricha miocenica* both appear to exhibit only state 2, though with different shapes for the spine table, while *Taricha lindoei* appears to exhibit state 1 as seen in some extant *Taricha*, although this may be an artifact of nearly two-dimensional preservation.

In addition to the difference in observations even within a single newt genus for this character, we suspect that the current list of character states is insufficient for describing the morphology of the neural crest and the spine table, when present. Taxa such as *Taricha*, for example, only show a broadening spine table at the posterior-most part of the neural crest (like an elongate, narrow, upside-down funnel), and may or may not exhibit sculpture, while taxa such as *Echinotriton* and *Tylotriton* have overall broader, near-triangular, extensive neural crest spine tables, and appear to exhibit sculpture throughout a mature individual’s trunk vertebrae. We suggest investigating differences of shape in the spine table in the future, and perhaps either adding these data as an additional character, or using them to better define or increase the number of character states for this character in future analyses. Other vertebral characters may similarly produce such issues, but we feel that the amount of expansion and sculpture of the neural crest exhibits the problem best.

Our unconstrained analyses (Figs. 8, 10) recovered a monophyletic Pleurodelini group, unlike in our constrained analyses; however, inclusion of all 40 taxa resulted in a massive polytomy between the Pleurodelini and various parts of what is molecularly recognized as the Molgini. Just as in the constrained analyses, the removal of “vertebrae-only” taxa

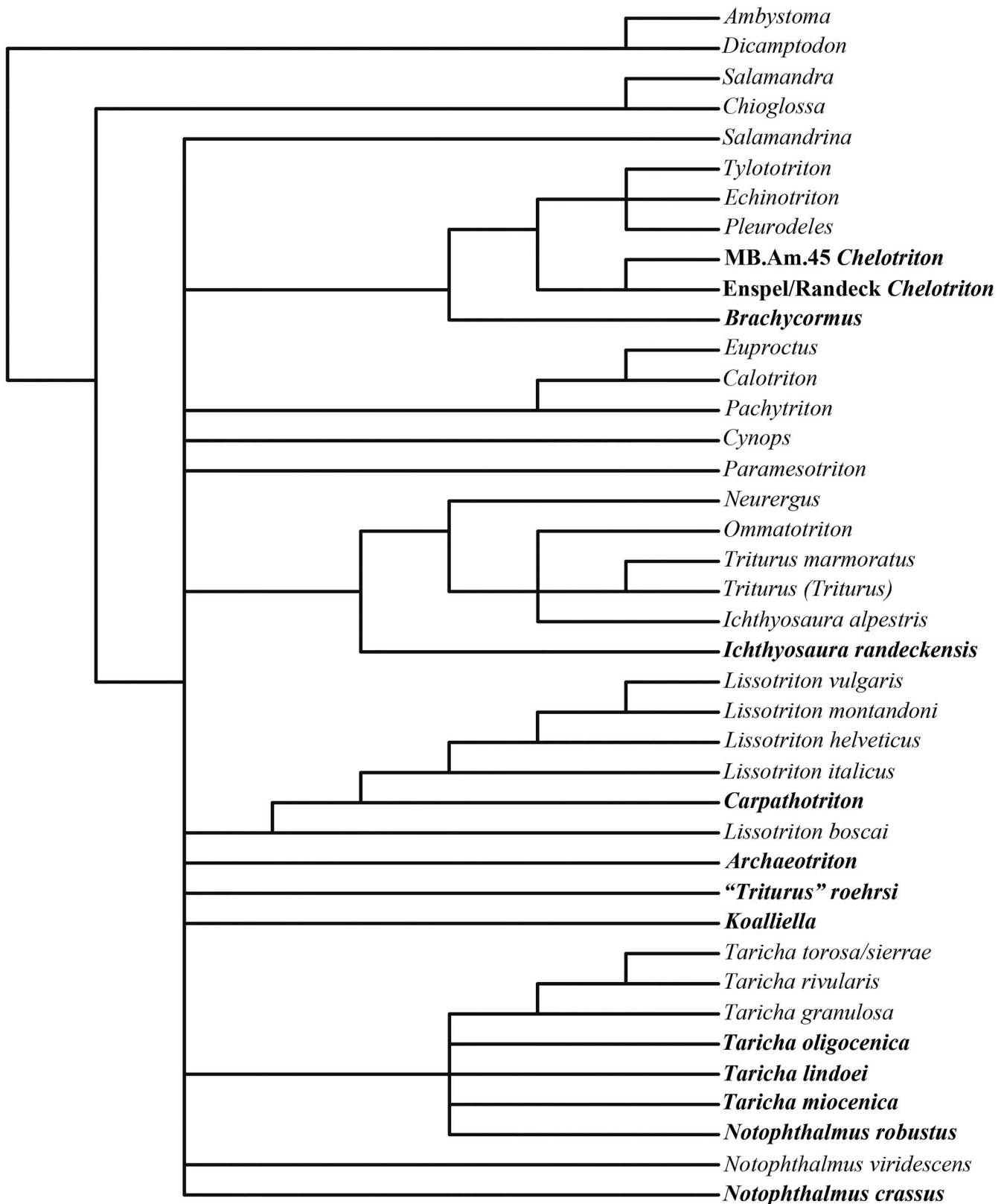


Figure 8. Strict consensus tree of 420 most parsimonious trees (length = 635 steps) from our unconstrained analysis with all 40 taxa. Extinct taxa are in bold.

greatly reduced the number of most parsimonious trees (from 420 to 32), and provided better resolution for the Molgini, separating out the non-North American Molgini, *Taricha*, and

Notophthalmus. One major issue with the unconstrained analyses is that *Notophthalmus viridescens* and, when included, *Notophthalmus crassus* do not form a group with

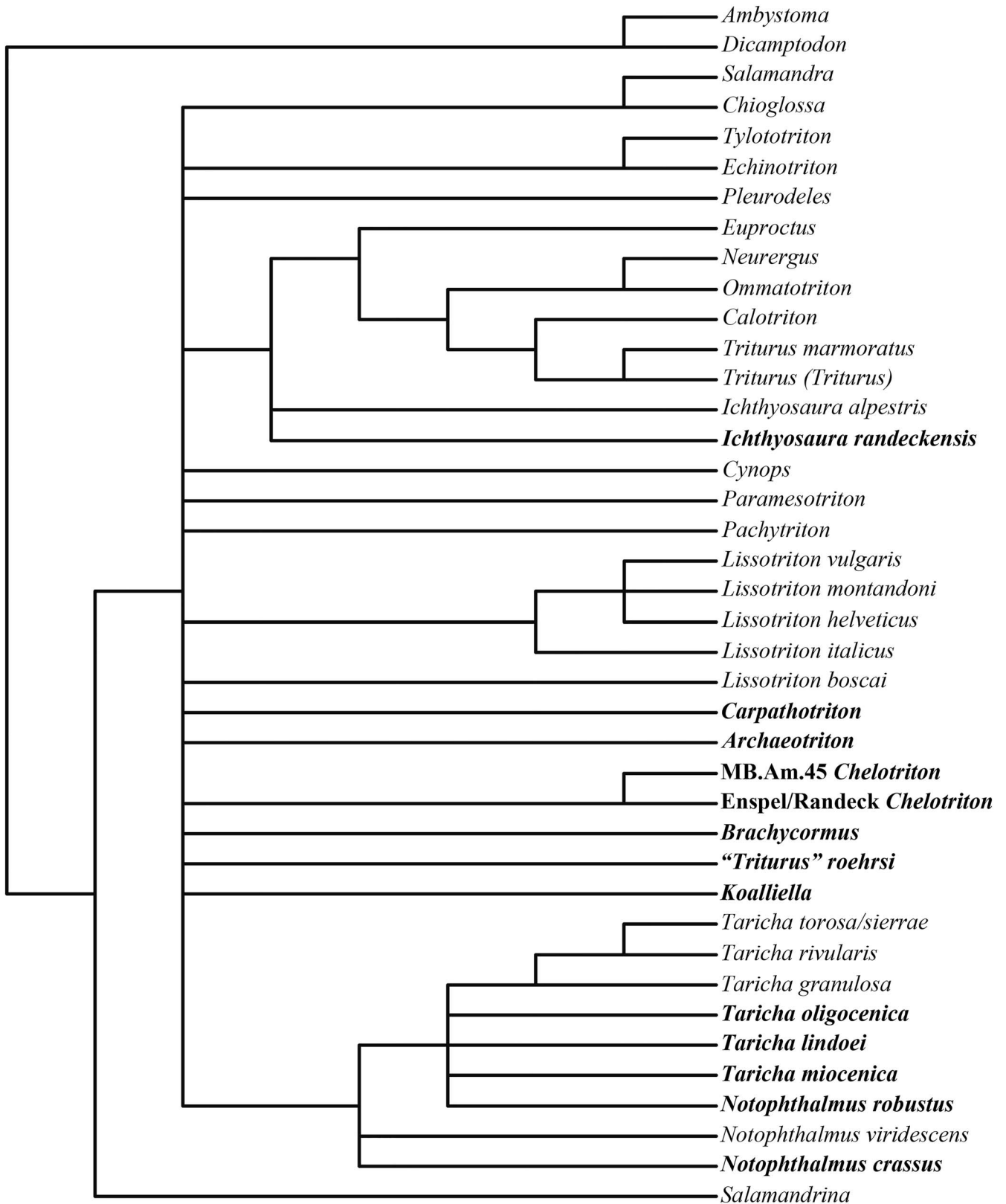


Figure 9. Strict consensus tree of 760 most parsimonious trees (length = 667 steps) from our molecularly constrained analysis of all 40 taxa. Extinct taxa are in bold.

Notophthalmus robustus, nor do they form a sister-group relationship with *Taricha* such that a North American Molgini clade is formed. Instead, *N. viridescens* and *N. crassus* form a

polytomy with all other North American newts when all taxa are included, while *N. viridescens* forms a trichotomy with *Taricha* and the non-North American Molgini. We suggest that our

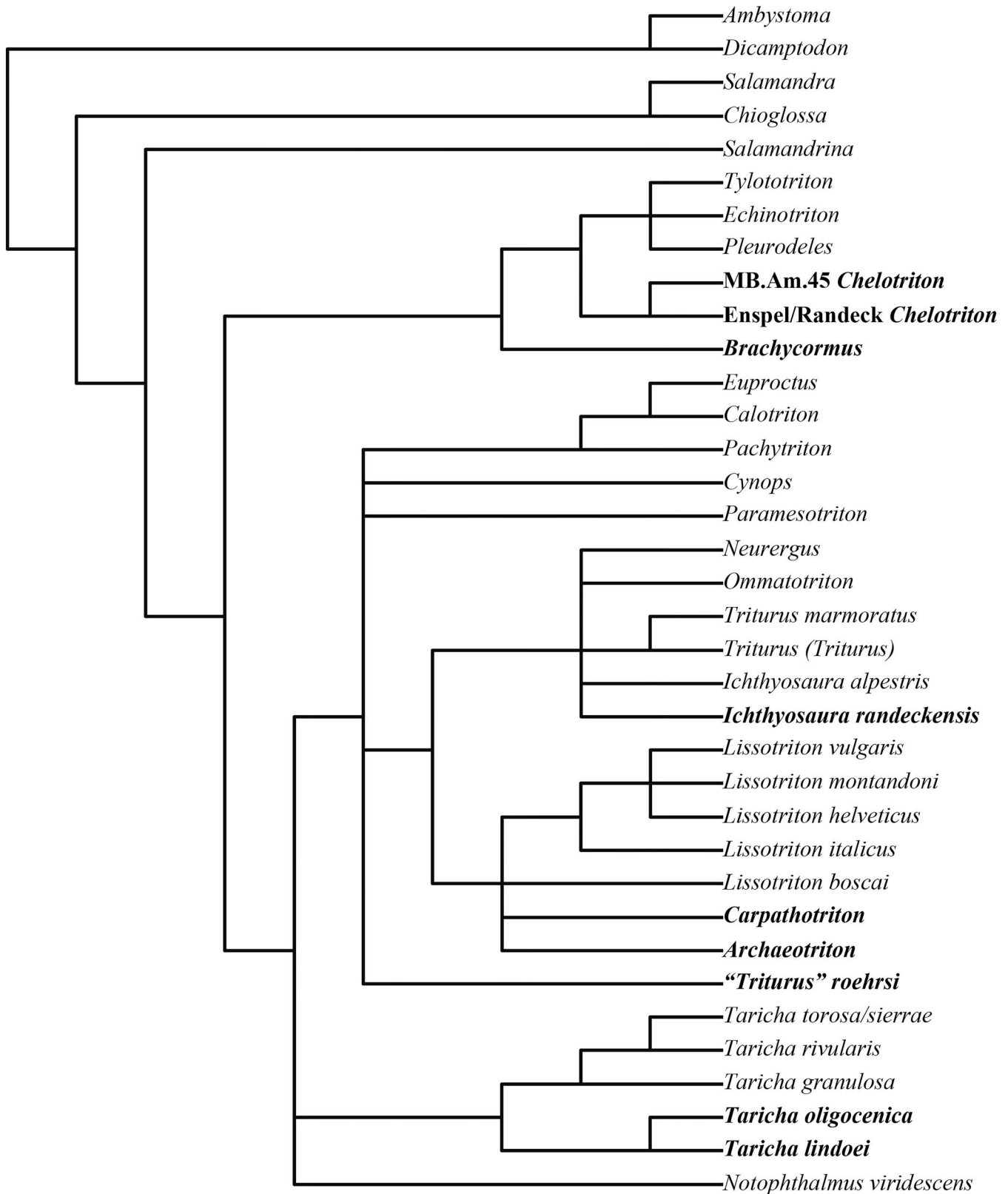


Figure 10. Strict consensus tree of 32 most parsimonious trees (length = 630 steps) from our unconstrained analysis without the “vertebrae-only” fossil taxa. Extinct taxa are in bold.

unconstrained morphological analyses fail to show a consensus North American clade as the result of a lack of characters for the post-cranial skeleton of *Notophthalmus*, combined with a deep

split of the *Taricha* and *Notophthalmus* lineages, resulting in significant autapomorphy evolution that likely began in either the late Oligocene or early Miocene.



Figure 11. Strict consensus tree of 16 most parsimonious trees (length = 662 steps) from our molecularly constrained analysis without the “vertebrae-only” fossil taxa. Extinct taxa are in bold.

In all four of our strict consensus trees (Figs. 8–11), we recover a group including all extant and fossil species of *Taricha*, the vertebrae-only *Taricha miocenica*, as well as,

curiously, *Notophthalmus robustus*, when they are included. Our strict consensus trees also did not place any fossil or extant North American newts within the Eurasian Molgini.

Estes (1981) noted that *N. robustus* is apparently less derived than other known species, and differs more from at least the extant species than those species do from each other. While *T. miocenica* was placed with other species of *Taricha*, its exact placement within the group is uncertain, possibly because it relies entirely on our vertebral characters; analyses including *N. robustus* and *N. crassus* face a similar problem. As such, we suggest a reexamination of the three “vertebrae-only” North American taxa because we did not investigate those taxa personally when assigning character states. We furthermore suggest the addition of extant taxa *Notophthalmus meridionalis* and *Notophthalmus perstriatus* to future analyses that look to investigate North American taxa specifically, especially when including fossil taxa. Clearly, the current state of unconstrained morphological analyses struggle with *Notophthalmus* overall; the addition of all species and species-level characters may improve the resolution in future studies.

We also suggest deeper investigation into the vertebral characters of the Salamandridae overall because the current state of characters may not necessarily explain the morphological similarities and differences within the group. We were unable to address this in our current study, and were also unable to code some of our original characters for non-North American taxa, because of insufficient specimen availability to account for possible variation. Future studies should build on our current analysis and incorporate more data, as available, while studying multiple individuals of each taxon.

Overall, we find support for *T. oligocenica*, *T. lindoei*, and *T. miocenica* as members of the *Taricha* group with a long history of >32 Ma. The curious and consistent placement of *N. robustus* warrants a reexamination of the taxon and the character states assigned to it, and we recommend the same for the remaining North American taxa (including the questionable taxon *N. slaughteri*) for the sake of confirming their morphologies. Improving the characters and character states for the vertebrae and ribs of salamandrid phylogenies should also be a priority for future analyses; other characters, such as the single geographic character, may also be possible to improve on when advancing these studies.

Functional morphology

Discussion.—The overall impression of *Taricha oligocenica* is that of a sturdy or robust, moderate-to-large-sized newt with a mosaic of defensive adaptations present in the Salamandridae. First is the frontosquamosal arch, which consists of an anteromedial projection from the squamosal and a posterolateral projection from the frontal that has been considered a defensive adaptation in the family Salamandridae (Naylor, 1978a; Brodie, 1983; Duellman and Trueb, 1986), the function of which is to lessen injury during predatory attack by increasing the skull’s resistance to crushing. The frontosquamosal arch also increases the difficulty of swallowing for predators similar to *Thamnophis*, which attempt to swallow their prey headfirst (Brodie, 1968a, 1983; Naylor, 1978a; Duellman and Trueb, 1986), or predators such as *Lithobates* and some fishes, which also attempt to swallow their prey whole (Brodie, 1968a; Naylor 1978a). Although not all salamandrids possess a complete, bony arch (some exhibit a narrow gap, or no frontosquamosal arch),

this structure is only found in the Salamandridae (Wake and Özeti, 1969; Naylor, 1978a; Duellman and Trueb, 1986). The ridges and grooves of the frontosquamosal arch, continuous with the relatively robust and rigid skull seen in salamandrids (compared to other salamanders), effectively strengthen the skull, especially when resisting lateral pressure, such as that experienced when being swallowed by predators, including bullfrogs and snakes (Naylor, 1978a). Additionally, the paired arches can form a protective shelf over the eyes of newts; this shelf can also be observed when these newts swallow or take a defensive posture (Brodie, 1977). As mentioned above, the extensive pitting of the skull and frontosquamosal arches of *T. oligocenica* is beyond that of living members of *Taricha*, but less than found in *Echinotriton* or *Tylostotriton*.

The most glaring differences between *T. oligocenica* and extant *Taricha* involve the heavy ossification of different parts of the skeleton in *T. oligocenica*, specifically the trunk region. As Naylor (1978a) has pointed out, only newts with complete bony frontosquamosal arches possess expanded spine tables on the vertebral neural crests (examples include *Notophthalmus*, *Cynops*, and *Tylostotriton*; Brodie, 1983; Duellman and Trueb, 1986). Although not all newts with bony arches possess extensive sculpture on these expansions, others may vary in degree of sculpture even within an individual, such as in *Taricha* (Naylor, 1978a, 1978b; Brodie, 1983; this study). These expansions are most likely defensive in nature (Naylor, 1978a; Brodie, 1983; Duellman and Trueb, 1986) because they have no muscle attachments and form interlocking series along the usually vulnerable spine of these salamanders. The amount of protection provided by these expansions likely differs by how extensively they cover the spine (Van Frank, 1955). *Taricha oligocenica* stands out in that its expansions are as extensive and sculptured as those of extant *Tylostotriton* and *Echinotriton*, perhaps even more so, as the spine tables of those taxa narrow anteriorly, while *T. oligocenica* has somewhat rectangular expansions (Van Frank, 1955, Estes, 1981; this study).

The elongate epipleural rib processes of *T. oligocenica* and *T. lindoei* are here proposed to provide a defensive role similar to the epipleural processes of *Tylostotriton*. Like *Tylostotriton*, *T. oligocenica* and *T. lindoei* possess singular, robust processes, directed dorsally and distally, on somewhat elongate (beyond the length of a simple rod) ribs, both of which terminate in blunt ends (Nussbaum and Brodie, 1982; Brodie et al., 1984; Heiss et al., 2009). Unlike in *Echinotriton*, *Pleurodeles*, and possibly fossil salamanders such as *Chelotriton* (Marjanović and Witzmann, 2015; Schoch et al., 2015), which possess even longer, pointed ribs, often with one or more pointed epipleural processes that function to pierce the skin and inject toxins into predators if compressed, these structures are unlikely to have protruded through the skin, and may have been used for muscle attachment and to apply pressure to toxin-containing granular gland clusters (risen on the skin of *Tylostotriton*) when compressed without piercing the skin or to help project toxin-concentrated parts of the body towards potential antagonists. The increased muscle attachment and overall robustness of the structures could also have provided extra resistance against crushing forces when attacked. Unfortunately, testing this latter hypothesis would involve significant biomechanical testing, which is beyond the scope of this study. It should also be noted

that epipleural processes are present throughout fossil and extant salamandrids (and even other salamanders) to some extent, with various types and levels of functionality (Nussbaum and Brodie, 1982; Brodie et al., 1984; Marjanović and Witzmann, 2015). It is therefore difficult to project the function of epipleural processes in fossil *Taricha* with complete confidence outside of their similarity to those of extant *Tylotriton verrucosus*.

The skin of all newts is toxic and sometimes fatal to potential predators; it is especially potent in the genus *Taricha* (Wakely et al., 1966; Brodie, 1968a, 1968b; Brodie et al., 1974; Hanifin, et al., 2004). Given the phylogenetic bracketing of *T. oligocenica* and *T. lindoei* with other toxic newt species (including both North American genera), the fossil species were also likely to have been toxic, although it is impossible to discern how potent the toxins actually were in these organisms. Naylor (1978a) was the first to propose a connection between the frontosquamosal arch and newt toxins on the basis that it is decidedly advantageous if an organism with toxic (not to mention distasteful) skin secretions also has defensive mechanisms that allow it to survive and decrease injury from predators experiencing the poison. In a now-famous encounter, one bullfrog (*Lithobates catesbeiana*) voluntarily ate an individual of *T. granulosa* (Brodie, 1968a). The defensive advantages of a robust, hardy body and toxic skin secretions became clear when the frog died within ten minutes and the newt emerged unscathed shortly after (Brodie, 1968a). While the toxicity of the fossil newts in this study is unknown, the skeleton of *T. oligocenica* in particular is more armored than that of *T. granulosa* (Van Frank, 1955), and is likely able to resist easy consumption from predators, as seen in extant *Taricha* (Brodie, 1968a, 1977; Naylor, 1979).

Conclusions

Our four phylogenetic analyses provided mixed results when compared to the molecular phylogenies of Zhang et al. (2008) and Pyron (2014), yet consistently nested *Taricha oligocenica*, *Taricha lindoei*, *Taricha miocenica*, and *Notophthalmus robustus* within a clade of North American newts. Future studies should attempt to find additional osteological characters for all fossil and extant species of North American newts for better resolution of morphological analyses, particularly for *Notophthalmus*, which appears to be problematic in morphological analyses.

Unfortunately, the morphological characters in this analysis did not resolve the positions of the fossil taxa relative to extant species of the genus, so their exact classification within the North American clade is uncertain. The use of muscular and behavioral characters does not help resolve fossil species, while a lack of species-level osteological characters, the presence of homoplasy in some potential characters, and the possibility of cryptic species complicate the ability of our analyses to discriminate between taxa.

A detailed morphological study of *T. oligocenica* and *T. lindoei* supports their classification as separate species more similar to *Taricha* than to any other known genus of newt. As in the phylogenetic analysis, this conclusion suggests that the genus *Taricha* has deep roots into at least the early Oligocene, where ancestors to living species may have diverged

32–33 Ma. Functionally, *T. lindoei* is similar to, though possibly smaller than, all extant taxa, and existed in a seasonal temperate environment similar to the environments in which Pacific newts are found today. *Taricha oligocenica*, on the other hand, represents a large, robust newt that was considerably more armored than extant *Taricha*, and lived in a milder climate nearer to the Oligocene coast.

Because we did not directly examine any specimens of *Taricha miocenica* or of fossil *Notophthalmus* outside of published literature (Tihen, 1974; Estes, 1981; Holman, 2006), it is of particular importance to examine and compare these fossils in detail with additional fossils of *Taricha* and *Notophthalmus*, along with skeletons of extant members of these genera, to examine their evolutionary relationships with modern North American salamandrids. The fact that *T. miocenica* and all fossils of *Notophthalmus* are only preserved as isolated vertebrae (Tihen, 1974; Estes, 1981) enhances the difficulty of such determinations, and our analyses and observations indicate further development of vertebral characters is clearly required. Despite the complications, only by performing such studies can we hope to draw concrete conclusions on the phylogenetic positions North American fossil newts relative to each other and to extant *Taricha* and *Notophthalmus*.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: <http://dx.doi.org/doi:10.5061/dryad.8m9t1>

References

- Albright, L.B. III, Woodburne, M.O., Fremd, T.J., Swisher, C.C. III, MacFadden, B.J., and Scott, G.R., 2008, Revised Chronostratigraphy and Biostratigraphy of the John Day Formation (Turtle Cove and Kimberly members), Oregon, with Implications for Updated Calibration of the Arikareean North American Land Mammal Age: *The Journal of Geology*, v. 116, p. 211–237.

- Atkins, J.B., and Franz-Odenaal, T.A., 2015, The evolutionary and morphological history of the parasphenoid bone in vertebrates: *Acta Zoologica* (Stockholm), v. 97, p. 255–263.
- Bestland, E.A., and Retallack, G.J., 1994, Geology and Paleoenvironments of the Painted Hills Unit, John Day Fossil Beds National Monument: National Park Service Open-File Report, v. 30, 211 p.
- Boardman, G.S., and Schubert, B.W., 2011, First Mio-Pliocene salamander fauna from the southern Appalachians: *Palaeontologia Electronica*, v. 14, 19 p.
- Brodie, E.D. Jr., 1968a, Investigations on the Skin Toxin of the Adult Rough-Skinned Newt, *Taricha granulosa*: *Copeia*, v. 2, p. 307.
- Brodie, E.D. Jr., 1968b, Investigations on the Skin Toxin of the Red-Spotted Newt, *Notophthalmus viridescens viridescens*: *American Midland Naturalist*, v. 80, p. 276.
- Brodie, E.D. Jr., 1977, Salamander antipredator postures: *Copeia*, v. 3, p. 523.
- Brodie, E.D. Jr., 1983, Antipredator Adaptations of Salamanders: Evolution and Convergence Among Terrestrial Species, in Margaris, N.S., Arianooutsou-Faraggitaka, M., and Reiter, R.J., eds., *Plant, Animal, and Microbial Adaptations to Terrestrial Environments*: New York, Plenum Publishing Corporation, p. 109–133.
- Brodie, E.D. Jr., Hensel, J.L., and Johnson, J.A., 1974, Toxicity of the Urodele Amphibians *Taricha*, *Notophthalmus*, *Cynops* and *Paramesotriton* (Salamandridae): *Copeia*, v. 2, p. 506.
- Brodie, E.D. Jr., Nussbaum, R.A., and DiGiovanni, M., 1984, Antipredator adaptations of Asian salamanders (Salamandridae): *Herpetologica*, v. 40, p. 56–68.
- Bruce, R.C., 2010, Proximate contributions to adult body size in two species of dusky salamanders (Plethodontidae: *Desmognathus*): *Herpetologica*, v. 66, p. 393–402.
- Buckley, D., and Sanchiz, B., 2012, Untrained versus specialized palaeontological systematics: a phylogenetic validity test using morphostructural conspicuity as character weight: *Spanish Journal of Palaeontology*, v. 27, p. 131–142.
- Caruso, N.M., Sears, M.W., Adams, D.C., and Lips, K.R., 2014, Widespread rapid reductions in body size of adult salamanders in response to climate change: *Global Change Biology*, v. 20, p. 1751–1759.
- Dillhoff, R.M., Dillhoff, T.A., Dunn, R.E., Myers, J.A., and Strömberg, C.A.E., 2009, Cenozoic paleobotany of the John Day Basin, central Oregon, in O'Connor, J.E., Dorsey, R.J., and Madin, I.P., eds., *Volcanoes to Vineyards: Geologic Field Trips through the Dynamic Landscape of the Pacific Northwest*: Boulder, Colorado, Geological Society of America, Field Guide, v. 15, p. 135–164.
- Dubois, A., and Raffaëlli, J., 2009, A new ergotaxonomy of the family Salamandridae Goldfuss, 1820: *Alytes*, v. 26, p. 1–85.
- Duellman, W.E., and Trueb, L., 1986, *Biology of Amphibians*: New York, McGraw Hill, 670 p.
- Estes, R., 1981, *Gymnophiona, Caudata*, in Wellenhofer, P., ed., *Handbuch der Paläoherpetologie*, pt. 2: Stuttgart and New York, Gustav Fischer Verlag, 115 p.
- Fitzinger, L.J.F.J., 1826, Neue Klassifikation der Reptilien nach ihren natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichniss der Reptilien-Sammlung des K. K. Zoologisch Museum's zu Wien: Wien, J.G. Hübner, 66 p.
- Fremd, T.J., 2010, Guidebook, SVP Field Symposium 2010, John Day Basin Field Conference, John Day Fossil Beds National Monument (and surrounding basin) Oregon, USA June 7–11, 2010: Society of Vertebrate Paleontology, Published Report, 153 p.
- Goin, C.J., Goin, O.B., and Zug, G.R., 1978, *Introduction to Herpetology*: San Francisco, W.H. Freeman, 527 p.
- Goldfuss, G.A., 1820, *Handbuch der Zoologie, Dritter Theil, zweite Abtheilung*: Nürnberg, Johann Leonhard Schrag, 512 p.
- Good, D.A., and Wake, D.B., 1992, Geographic variation and speciation in the torrent salamanders of the Genus *Rhyacotriton* (Caudata: Rhyacotritonidae): Berkeley, University of California Publication in Zoology, v. 126, p. 1–91.
- Gray, J.E., 1825, A synopsis of the genera of reptiles and Amphibia, with a description of some new species: *Annals of Philosophy, Series 2*, London, v. 10, p. 193–217.
- Gray, J.E., 1850, *Catalogue of the specimens of Amphibia in the collection of the British Museum, Part II. Batrachia Gradientia, etc.*: London, Spottiswoodes & Shaw, 72 p.
- Haeckel, E.H.P.A., 1866, *Generelle Morphologie der Organismen*, v. Volume 2: Berlin, Georg Reimer, p. 17–150.
- Hanifin, C.T., Brodie, E.D. III, and Brodie, E.D., 2004, A predictive model to estimate total skin tetrodotoxin in the newt *Taricha granulosa*: *Toxicon*, v. 43, p. 243–249.
- Heiss, E., Natchev, N., Salaberger, D., Gumpenberger, M., Rabanser, A., and Weisgram, J., 2009, Hurt yourself to hurt your enemy: new insights on the function of bizarre antipredator mechanism in the salamandrid *Pleurodeles waltl*: *Journal of Zoology*, v. 280, p. 156–162.
- Holman, J.A., 2006, *Fossil Salamanders of North America*: Bloomington, Indiana University Press, 233 p.
- Irmis, R.B., 2007, Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs: *Journal of Vertebrate Paleontology*, v. 27, p. 350–361.
- Kuchta, S.R., 2007, Contact zones and species limits: hybridization between lineages of the California Newt, *Taricha torosa*, in the Southern Sierra Nevada: *Herpetologica*, v. 63, p. 332–350.
- Maddison, W.P., and Maddison, D.R., 2011, Mesquite: a modular system for evolutionary analysis: Version 2.75, <http://mesquiteproject.org>.
- Marjanović, D., and Witzmann, F., 2015, An extremely peramorphic newt (Urodela: Salamandridae: Pleurodelini) from the latest Oligocene of Germany, and a new phylogenetic analysis of extant and extinct salamandrids: *PLoS ONE*, v. 10, e0137068, <https://doi.org/10.1371/journal.pone.0137068>
- McCloughry, J.D., Wiley, T.J., Ferns, M.L., and Madin, I.P., 2010, Digital Geologic Map of the Southern Willamette Valley, Benton, Lane, Linn, Marion and Polk Counties, Oregon: Oregon Department of Geology and Mineral Industries Open-File Report 0-10-03, 113 p.
- Meyer, H., 1973, The Oligocene Lyons Flora of northwestern Oregon: *The Ore Bin*, v. 35, p. 37–51.
- Meyer, H.W., and Manchester, S.R., 1997, The Oligocene Bridge Creek Flora of the John Day Formation, Oregon: University of California Publications in the Geological Sciences, v. 141, p. 1–195.
- Myers, J., Kester, P., and Retallack, G.J., 2002, Paleobotanical record of Eocene–Oligocene climate and vegetational change near Eugene, Oregon, in Moore, G.W., ed., *Field Guide to Geologic Processes in Cascadia*: Oregon Department of Geology and Mineral Industries Special Paper 36, p. 145–154.
- Naylor, B.G., 1978a, The frontosquamosal arch in newts as a defence against predators: *Canadian Journal of Zoology*, v. 56, p. 2211–2216.
- Naylor, B.G., 1978b, The Systematics of Fossil and Recent Salamanders (Amphibia: Caudata) with Special Reference to the Vertebral Column and Trunk Musculature [Ph.D. Dissertation]: Edmonton, Alberta, University of Alberta, 857 p.
- Naylor, B.G., 1979, A New Species of *Taricha* (Caudata: Salamandridae), from the Oligocene John Day Formation of Oregon: *Canadian Journal of Earth Sciences*, v. 16, p. 970–973.
- Naylor, B.G., 1982, A new specimen of *Taricha* (Amphibia: Caudata) from the Oligocene of Washington: *Canadian Journal of Earth Sciences*, v. 19, p. 2207–2209.
- Naylor, B.G., and Fox, R.C., 1993, A new ambystomatid salamander, *Dicamptodon antiquus* n.sp. from the Paleocene of Alberta, Canada: *Canadian Journal of Earth Sciences*, v. 30, p. 814–818.
- Nussbaum, R.A., and Brodie, E.D. Jr., 1982, Partitioning of the salamandrid genus *Tylototriton* Anderson (Amphibia: Caudata) with a description of a new genus: *Herpetologica*, v. 38, p. 320–332.
- Nussbaum, R.A., Brodie, E.D. Jr., and Datong, Y., 1995, A taxonomic review of *Tylototriton verrucosus* Anderson (Amphibia: Caudata: Salamandridae): *Herpetologica*, v. 51, p. 257–268.
- Peabody, F.E., 1959, Trackways of living and fossil salamanders: University of California Publications in Zoology, v. 63, p. 1–71.
- Pollett, K.L., MacCracken, J.G., and MacMahon, J.A., 2010, Stream buffers ameliorate the effects of timber harvest on amphibians in the Cascade Range of southern Washington, USA: *Forest Ecology and Management*, v. 260, p. 1083–1087.
- Pyrn, R.A., 2014, Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians: *Systematic Biology*, v. 63, p. 779–797.
- Rasmussen, D.L., 1977, Geology and Mammalian Paleontology of the Oligocene-Miocene Cabbage Patch Formation, Central-Western Montana [Ph.D. dissertation]: Lawrence, Kansas, University of Kansas, 794 p.
- Rasmussen, D.L., and Prothero, D.R., 2003, Lithostratigraphy, biostratigraphy, and magnetostratigraphy of Arikarean strata west of the Continental Divide in Montana, in Reynolds, R.G., and Flores, R.M., eds., *Cenozoic Systems of the Rocky Mountain Region*: Denver, Colorado, Rocky Mountain SEPM, p. 479–499.
- Rathke, M.H., 1833, Fünftes Heft, in F. Eschscholtz, *Zoologischer Atlas, enthaltend Abbildungen und Beschreibungen neuer Thierarten, während das Flottcapitains v. Kotzebue zweiter Reise um die Welt, auf der Russisch-Kaiserlichen Kriegsschiff Predpriate in den Jahren 1823–1826 beobachtet*, Fünftes Heft: Berlin, G. Reimer, 28 p.
- Reading, C.J., 2007, Linking global warming to amphibian declines through its effects on female body condition and survivorship: *Oecologia*, v. 151, p. 125–131.
- Retallack, G.J., 2008, Cenozoic cooling and grassland expansion in Oregon and Washington: *Paleobios*, v. 28, p. 89–113.
- Retallack, G.J., Bestland, E.A., and Fremd, T.J., 2000, Eocene and Oligocene paleosols of central Oregon: *Geological Society of America Special Paper* 344, 192 p.

- Retallack, G.J., Orr, W.N., Prothero, D.R., Duncan, R.A., Kester, P.R., and Ambers, C.P., 2004, Eocene–Oligocene extinction and paleoclimatic change near Eugene, Oregon: *Geological Society of America Bulletin*, v. 116, p. 817–839.
- Schoch, R.R., and Rasser, M.W., 2013, A new salamandrid from the Miocene Randeck Maar, Germany: *Journal of Vertebrate Paleontology*, v. 33, p. 58–66.
- Schoch, R.R., Poschmann, M., and Kupfer, A., 2015, The salamandrid *Chelotriton paradoxus* from Enspel and Randeck Maars (Oligocene–Miocene, Germany): *Palaeobiodiversity and Palaeoenvironments*, v. 95, p. 77–86.
- Scopoli, G.A., 1777, *Introductio ad Historiam Naturalam, Sistens Genera Lapidium, Planatarum, et Animalium Hactenus Detecta, Characteribus Essentialibus Donata in Tribus Divisa, Subinde ad Leges Naturae*: Prague, Gerle, 506 p.
- Shubin, N., Wake, D.B., and Crawford, A.J., 1995, Morphological variation in the limbs of *Taricha granulosa* (Caudata: Salamandridae): evolutionary and phylogenetic implications: *Evolution*, v. 49, p. 874–884.
- Smith, G.A., Manchester, S.R., Ashwill, M., McIntosh, W.C., and Conrey, R.M., 1998, Late Eocene–early Oligocene Tectonism, Volcanism, and Floristic Change near Gray Butte, Central Oregon: *Geological Society of America Bulletin*, v. 110, p. 759–778.
- Swofford, D.L., 2002, PAUP*, *Phylogenetic Analysis Using Parsimony (*and Other Methods)* [Software]: Version 4.0a152; 2014, Sinauer Associates, Sunderland, Massachusetts.
- Thormahlen, D.J., 1984, *Geology of the Northwest One-quarter of the Prineville Quadrangle, Central Oregon* [Masters Thesis]: Corvallis, Oregon State University, 106 p.
- Tihen, J.A., 1974, Two new North American Miocene salamandrids: *Journal of Herpetology*, v. 8, p. 211–218.
- Titus, T.A., and Larson, A., 1995, A molecular phylogenetic perspective on the evolutionary radiation of the salamander family Salamandridae: *Systematic Biology*, v. 44, p. 125–151.
- Van Frank, R., 1955, *Palaeotaricha oligocenica*, new genus and species, an Oligocene salamander from Oregon: *Breviora*, v. 45, p. 1–12.
- Venczel, M.A., 2008, New salamandrid amphibian from the Middle Miocene of Hungary and its phylogenetic relationships: *Journal of Systematic Palaeontology*, v. 6, p. 41–59.
- Wake, D.B., and Özeti, N., 1969, Evolutionary relationships in the family Salamandridae: *Copeia*, v. 1, p. 124–137.
- Wakely, J.F., Fuhrman, G.J., Fuhrman, F.A., Fischer, H.G., and Mosher, H.S., 1966, The occurrence of tetrodotoxin (tarichatoxin) in Amphibia and the distribution of the toxin in the organs of newts (*Taricha*): *Toxicon*, v. 3, p. 195–203.
- Weaver, W.G. Jr., 1963, Variations in the prevomerine tooth patterns in the salamander genus *Taricha*: *Copeia*, v. 3, p. 562–564.
- Zhang, P., Papenfuss, T.J., Wake, M.H., Qu, L., and Wake, D.B., 2008, Phylogeny and biogeography of the family Salamandridae (Amphibia: Caudata) inferred from complete mitochondrial genomes: *Molecular Phylogenetics and Evolution*, v. 49, p. 586–597.

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