THE OLIGOCENE FOSSIL CAUDATES OF OREGON: CLASSIFICATION, ANALYSIS, AND INSIGHTS ON THE PALEOECOLOGY AND CONSERVATION BIOLOGY OF PACIFIC NEWTS

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THESIS ABSTRACT

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Title: The Oligocene Fossil Caudates of Oregon: Classification, Analysis, and Insights on the Paleoecology and Conservation Biology of Pacific Newts

Newts, abundant worldwide, have unclear pre-Pliocene evolution and phylogenetic relationships. North America has a sporadic pre-Pliocene newt record. Several undescribed fossils can address this lack of information. I built a character matrix of >70 morphological characters for extant newts and two fossil species, *Taricha oligocenica* and *Taricha lindoei.* Phylogenetic analyses were used to investigate the relationships of the fossil taxa within newts. The morphology of the fossil taxa was compared with extant North American newts to redescribe the fossil specimens. The past ecology and biogeography of North American fossil newts was compared with their current ecologies and distribution to better understand their evolution and dispersal and to predict possible changes for newts in the face of environmental change. Results indicate that *T. oligocenica* and *T. lindoei* are closely-related species nested within *Taricha*, but their relationships with extant species are unresolved; the genus itself is rooted at least 32 Ma.

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CHAPTER I

INTRODUCTION

Salamanders have been abundant vertebrates playing important ecological roles as migratory, mid-level vertebrate predators, for at least 150-200 million years (Gao and Shubin, 2001). Today, salamanders have a wide distribution throughout the New World, Europe, and temperate eastern Asia (Duellman, 1999). Despite their abundance, climate change, human activity, and infection have pushed this ecologically diverse group into global decline (Lannoo et al., 2005; Pyron and Wiens, 2011; Denoël et al., 2013). For many salamander groups, their evolution, phylogenetic relationships, and times of origin are unclear (Tihen, 1958; Wake and Özeti, 1969; Naylor, 1978; Naylor, 1979; Estes, 1981; Duellman and Trueb, 1986; Dubois and Raffaëlli, 2009; Pyron and Wiens, 2011). The fossil record of caudates can help clarify such gaps in knowledge about this ecologically important group; fossil salamanders therefore represent an invaluable tool for the study of salamanders through time. Unfortunately, the pre-Pliocene fossil record of North American salamanders is sparse, especially west of the Rocky Mountains. Salamander fossils are often only represented by isolated vertebrae or other fragmentary elements, but 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; McClaughry et al., 2010). Additional, currently undescribed specimens include fossils from new localities near Gray Butte, Oregon and Lyons, Oregon, and a large individual from Goshen, Oregon. This work involves the description of new specimens and the redescription of previously examined material. The use of fossil caudates are used to examine the evolutionary relationships of North American salamanders, particularly for the Family Salamandridae, as the migration of salamandrids to North America and their subsequent divergence into the genera *Taricha* and *Notophthalmus* is poorly understood (Tihen, 1974; Naylor, 1979; Naylor and Fox, 1993).

Previous morphological comparisons with extinct and extant North American salamanders have recognized at least two species of fossil salamander 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). Further east, vertebrae from a third species, *Taricha miocenica*, have been uncovered in Montana's Late Oligocene (Arikareean; 24-26 Ma) Middle Cabbage Patch Beds (Tihen, 1974; Rasmussen, 1977; Rasmussen and Prothero, 2003). *Taricha miocenica* therefore appears in beds younger than those of *T. oligocenica* and *T. lindoei*. Van Frank's *T. oligocenica* and Naylor's *T. lindoei* are found in beds assigned to the Rupelian Stage (33-30 Ma; Early Oligocene); dates by Retallack et al. (2000) and Retallack et al. (2004) suggest correspondence with the Orellan NALMA of the Early Oligocene for *T. oligocenica* and *T. lindoei* (Albright et al., 2008). Another *Taricha* specimen from the Early Oligocene (33-32 Ma) Gumboot Mountain strata in Washington, identified to genus only, was described by Naylor (1982). The only other published evidence of these newts in the fossil record are fossil trackways from the Late Miocene of California and the Late Miocene of Kansas, which have been attributed to *Taricha* (Peabody, 1959; Holman, 2006).

The goal of this thesis is to identify Oregon's fossil salamanders and to determine diagnostic skeletal characters for use in future phylogenetic analyses with extinct and extant North American salamandrids. Furthermore, I will reexamine 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. Finally, I will use information gained from body size, morphology, and paleoecology of the fossil salamanders to examine possible applications to the conservation biology of living salamanders, given climate change and the global decline in amphibian populations (Blaustein and Wake, 1990; Alford and Richards, 1999; Gibbons, 2000; Stuart et al., 2004; Lannoo et al., 2005; Blaustein and Bancroft, 2007; Pyron and Wiens, 2011; Denoël et al., 2013).

All of this work will be performed incorporating 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, I hope 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? Do these salamanders represent separate and valid species, or an ontogenetic sequence of a single taxon? Are there any characters useful for a morphology-based phylogenetic analysis of fossil and extant salamandrids? Are there any insights to be gained 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?

Distribution of Fossil Salamandrids in North America

The fossil record of salamandrids in North America is sparse, yet it extends surprisingly far back into the Oligocene (33-32 Ma). The earliest appearances of fossil newts in North America are *Taricha oligocenica* and *Taricha lindoei*, both known from the early Oligocene of Oregon (Van Frank, 1955; Naylor, 1979). Another specimen from the Early Oligocene (Orellan, 33-32 Ma) Gumboot Mountain strata in Washington was described by Naylor (1982) as a member of the "*Palaeotaricha*" group. A third species, *Taricha miocenica*, is known from Montana's Middle Cabbage Patch Beds (24-26 Ma, Late Oligocene; Rasmussen and Prothero, 2003). Collections at the University of California Museum of Paleontology also contain a number of specimens assigned to the genus *Taricha*, including: trackways from the Late Miocene age Mehrten Formation, Tuolumne County, California (Peabody, 1959); a caudal vertebra from the Late Miocene age Mole Quarry of the Ricardo Formation, Kern County, California; and isolated postcrania from a Pleistocene age site in Contra Costa County, California (Olori and Bell, 2007). No fossils of *T. miocenica* have been examined for this study, though Tihen (1974) noted a mix of characters from both North American newt genera in *T. miocenica*, but assigned fossil specimens to the genus *Taricha*. If these classifications are correct, then *T. miocenica* represents one of the two occurrences of *Taricha* (along with the Kansas Mio-Pliocene trackways) east of the Rocky Mountains. 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), which was considered ancestral to only the modern *Taricha* taxa. However, the age and mix of character states represented in *T. oligocenica* and *T. miocenica*, along with eastern range extension (relative to the Rocky Mountains) of *T. miocenica*, suggest that these two taxa may be representatives of an ancestral lineage for both North American newt genera. More research on *T. miocenica* will be needed to resolve this matter. Interestingly, *T. lindoei*, which appears to be most similar to extant taxa, occurs in older beds than *T. miocenica* and *T. oligocenica*. This reversal of the stratigraphic order is easily explained by preservational bias; the fossil record of *Taricha* is extremely sparse. The single specimen from Washington, probably representing *T. oligocenica*, comes from the earliest Oligocene (Naylor, 1982). It seems likely that *T. oligocenica* and *T. lindoei* existed at the same time, given the evidence provided in the fossil record.

There are currently four species of *Notophthalmus* known in the fossil record, and all identifications are from isolated bones (mostly vertebrae). *Notophthalmus crassus* from the Early Miocene beds in the Batesland Formation of South Dakota (Tihen, 1974), *Notophthalmus robustus* from the Early Miocene of Florida (Estes, 1981), and *Notophthalmus slaughteri* from the Middle Miocene of Texas are extinct species (Holman, 2006), while *Notophthalmus viridescens* makes its first documented appearance in the Pleistocene of Maryland, West Virginia, Virginia, and Pennsylvania (Estes, 1981; Holman, 2006). Additionally, postcrania from the Gray Fossil Site of Tennessee are assigned to *Notophthalmus* (Boardman and Schubert, 2011), and a vertebra from the Pleistocene of Florida is assignable to either *N. viridescens* or *N. perstriatus*, which possess very similar vertebrae. A number of additional Pleistocene fossils from Texas have been identified to the generic level (Holman, 2006).

Geologic Setting

Southern Willamette Valley

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 convergence of oceanic crust obliquely subducts beneath the North American continental plate for much of the Cenozoic (McClaughry et al., 2010. This has resulted in a complicated forearc basin that has locally accumulated over 7,000 m of sedimentary and volcanic strata since the Paleocene (Retallack et al., 2004; McClaughry et al., 2010). The north- to northwest-flowing Willamette River and its major tributaries from the west (Long Tom, Luckiamute, and Mary's rivers) and the east (Calapooia, Coast Fork, North Santiam, and South Santiam rivers) drains the Southern Willamette Valley (McClaughry et al., 2010). The exposed rocks of the Southern Willamette Valley, which includes 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, represent an excellent record of depositional and deformational history through the Cenozoic along the aforementioned continental margin (Fig. 1; Retallack et al., 2004; McClaughry et al., 2010).

Willamette and Lyons Floras and the Mehama Formation

The Mehama Formation of the Little Butte Volcanics, within which the Willamette and Lyons floras and all Western Oregon salamander fossils are preserved, is a well-bedded sequence of volcaniclastic, indurated, dark gray, green, yellow-brown, or white sandstone, mudstone, conglomerate, and pebble breccia (Fig. 1). The sandstone, conglomerate, and breccia are typically massive, while the mudstone is similar to the underlying Fisher Formation in its regular bedding, the presence of carbon-rich horizons, and locally occurring pumiceous tuff (Retallack et al., 2004). Units within the Mehama Formation are locally fossiliferous (Fig. 1; McClaughry et al., 2010). It is important to note that, at this time, the Mehama Formation represents the generally nondescript volcaniclastic sedimentary rocks that occur between the more distinctive features of the Little Butte Volcanics, such as mapped formations, marker beds, and volcanic centers (McClaughry et al., 2010). This is opposed to the classic use of the term "formation," which is a formal lithostratigraphic unit, usually representing a tabular body of known position.

Fossils (mostly leaves, acorns, and catkins) are found in regularly, thinly bedded shales and in coarse-grained sandstone as gray, black, or brown compressions or impressions (Fig. 2; Retallack et al., 2004; McClaughry et al., 2010). The latest work done in this area, by Retallack et al., (2004) and Myers et al. (2002), suggests a flora of about 60 species representative of a forested Oligocene lacustrine assemblage. Included in this assemblage are a large number of holdovers from the Late Eocene, such as *Magnolia*, *Gingko*, *Fagus oregona*, and *Meliosma*, but the overall assemblage is dominated by early Oligocene taxa such as *Sequoia affinis*, *Pinus johndayensis*, and *Quercus consimilis* (Myers et al. 2002).

Along with the latest Eocene-earliest Oligocene Goshen flora (between 34.85 and 32.8 Ma, ^{40}Ar/^{39}Ar dates), the early Oligocene Willamette flora (>30.64 Ma) is regarded

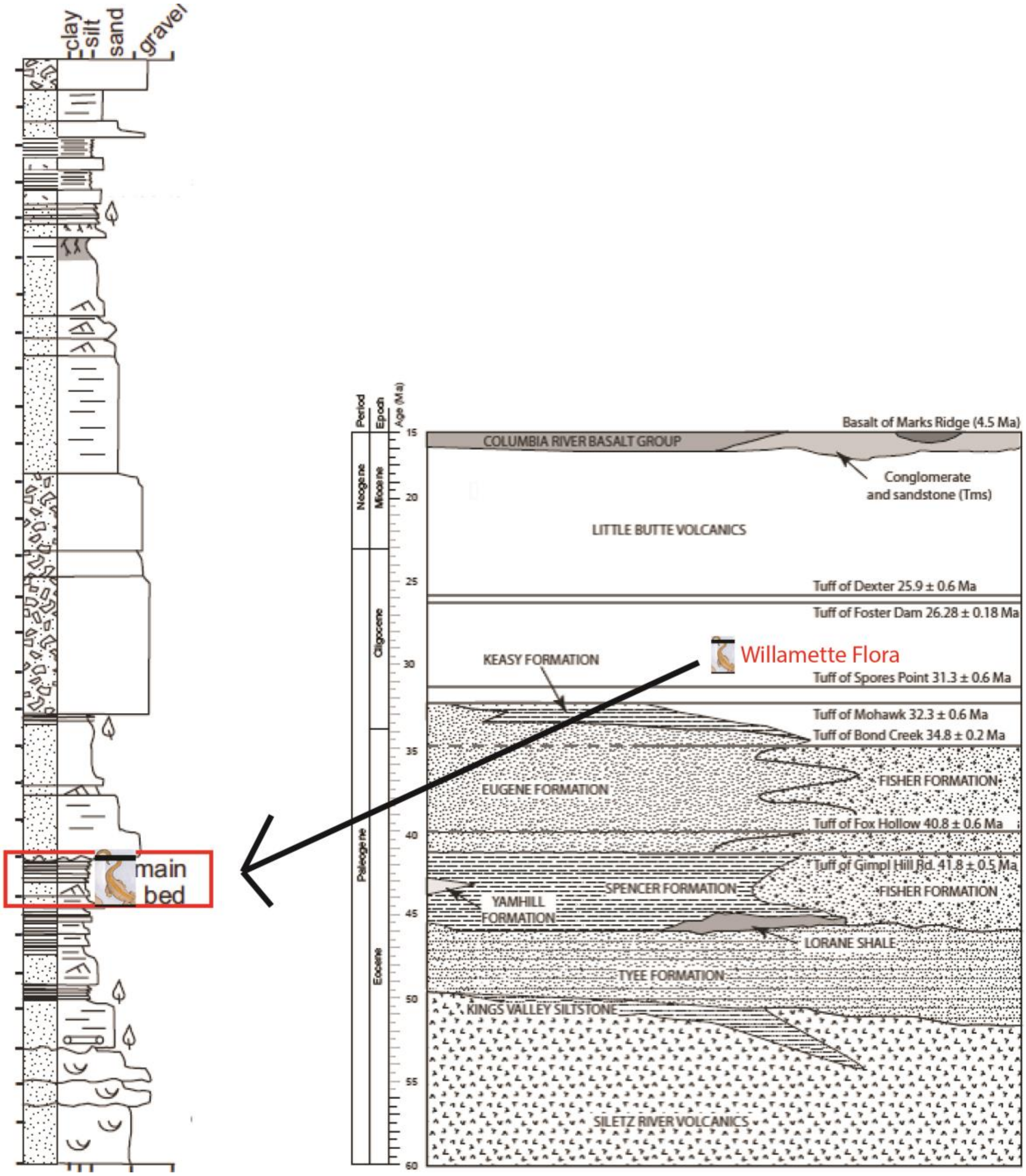


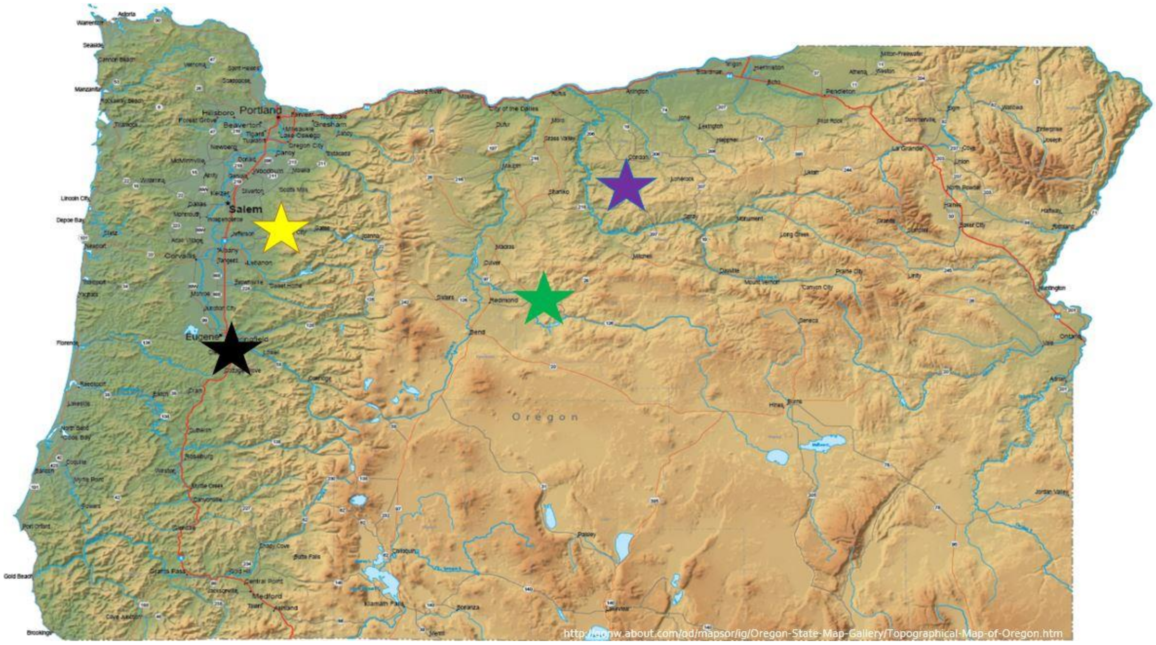
Figure 1. Stratigraphy of the Southern Willamette Valley. Left side: stratigraphic section from the Mehama Formation, with main beds containing all known salamander fossils from the area bordered by red box. Right side: general stratigraphy of the entire Southern Willamette Valley, with salamander symbol representing location of salamander fossils and the Willamette Flora. Leaves indicate other fossil flora localities. Modified from Retallack et al. (2004).

Figure 2. Outcrop of the Mehama Formation near Goshen, Oregon. This photograph exhibits the thinly bedded shales (bottom left of outcrop) that have produced most of the Willamette flora and several salamander fossils. Photo by Gregory Retallack.

as a critical indicator of climatic and vegetational shift across the Eocene-Oligocene transition (Retallack, 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; Fig. 1; Myers et al., 2002; Retallack et al, 2004; McClaughry et al, 2010). The presence of thick andesitic debris flow deposits suggests that the Willamette Flora (and the salamanders found with it) grew in an unstable environment adjacent to the increasingly active Western Cascades (Myers et al., 2002). Overall, the Willamette flora typifies a mesic warm temperature, mixed broadleaf and conifer forest, with a mean annual temperature of 13.5°C (less than 6°C cooler than Goshen flora conditions), and 1500mm of seasonal rainfall (Myers et al., 2002; Retallack et al., 2004). Many of the previous localities for both the Goshen and Willamette floras have been destroyed by road construction, though a few exposed blocks of the type Goshen locality can still be found at the surface, and a single road cut remains of the known Willamette flora localities (Fig. 3; named the "North Goshen locality" in Steere, 1958; Myers et al. 2002; Retallack et al. 2004;).

Only one small salamander specimen has been recovered from the sandstone of the Mehama Formation; the rest are found in the dark gray or whitish tan shales of the same formation. The presence of fossil *Taricha* agrees with the interpretation of the bedded shales as a lake margin deposits, as this genus and the majority of this family feeds in a freshwater environment; species of the genus *Taricha* prefers slow moving or still water conditions (Wake and Özeti, 1969; Goin et al., 1978; Naylor, 1978a; Naylor, 1978b; Naylor, 1979; Retallack et al., 2004; Pollett et al. 2010).

The Lyons flora, located in Northwestern Oregon (Fig. 3; southeast of the town of Lyons, Oregon in the upper Thomas Creek area), is comprised of at least 24 floral fossil 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 which has been silicified (Meyer, 1973). The stratification of the beds, abundance of fossil leaves, and the presence of one water plant (*Nymphoides*) in the fossil record suggest a shallow, quiet lacustrine environment (Meyer, 1973). Meyer



http://www.about.com/od/mapsor/ig/Oregon-State-Map-Gallery/Topographical-Map-of-Oregon.htm

Figure 3. Topographical map of Oregon with Oligocene fossil salamander localities. The black star is Goshen, the yellow star is Lyons, the green star is Gray Butte, and the purple star is Wheeler High School. Map modified from Angela Brown and About.com (2014).

(1973) compared the Lyons flora to other well-studied Tertiary floras, and determined it to be “middle Oligocene” in age based on its taxonomic similarities to the Rujada and Bridge Creek floras. Much like the Willamette flora, the Lyons flora is a mosaic of subtemperate holdovers from the Eocene and earliest Oligocene, and later Oligocene temperate plants, likely because of the flora’s close proximity to the Oligocene sea. However, the Lyons flora appears to be more similar to the Bridge Creek flora than to other Tertiary floras (Meyer, 1973). The presence of *Holmskioldia speirii* in particular is indicative of these later early Oligocene floras (Meyer, 1973). Retallack and others (2004) have listed the Lyons flora among the forested Oligocene lacustrine floras. At this time, one definite salamander fossil, consisting of part and counterpart, have been recovered from the same beds as the Lyons flora.

Bridge Creek Flora and the John Day Formation

The John Day Formation is a complex series of strata with a unique record of the long term change (around 20 million years) of climate and biotas for the Pacific Northwest of North America (Fig. 4; Fremd, 2010). Located in the Blue Mountains physiographic province, the John Day Formation is exposed in a number of basins in North-Central and Central Oregon (Fremd, 2010).

The lower John Day Formation Big Basin Member is recognized by its distinctive red and tan claystone and globally famous paleobotanical localities, which have also produced the vast majority of Eastern Oregon caudate fossils. Radiometric dates indicate that the Big Basin Member preserves roughly nine million years of deposition, from around 39-30 Ma. The lowest date, from the Member A ash-flow tuff of Peck (1964) and Robinson (1975) at the base of the Big Basin Member, has dates from two locations: the Clarno area, which is dated at 39.22 ± 0.03 Ma, and the Painted Hills area, which is dated at 39.72 ± 0.03 Ma (Fig. 4; Bestland and Retallack, 1994; Retallack et al., 2000; McClaughry et al., 2009). The uppermost Big Basin Member does not have an exact date, but a date of 29.75 ± 0.016 Ma from the lowermost sanidine tuff of the overlying Turtle Cove Member in the Painted Hills (Bestland and Retallack, 1994), combined with Albright et al.'s (2008) magnetostratigraphy with the sanidine tuff of the Painted Hills, fairly constrains the Big Basin/Turtle Cove boundary within Chron 12n, or about 30.6 Ma. The Bridge Creek Flora type localities, which are near the Eocene-Oligocene boundary, can be found 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), as it is sandwiched between the underlying Biotite Tuff (32.99 ± 0.11 Ma) and the Overlook Tuff overlying (32.66 ± 0.03 Ma; Fig. 4).

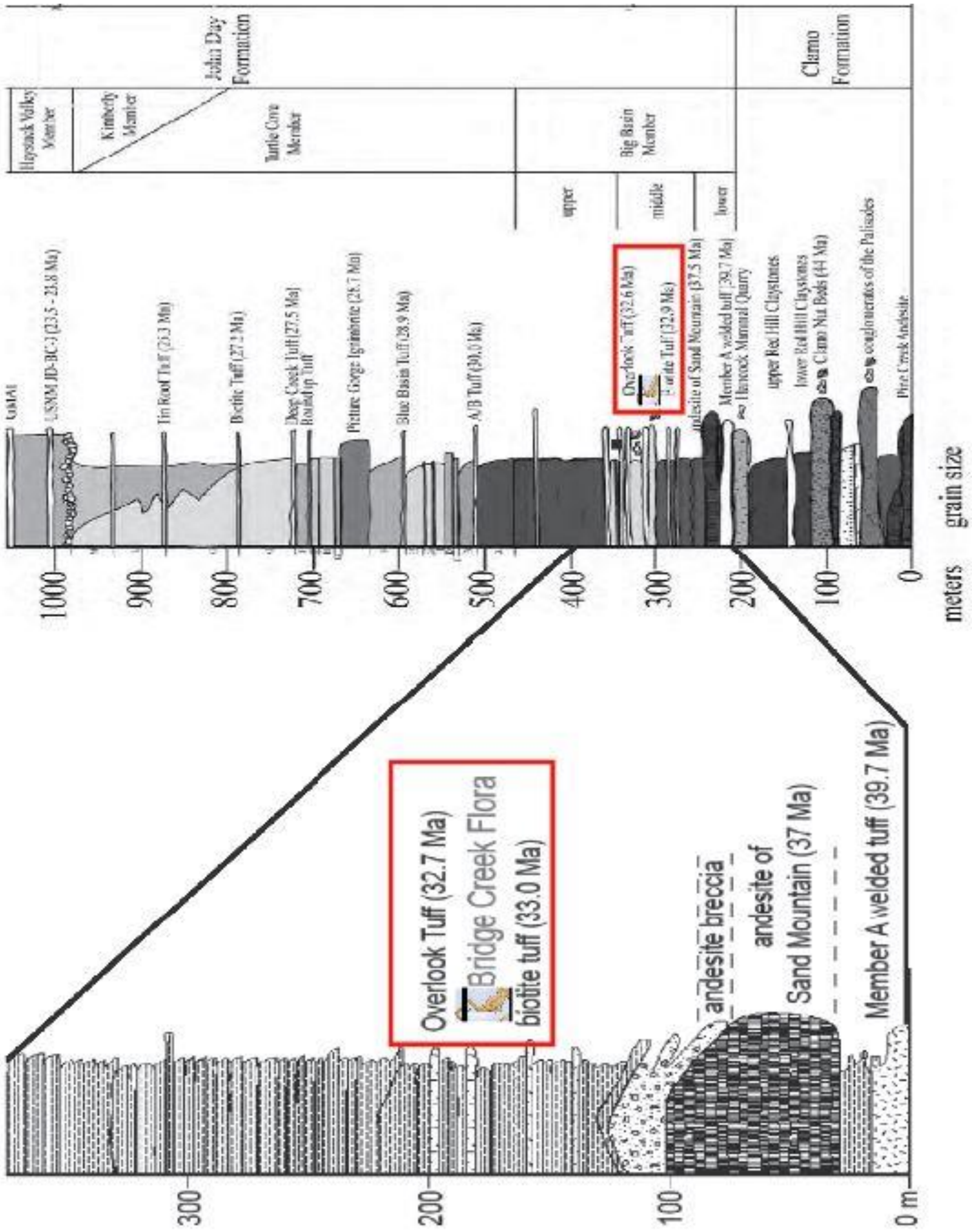


Figure 4. Composite stratigraphy of the John Day Formation. Modified from Fremd (2010). Detailed stratigraphy of the Big Basin Member of the John Day Formation, from the Painted Hills Unit, based on Bestland and Retallack (1994) and Retallack et al. (2000). Red boxes indicate location of salamander fossils within the stratigraphy.

The fossil salamanders found in the Big Basin Member of the John Day Formation have been unearthed at the Wheeler High School exposures in the town of Fossil, Wheeler County, Oregon (Naylor, 1979). Of the fossils from Wheeler High School, the vast majority are leaves of plants like *Metasequoia*, *Alnus,* and *Quercus*, but several vertebrates, including a species of bat, numerous fishes, and several amphibians have also been unearthed, most of which have gone unstudied (Brown, 1959; Meyer and Manchester, 1997; Dillhoff et al., 2009; Fremd, 2010). Plant, vertebrate, and invertebrate fossils preserved in these rocks are consistent with a cooler temperate climate than found in the Willamette flora, with less Eocene subtropical holdovers present (Meyer and Manchester, 1997; Retallack, 2008; Dillhoff et al., 2009). Salamander fossil-bearing beds are between 32.99 and 32.66 Ma, placing these fossils solidly in the Orellan NALMA (Bestland and Retallack, 1994; Retallack et al., 2000; Albright et al., 2008).

New Locality: Gray Butte and the John Day Formation

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 (Fig. 3), 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 (Fig. 5). Like the Bridge Creek flora, these plants (and now, this salamander) were deposited within the John Day Formation, and are between 33-32 Ma, according to a combination of the ^{40}Ar/^{39}Ar dates of the overlying alkali-olivine basalt, correlative stratigraphy between the Gray Butte area with the western facies of the John Day Formation (Fig. 5), and the respective compositions of the Kings Gap, Sumner Spring, Nichols Spring, Canal, and Trail Crossing floras (Smith et al., 1998). These floras collectively number 51 genera and 55 species of plants, and cover the climatic change from the subtropical Late Eocene to the cooler, drier temperate environment that emerged during the Early Oligocene of Oregon (Smith et al., 1998).

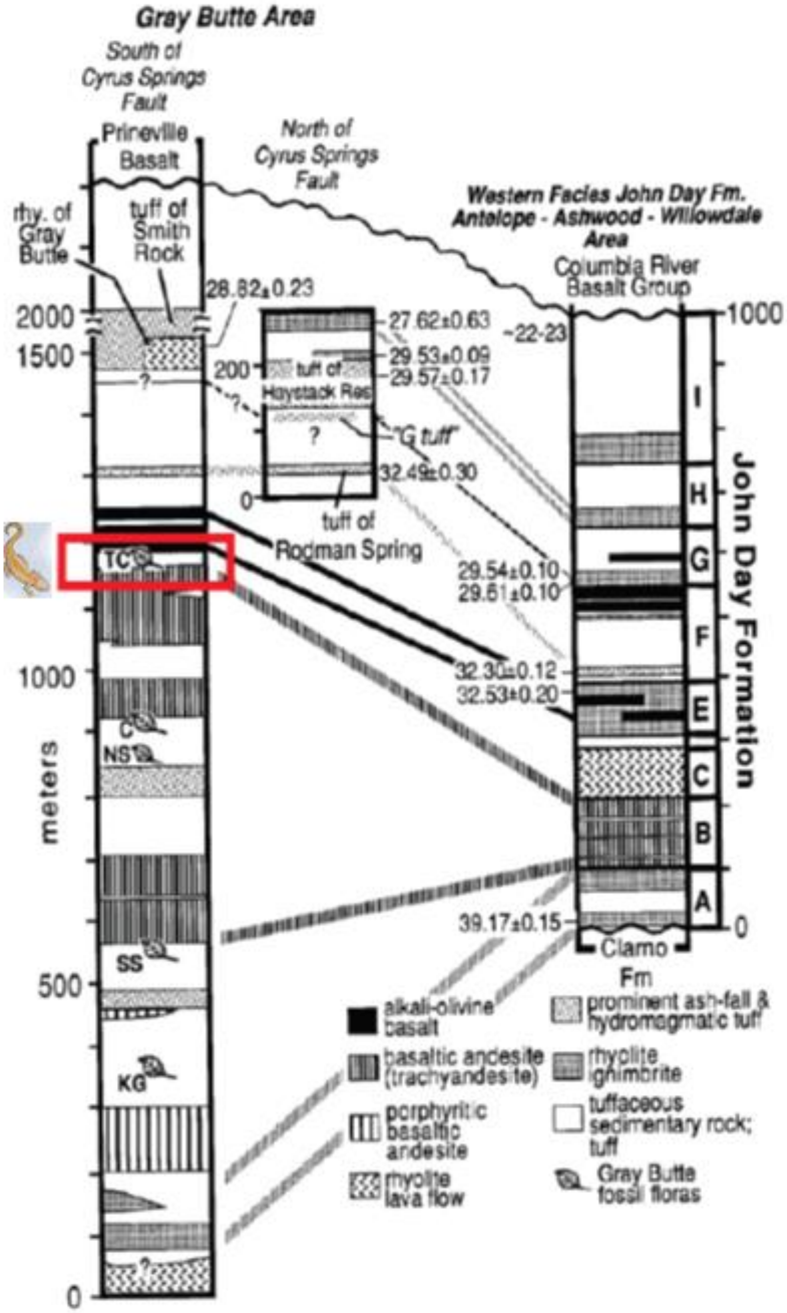


Figure 5. Stratigraphy of the Gray Butte Area. Correlated with the western facies of the John Day Formation, with the location of the Trail Crossing Flora indicated by a red box. Modified from Smith et al., 1998.

CHAPTER II

METHODS

Systematic Paleontology and Comparative Morphology

Given the rarity of complete or near-complete fossil salamander skeletons in North America, particularly for the Family Salamandridae, a large portion of this thesis compares fossils to each other and to extant salamander skeletal material to make diagnoses for the fossil specimens. In addition to using fossils housed at the University of Oregon Museum of Natural History (UOMNH) and John Day Fossil Beds National Monument (JODA), this thesis involved traveling to the University of California-Berkeley to examine additional salamandrid fossils from Oregon and to examine the modern salamander skeletal collections housed in the Museum of Paleontology (UCMP) and the Museum of Vertebrate Zoology (UCMVZ), respectively. I provide a list of institutional abbreviations for this thesis in Table 1 and a list of specimens examined in Table 2. I examined skeletons and isolated bones of eight *Taricha granulosa*, a single *Taricha sierra*, 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*. I 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). I paid special attention to details of the skull when possible, as 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 morphology of these structures is described in the systematic descriptions and incorporated into the phylogenetic analysis as characters.

Table 1. Institutional abbreviations.

Institution	Abbreviations
University of Oregon Museum of Natural History	UOMNH
John Day Fossil Beds National Monument	JODA
University of Alberta Laboratory for Vertebrate Paleontology	UALVP
University of California - Berkeley Museum of Paleontology	UCMP
University of California - Berkeley Museum of Vertebrate Zoology	UCMVZ

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 Kuchta (2007) to the morphometrics of *T. torosa* and *T. sierra* whenever possible (Fig 6). While the small sample size and limited variety of age classes for fossils make it unlikely that morphometrics can be analyzed in the manner of Good and Wake (1992) and Kuchta (2007), these measurements can still be useful for determining body proportions and predicting the size of individual specimens. These measurements include snout-vent length (SVL), tail length (TL), snout-gular length (SG), head width (HW), eye width (EW), eye-eye (E-E), eye-nostril (E-N), axilla-groin length (AG), trunk width (TW), forelimb length (FLL), hind limb length (HLL), and foot length (FL). I 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

Table 2. List of specimens with collection numbers. Institutional abbreviations are listed in Table 1; dagger symbol (†) indicates fossil taxa.

Specimen #	Taxon
UOMNH F-5405	*T. oligocenica* †
UOMNH F-30648	*T. oligocenica* †
UOMNH F-36412	*T. oligocenica* †
UOMNH F-55196	*T. oligocenica* †
UOMNH F-59812 A-B	*T. oligocenica* †
UOMNH F-35553	*T. lindoei* †
UOMNH F-59813	*T. lindoei* †
UOMNH F-30616	*T. lindoei* †
UOMNH F-109709	*T. lindoei* †
UOMNH F-109710	*T. lindoei* †
UOMNH F-110577	*T. lindoei* †
UOMNH F-111395 A-B	*T. lindoei* †
UOMNH F-37883 A-B	*T. lindoei* †
JODA 10429 A-B	*T. lindoei* †
JODA 1230	*T. lindoei* †
UCMP 137464	*T. lindoei* †
UCMP 137465	*Taricha sp.* †
UCMP 137466	*T. lindoei* †
UCMP 118876	*T. granulosa*
UCMVZ 67956	*T. granulosa*
UCMVZ 67969	*T. granulosa*
UCMVZ 218168	*T. granulosa*
UCMVZ 218169	*T. granulosa*
UCMVZ 218170	*T. granulosa*
UCMVZ 218171	*T. granulosa*
UCMVZ 218172	*T. granulosa*
UCMP 81746	*T. rivularis*
UCMVZ 78190	*T. rivularis*
UCMVZ 111544	*T. rivularis*
UCMVZ 111546	*T. rivularis*
UCMVZ 111548	*T. rivularis*
UCMVZ 68232	*T. rivularis*
UCMVZ 68233	*T. rivularis*
UCMVZ 68234	*T. rivularis*
UCMVZ 68235	*T. rivularis*
UCMVZ 68236	*T. rivularis*
UCMVZ 68237	*T. rivularis*
UCMVZ 78191	*T. rivularis*

Table 2 (continued).

Specimen #	Taxon
UCMP 81747	*T. torosa*
UCMVZ 4480	*T. torosa*
UCMVZ 68179	*T. torosa*
UCMVZ 68180	*T. torosa*
UCMVZ 68181	*T. torosa*
UCMVZ 68182	*T. torosa*
UCMVZ 129891	*T. torosa*
UCMVZ 129892	*T. sierrae*
UCMP 117050	*N. viridescens*
UCMP 118873	*N. viridescens*
UCMP 118874	*N. viridescens*
UCMVZ 185290	*N. viridescens*

tissue reference points (Good and Wake, 1992; Kuchta, 2007), and are here adjusted to use osteological landmarks that represent similar measurements for fossil taxa. Here, the anterior edge of the premaxilla to the posterior edge of the pelvic girdle is listed as SVL, the anterior edge of the premaxilla to the anterior portion of the atlas is listed as SG, and the length of the trunk between the forelimb and the hindlimb is listed as AG.

All University of Oregon (UO) and John Day Fossil Beds National Monument (JODA) fossil salamander photos have been taken with a Nikon D-90 at a focal length of 90mm. University of California-Berkeley specimens were photographed using either a Nikon optiphot 2-pol polarizing microscope with a Nikon digital sight ds-fi2 attachment, or a Nikon Coolpix L24 digital camera.

Chapter III is a systematic description and discussion of all known fossil caudates from the Goshen, Lyons, Prineville, and Wheeler High School (Fossil, Oregon) localities (Fig. 3) in the state of Oregon. The specimens are housed in collections at the University of Oregon Museum of Natural and Cultural History, University of California – Berkeley

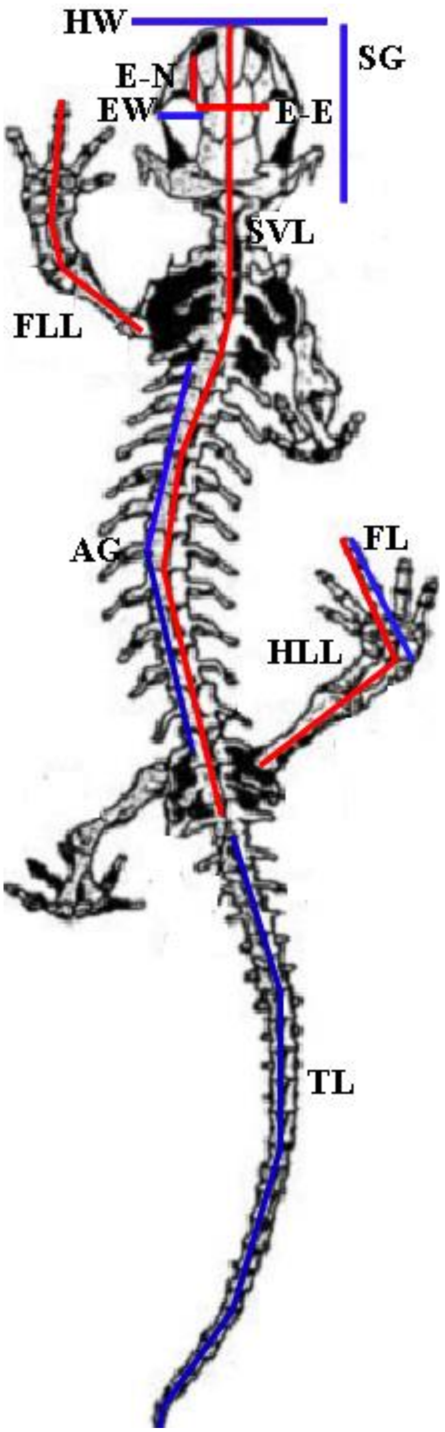


Figure 6. Generalized salamander skeleton, with measurements used. Measurements labelled with black line and abbreviations. Skeleton modified from Holman (2006).

Museum of Paleontology, and John Day Fossil Beds National Monument. All taxa are described using examples and are diagnosed based on literature and personal observations. The intention is to describe or redescribe, identify, and analyze the caudate fossils collected from Oregon localities. This includes 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.

Phylogenetic Analysis

The phylogenetic analyses of this thesis were performed by coding characters in Mesquite (Maddison and Maddison, 2011), then running a simple parsimony analysis in the Tree analysis using New Technology (TNT) program (Goloboff et al., 2000). A total of 73 characters and 12 taxa were analyzed in a matrix using all characters; a smaller analysis using only the 41 osteological characters from the larger analysis was also performed for the 12 taxa. Characters not present or inapplicable (some soft tissue characters when coding fossil taxa) were coded with question marks. A number of characters (11, 12, 13, 19, 22, 23, 44, 54, 56, 58, 65, and 67) are ordered and are coded as such for the parsimony analysis in TNT. Bracketed numbers indicate a character's original number from its referenced source. The simple parsimony analysis performed 100 repetitions using the sectorial search algorithm setting, with all characters weighted equally. Standard (sample with replacement) bootstrap support with 100 replications, Consistency Index, and Retention Index were also calculated in TNT. Strict consensus trees were calculated in TNT as well.

Much of these cladistic analyses use personal observations, combined with characters first established in Wake and Özeti (1969), Titus and Larson (1995), Venczel (2008), and Schoch and Rasser (2013). Naylor (1979b) made a few adjustments to the morphology-based phylogeny of Wake and Özeti (1969), some of which are adapted in this analysis. Since direct observations on *Tylototriton*, *Pleurodeles, Euproctus,* and *Cynops* have not been made because of lack of specimen availability, characters on these taxa are coded according to Wake and Özeti (1969), Titus and Larson (1995), Venczel (2008), Schoch and Rasser (2013), and Naylor (1979b). A description of the morphologic characters is included in Chapter IV. As in Titus and Larson (1995), one behavioral character with morphological correlates, courtship pattern (Salthe, 1967), is included in the analysis. Several soft-body characters (skin texture, lung reduction, etc.) are included in this matrix; such characters are here coded as unknown for fossil taxa. Characters 1-29, 32-40, 53, 54, and 73 are considered osteological, while characters 30, 31, 41-52, and 55-72 are soft tissue or behavioral.

The morphological trees are rooted using one outgroup: *Salamandra salamandra*, a member of the non-newt salamandrid group known as “true salamanders.” To discern the placement of fossil taxa within the newts for this analysis, several additional newt genera representing “primitive” Asian (*Tylototriton*, *Pleurodeles*) and “modern” Eurasian (*Triturus*, *Euproctus*, *Cynops*) taxa were included with the modern North American genera (*Taricha*, *Notophthalmus*). Within *Taricha*, *T. sierrae* was not included in the analysis, as there was not enough morphological character data available, and few positively identified skeletal specimens available to distinguish the species from *T. torosa*.

CHAPTER III

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, as opposed to the even higher neural spine and dermal cap of *Notophthalmus* (Wake and Özeti, 1969; Naylor, 1978b). The genus *Taricha* also possesses concave inter-prezygapophyseal neural arch margins, in contrast with the linear to convex inter-prezygapophyseal neural arch margins of *Notophthalmus* (Boardman and Schubert, 2011). The premaxillae are fused, nasals are separated, the rib processes do not extend past the body wall (no costal grooves), caudosacral ribs 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. The interradial cartilage is reduced (Estes, 1981).

Discussion: Genus *Taricha*'s closest relative is *Notophthalmus,* the only other North American newt genus. The North American genera are thought to be in a group derived from a *Tylototrition*-like ancestor (Wake and Özeti, 1969). It is important to note that extinct species *Taricha oligocenica* (Van Frank, 1955) and *Taricha miocenica* (Tihen, 1974) do possess pitted dermal caps on the dorsal side of their vertebrae, leading to questions about the ancestral state of North American newts. Work by Weaver, (1963) has determined that the shape of the prevomerine tooth row of extant *Taricha* can be used to distinguish *Taricha granulosa*, which displays a V pattern, from *Taricha torosa, Taricha sierra,* and *Taricha rivularis*, which all display a Y pattern.

Taricha oligocenica Van Frank, 1955

Palaeotaricha oligocenica Van Frank, 1955

Taricha (Palaeotaricha) oligocenica (Van Frank, 1955): Tihen, 1974

Taricha oligocenica (Van Frank, 1955): Estes, 1981

Holotype: UOMNH F-5405, a mostly complete skeleton, Early Oligocene, Mehama Formation, Lane County, Oregon, UO 11026 Goshen (Fig. 8).

Referred material: Mehama Formation, Lane County, Oregon, UO 11026 Goshen: UOMNH F-5405, a nearly complete skeleton (Fig. 7A-B); UOMNH F-36412, a carbonized imprint preserving a few highly carbonized vertebrae representing a young, but metamorphosed individual (Fig. 8A); UOMNH F-30648, a partial skeleton preserving the dorsal side of the skull and anterior vertebral column representing a young adult (Fig. 8B); UOMNH F-55196, partial skeleton preserving the ventral side of the salamander, but missing the skull, atlas, and left forelimb (Fig. 9A). Mehama Formation, Linn County, Oregon, UO 4356 Thomas Creek Drive: UOMNH F-59812 A-B, a near complete but crushed skeleton in part and counterpart (Fig. 9B).

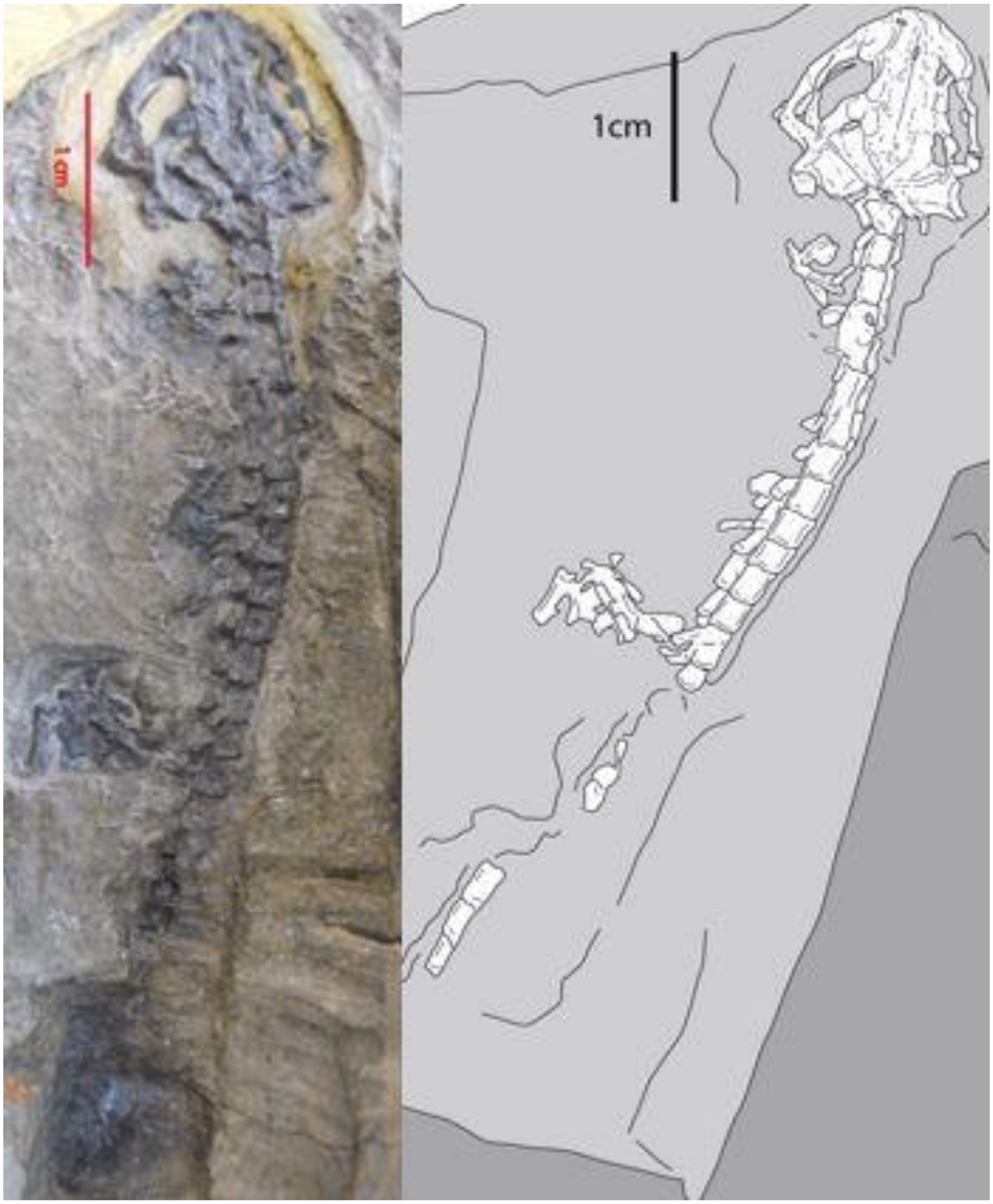


Figure 7. Dorsal view of UOMNH F-5405, type specimen of *T. oligocenica*. A, photograph. B, sketched reconstruction. Sketch done by Elizabeth White.

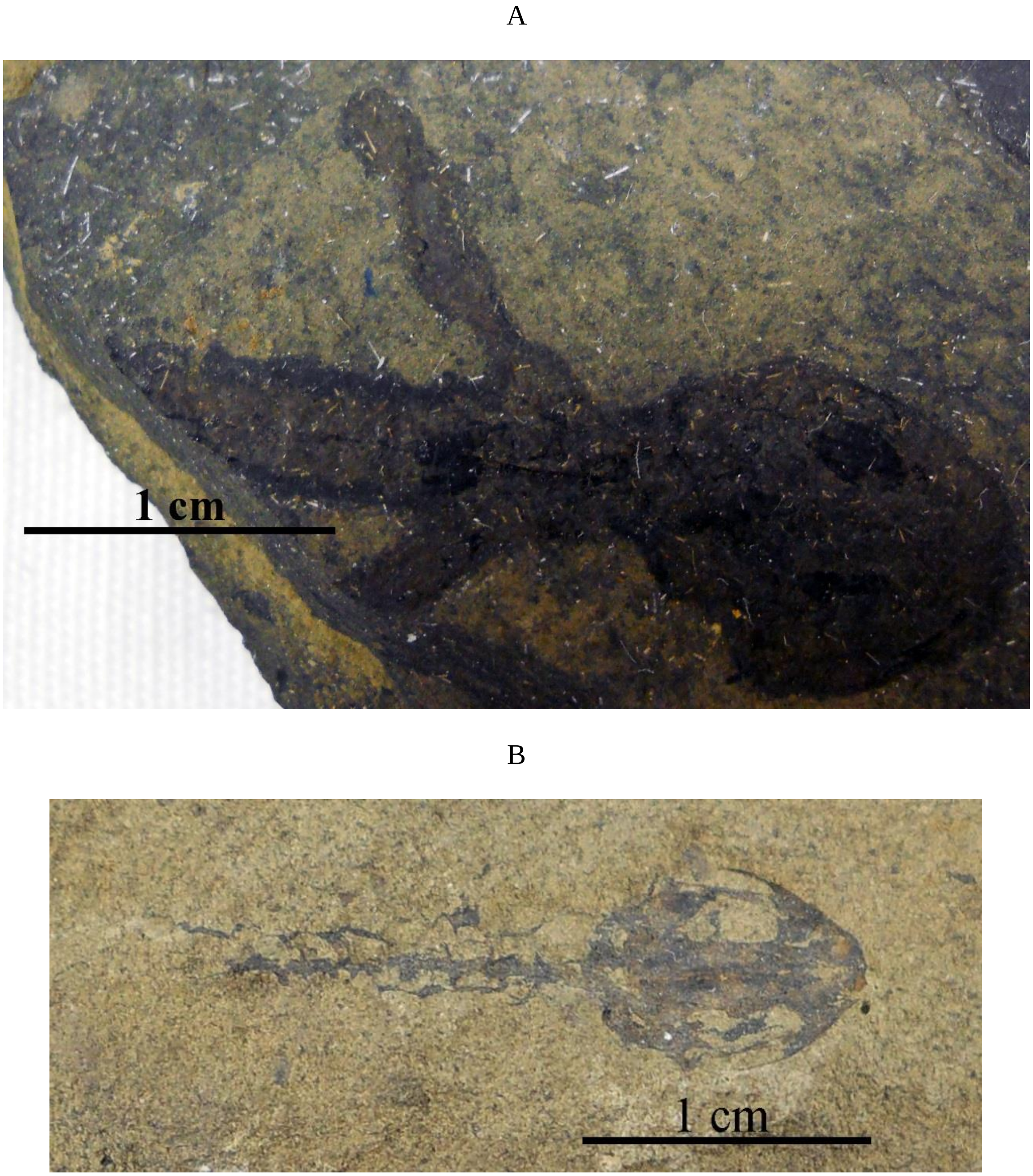


Figure 8. UOMNH F-36412 (A) and UOMNH F-30648 (B). These newt fossils are interpeted young adults.

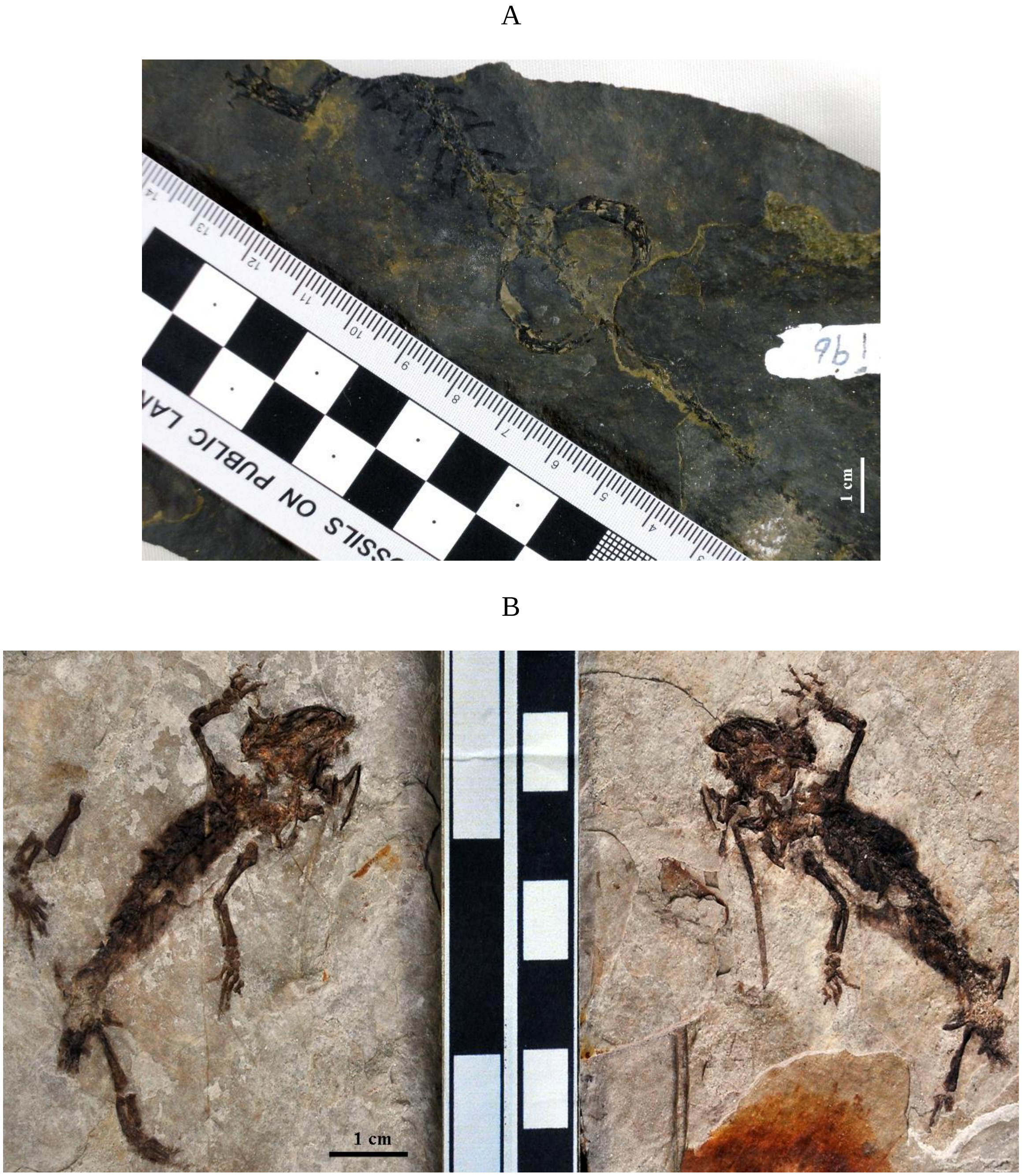


Figure 9. UOMNH F-55196 (A), and UOMNH F-59812 A-B (B), two large specimens of *T. oligocenica*. These fossils are interpreted as mature adults. UOMNH F-59812 A-B represents the best specimen found associated with the Lyons flora.

Range: Early Oligocene, Oregon

Diagnosis: Possesses a broad, expansive cap of dermal bone on the neural spines of the vertebrae. Differs from *Taricha miocenica* in having a broader, rectangular, as opposed to V-shaped dermal cap (Tihen, 1974; Estes, 1981; Holman, 2006). All other species of *Taricha* lack dermal caps on the neural spines of their vertebrae (Fig. 10). *T. oligocenica* also differs from *T. lindoei*, *T. granulosa*, *T. torosa*, *T. sierrae*, and *T. rivularis* in possessing a higher, differently shaped atlas that extends horizontally (flatly) towards the anterior end of the vertebra before a short anteroventral slope, followed by a near-vertical drop ventrally towards the condylar facets, and possesses an anteriorly narrowing, expanded dorsal cap (Fig. 11). Additionally differs from *T. lindoei* and all extant *Taricha* by exhibiting a narrow scapular portion of the scapulocoracoid (Van Frank, 1955; Naylor, 1979; Naylor 1982; Holman, 2006). *T. oligocenica* has more sculpturing in the dermal bones of the skull roof, particularly the frontals, parietals, squamosals, and frontosquamosal arch, than exhibited in extant *Taricha*. *T. oligocenica* also possesses a less tapered skull than *T. lindoei*. *T. oligocenica* and *T. lindoei* both possess elongate accessory rib process, distinguishing them from the short rib processes of extant *Taricha*.

Description: The maxillae of UOMNH F-5405 and UOMNH F-30648 extend similarly to extant *Taricha* and far further than in extant *Notophthalmus*. However, they do nearly but not quite extend to the quadrate, contrary to the original description by Van Frank (1955), who asserted that the maxillae were fused to the quadrate in the type specimen (UOMNH F-5405). 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. 7) 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).

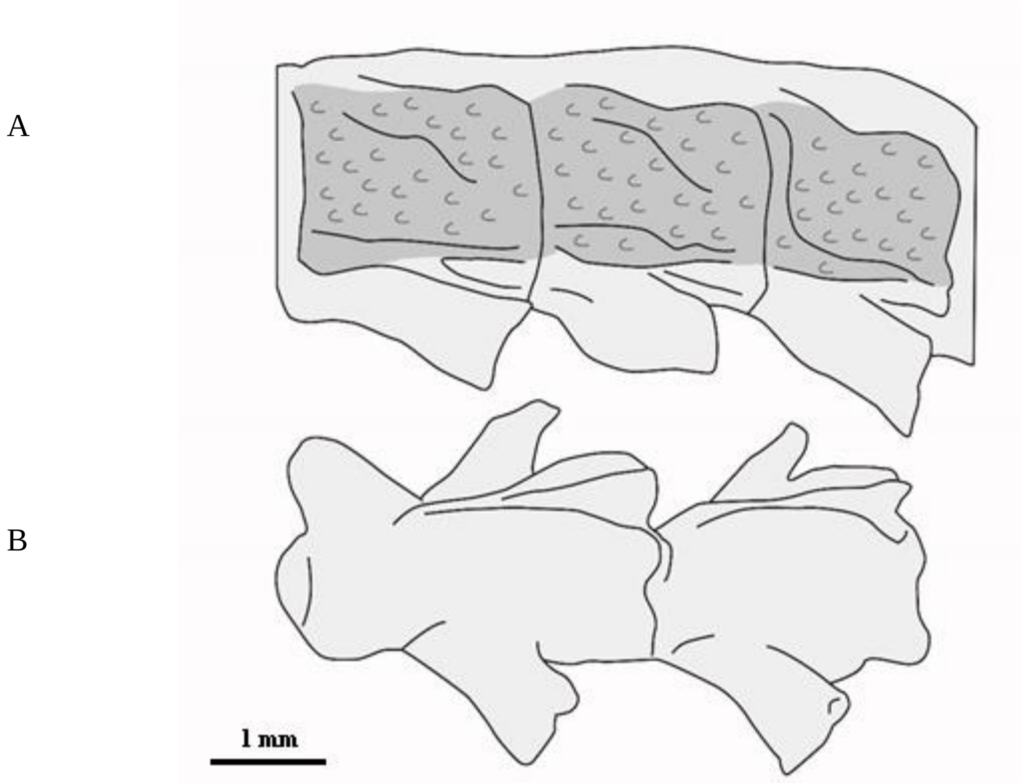


Figure 10. Traces of trunk vertebrae of *Taricha oligocenica* (A) and *Taricha torosa* (B) in dorsal view. Anterior to the left. Notable differences include the expansive rectangular caps of dermal armor present in *T. oligocenica*, but absent in *T. torosa*.

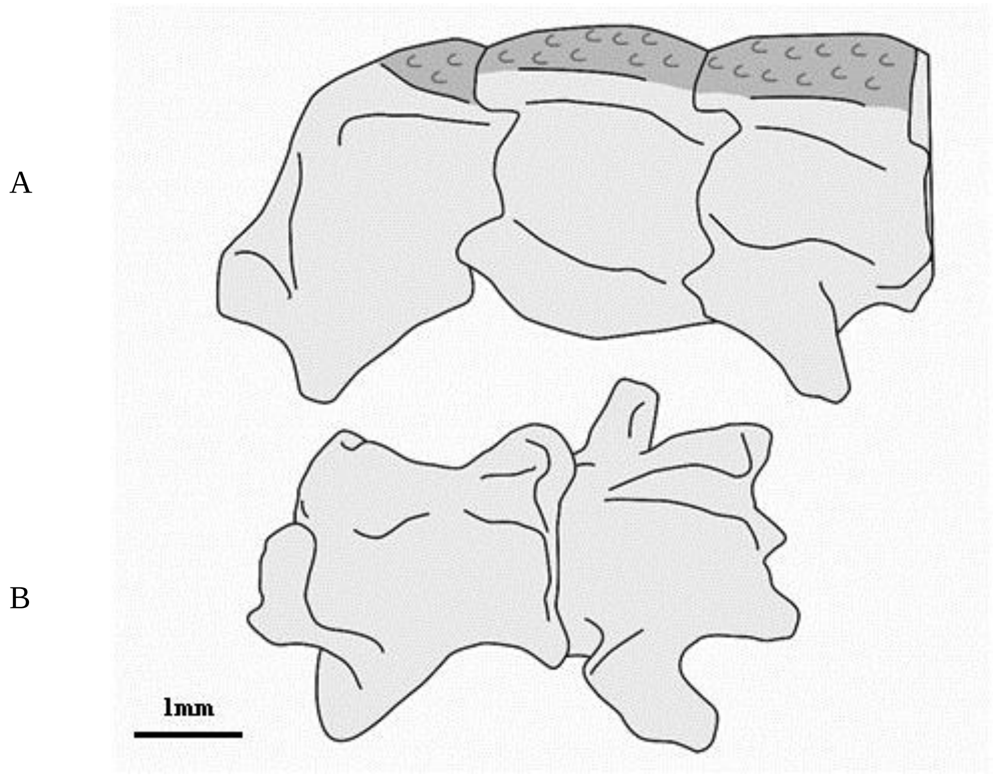


Figure 11. Traces of atlases of *Taricha oligocenica* (A) and *Taricha torosa* (B) in lateral view. Anterior to the left. Note the dermal cap on the posterior half of the atlas on *T. oligocenica*, along with the horizontal dorsal side and the abrupt, near-vertical drop to the condylar facets.

The vertebrae are opisthocoelous with laterally expansive rectangular dermal caps that are broad, flat, and somewhat sculptured (Fig. 10). These caps extend over the entirety of the trunk vertebra, including the atlas, and abut each other both anteriorly and posteriorly (Figs. 10-11). While previously, only the type specimen was known to possess these caps, this character is confirmed to be similarly expansive and identical in shape in UOMNH F-59812 A-B (Fig. 9B). The neural spines are high (higher than found in extant *Taricha*; Van Frank, 1955; Tihen, 1974) and elongate; and there are 14 presacral vertebrae, which are shorter when compared to extant *Taricha* of a similar size to the type specimen (approximately 135 mm total length). The atlas differs significantly from that of recent *Taricha*; as opposed to the anteroventrally sloping, robust neural crest of extant *Taricha*, the atlantal neural crest of *T. oligocenica* not only possesses an expanded dorsal cap that narrows anteriorly towards the skull, but also extends horizontally on the dorsal side of the vertebra towards the anterior end of the atlas, before forming a short anteroventral slope, then an abrupt ventral drop to the condylar facets (Fig. 11).

The ribs of *T. oligocenica* possess long uncinate processes that decrease in size successively towards the tail (Fig. 12). Van Frank (1955) noted that the number of these accessory 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); and 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 (Fig. 12), more so than in F-5405, which has a plastic compound obscuring the view of this character. It is difficult to tell if the number of the accessory rib processes is variable in individuals for the fossil taxa, as not all of the ribs are preserved in each specimen.

Comparison of the forelimbs and hindlimbs 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, the podials of *T. oligocenica* are fully ossified in adulthood (Fig. 13); this differs from extant *Taricha*, where the podials fully ossify only rarely, even in older individuals (Shubin et al., 1995). This difference in podial ossification may indicate that UOMNH F-5405, F-55196, and F-59812 A-B are old individuals, or may represent a legitimate character differentiation *T. oligocenica*. Unfortunately, only UOMNH F-5405, F-55196, and F-59812 A-B preserve the podials, so even with younger individuals available for study (UOMNH F-36412 and F-30648; Fig. 8A-B), it is not possible to discern whether this difference is due to age or a species level difference in morphology. 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-551196 (pes only; Fig. 13A), and F-59812 A-B (Fig. 13B). Van Frank (1955) described the pattern of bones in the tarsus (tarsal basale formula) in the type specimen of *T. oligocenica* as having an arrangement of 1, 2, 3, 4+5. While this appears to be the case, the specimen is obscured ventrally by epoxy yellowed by age, so it is difficult to confirm if this is an original arrangement or a result of taphonomy. If Van Frank's assessment is accurate and not a result of taphonomy, this tarsus arrangement contrasts with the pattern typically seen in extant *Taricha*, which have an arrangement of 1+2, 3, 4, 5. However, there is great variation in the patterns of the carpus and tarsus bones, even within a single population of *T. granulosa* (Shubin et al., 1995). While there is a preferred arrangement within a species (Shubin et al., 1995), a large sample size is required to take variation into account and determine a most common arrangement. With only two other specimens of *T. oligocenica* preserving bones of the tarsus (UOMNH F-55196 and F-59812 A-B), the sample size is not nearly large enough to such a study at this time, and even within this sample, UOMNH F-59812 appears to have the formula seen in extant *Taricha* (1+2, 3, 4, 5) (Fig. 13B). Given the variation found in extant populations and the small sample size of fossil specimens, this thesis does not utilize the tarsus bone arrangement as a character for use in phylogenetic analysis. The arrangement of the carpus bones is are 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 length of the more complete fossils (F-5405, F-59812 A-B) appears to be between ten times the skull width and ten times the snout-gular length (Table 3). 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 13mm, while the snout-gular length is 14mm. Naylor (1979) made similar calculations, determining that total body length in *Taricha* was approximately 12 times the skull width, but these calculations were done with specimens that still possessed soft tissues, and therefore appear to overpredict the total body length of specimens with only skeletal material remaining.

Discussion: Van Frank (1955) originally described the type specimen of *Taricha oligocenica* (Fig. 7) as a new genus and species, *Palaeotaricha oligocenica*, citing several differences he observed from extant *Taricha*, including: 1) a maxilla/quadrate suture, 2) a slightly different arrangement of tarsal bones, 3) dermal bone caps on the neural arches, 4) long uncinate 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 last of these traits is highly variable within species (Holman, 2006). Later, additional preparation led to the elimination of some differences (maxilla-quadrate suture, prepubic

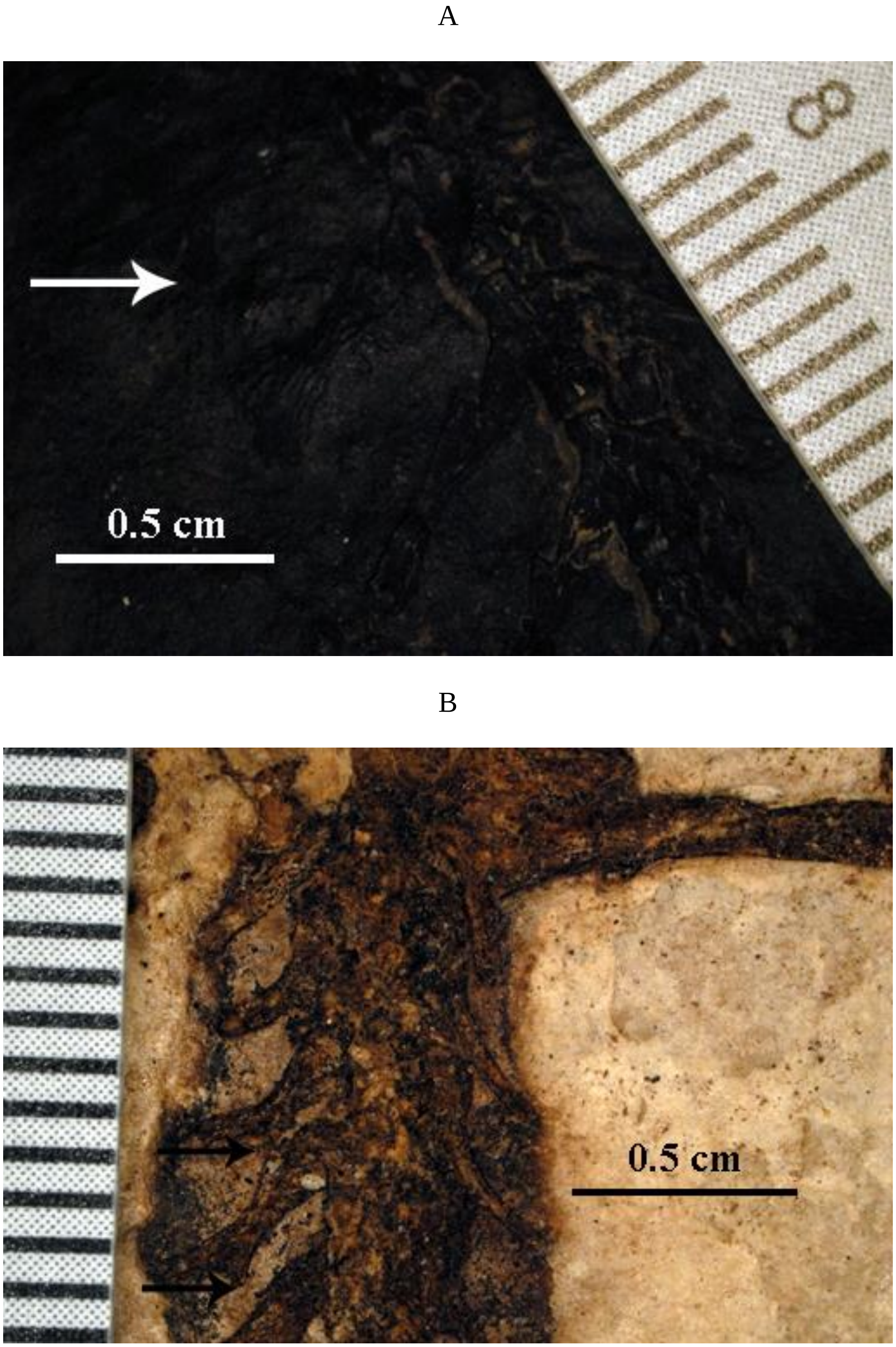


Figure 12. Images of the long, robust uncinate rib processes of *T. oligocenica* in UOMNH F-55196 (A) and UOMNH F-59812 B (B).

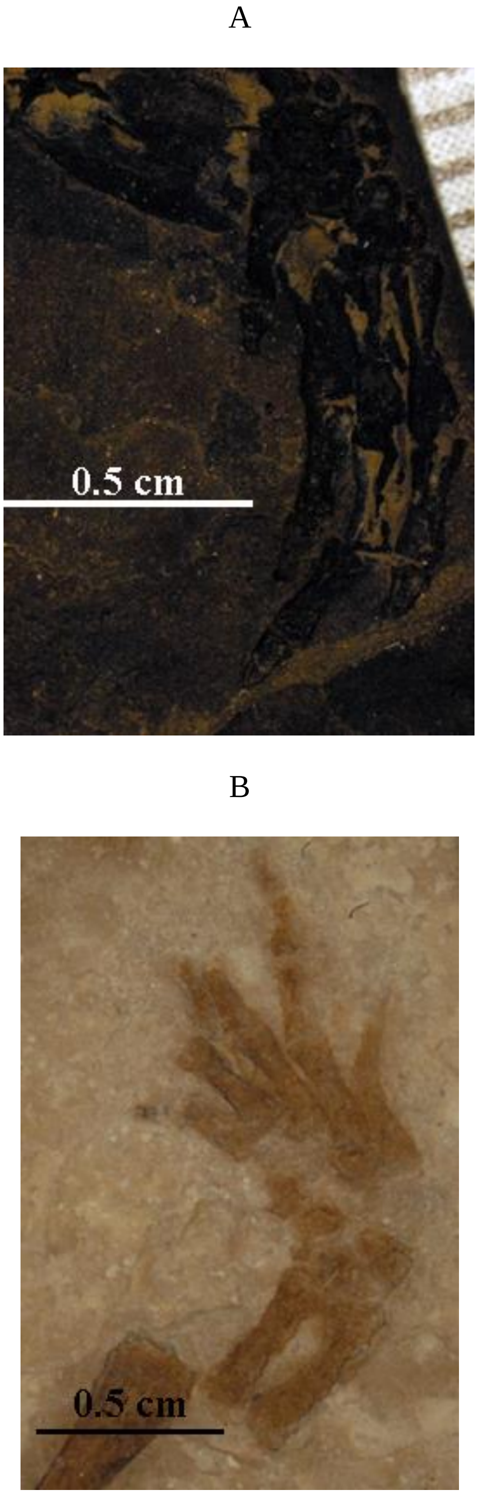


Figure 13. Images displaying the well-ossified tarsus of *T. oligocenica*. Top: UOMNH F-55196; Bottom: UOMNH F-59812 A. Note the preservation of newt swimming position in top picture, indicating that mature adult members of the species were at least semi-aquatic in their life histories.

Table 3. Measurements of fossil *Taricha*. Some specimens were 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 they structure is partial and therefore larger than the available measurement. All measurements in millimeters.

Specimen #	I.D.	HW	SG	SVL	AG	TL	HLL	FL	FLL	TW	E-E	EW	E-N	Approximate Length
UOMNH F-5405	*Taricha oligocenica*	13	14	60	34	>60	23	11	23	10	?	?	?	135
UOMNH F-36412	*T. oligocenica*	8	8	?	?	?	?	?	?	?	3	2	2	85
UOMNH F-30648	*T. oligocenica*	8	7.5	?	?	?	?	?	?	?	3	2	2	85
UOMNH F-55196	*T. oligocenica*	?	?	?	40	>85	32	13.5	32	14	?	?	?	170
UOMNH F-59812 A-B	*T. oligocenica*	13	15	62	35	?	24	12.5	24	10	?	?	?	140
UOMNH F-35553	*Taricha lindoei*	9.5	10.5	43	28	>25	>6	?	>5	?	3.5	2	?	100
UOMNH F-59813	*T. lindoei*	6	8	33	18	>13	>12	?	16	6	?	?	?	65
UOMNH F-30616	*T. lindoei*	9.5	11	45	30	?	?	?	?	?	3.5	2	?	100
UOMNH F-110577	*T. lindoei*	9.5	11	?	?	?	?	?	?	?	3.5	2	3	100
UOMNH F-38883 A-B	*T. lindoei*	11	11	54	30	>40	?	?	?	?	?	?	?	105
JODA 10429 A-B	*T. lindoei*	9	10	?	?	?	?	?	?	?	?	?	?	95
JODA 1230	*T. lindoei*	7	9	?	?	?	?	?	?	?	?	?	?	75
UCMP 137466	*T. lindoei*	7	9	?	?	?	?	?	?	?	?	?	?	75

process morphology), so 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 several 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, as he was unconvinced that there was enough evidence to differentiate any of the fossils from extant taxa at a subgeneric level. Curiously, the long accessory 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); yet 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 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 accessory rib processes. The most recent taxonomy of Family Salamandridae in Dubois and Raffaëlli (2009) has 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 study subsequent to the original descriptions of these species (in which *T. oligocenica* and *T. lindoei* are described from one specimen each).

Taricha lindoei Naylor, 1979

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

Referred material: 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. 14). 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. 15B); 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. 15A); 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. 15C); JODA 10429 A-B, flattened skull and first several vertebrae compressed onto block; JODA 1230, a block with skeletal impressions (Fig. 15D). UCMP John Day Formation locality V5636, Fossil, Wheeler County, Oregon: UCMP 137466, an anterior salamander impression/compression; UCMP 137464, partial skeleton compression. Despite the separate locality numbers of each institution, all specimens come from the Wheeler High School beds in Fossil, Wheeler County, Oregon.

Range: Early Oligocene, Oregon

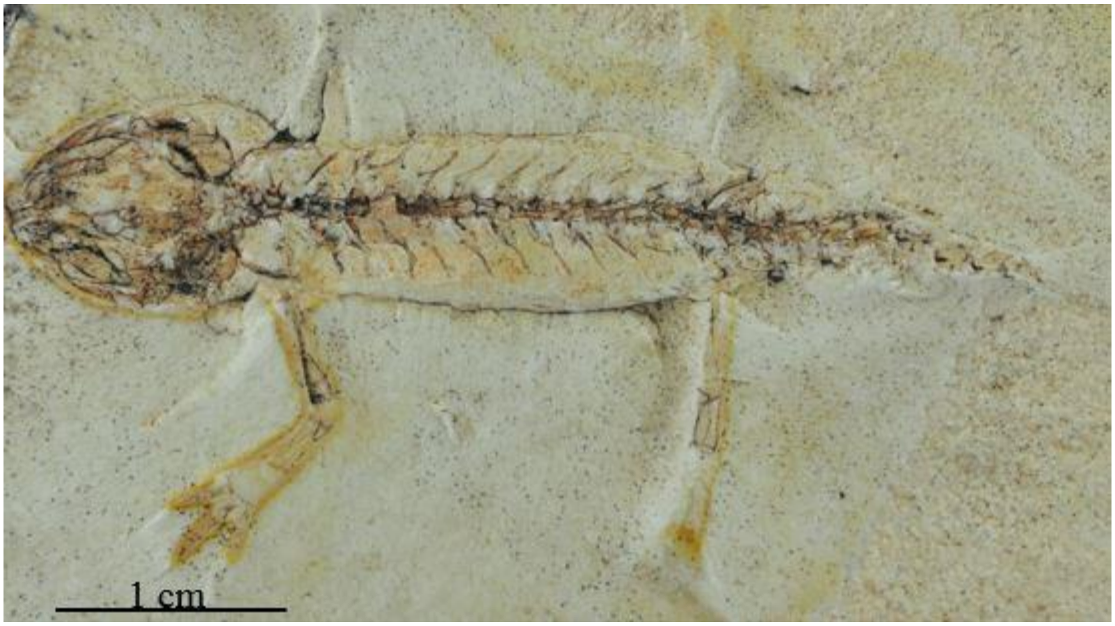


Figure 14. UOMNH F-59813, the only specimen of *T. lindoei* from Gray Butte. This specimen is not only the smallest articulated individual of *Taricha* in the fossil record, but also preserves a soft tissue outline for much of the specimen's body.

Diagnosis: Differs from *T. oligocenica* and *T. miocenica* in lacking caps of sculptured dermal bone on the neural spines of the vertebrae. Additionally different from *T. oligocenica* in atlas shape, broader scapular region of the scapulocoracoid, narrower anterior portion of the skull, and only minor sculpturing on the posterior end of the skull. Differs from *Taricha granulosa*, *Taricha torosa*, and *Taricha rivularis* in possessing prominent accessory pectoral rib processes, but is similar to *T. oligocenica* in this regard. Differs from other *Taricha* in having an elongate, anteriorly narrowed skull; however, the posterior region of the skull remains wide, differentiating this salamander from *Notophthalmus*. Concave inter-prezygapophyseal margins also differentiate *T. lindoei* from *Notophthalmus*.

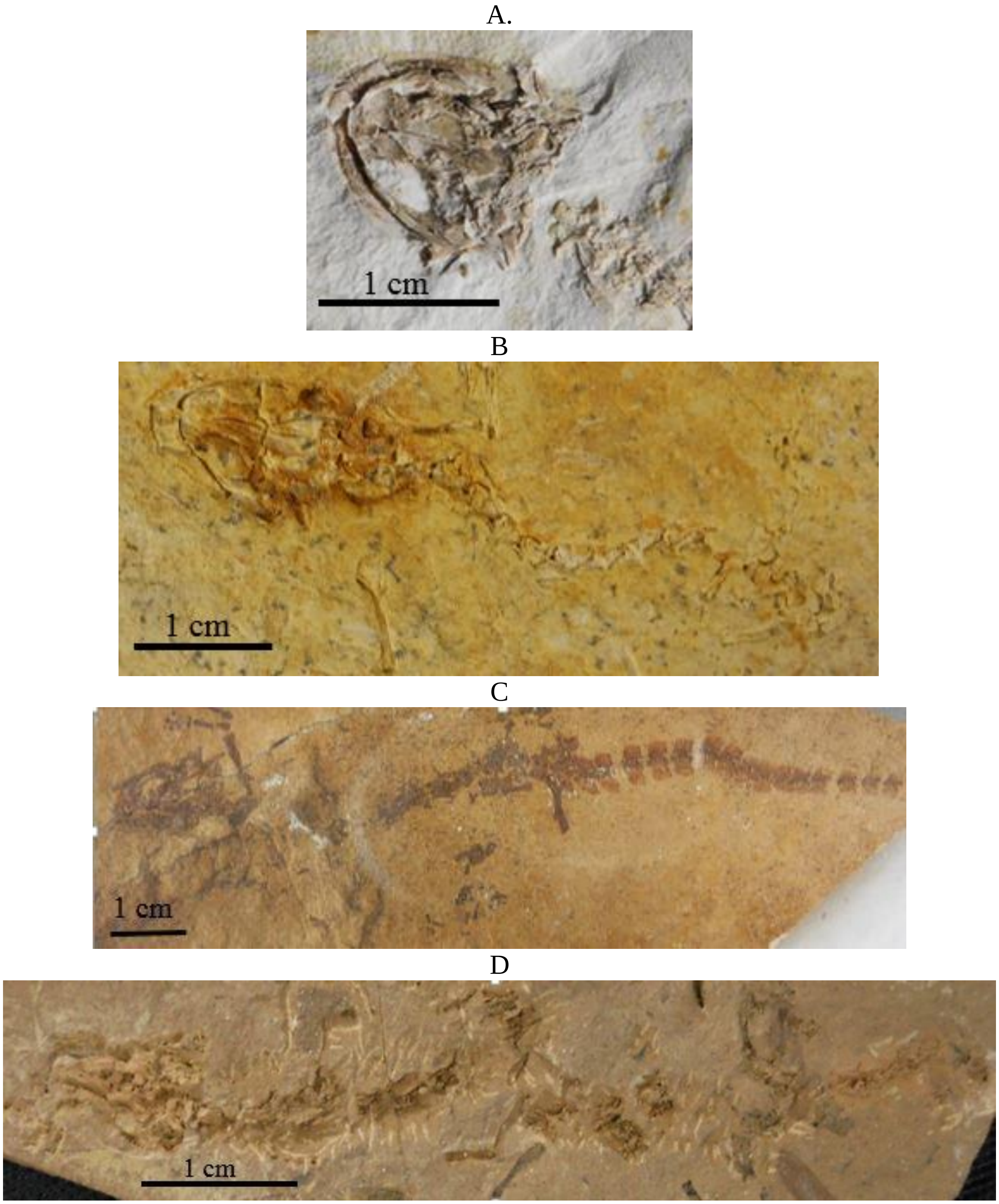


Figure 15. *Taricha lindoei*, specimens UOMNH F-110577 (A), UOMNH F-30616 (B), UOMNH F-37883A (C), and JODA 1230 (D). All specimenes were found associated with the Early Oligocene Bridge Creek Flora in Wheeler County, Oregon.

Description: The vertebrae of *Taricha lindoei* are opisthocoelous, as in all salamandrids, with long, thin, low neural crests that do not possess dermal caps, and concave inter-prezygapophyseal neural arch margins. The type specimen (UALVP 13870), UOMNH F-35553, and UOMNH F-59813 (Fig. 14) 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; Naylor 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; Naylor 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; Naylor, 1979). Furthermore, *T. lindoei* has a similar vertebral length and width to *Taricha miocenica* described in Tihen (1974), though the neural spine is much higher in the latter (Naylor, 1979; Estes, 1981). The atlas of *T. lindoei* is robust and slopes anteriorly, as in extant *Taricha* (Naylor, 1978b; Naylor, 1979). The scapular part of scapulocoracoid is broad, as in extant *Taricha* and unlike in *T. oligocenica* (Naylor, 1979; Holman, 2006). The uncinate (accessory) processes of the pectoral ribs are longer than those of extant *Taricha* species, as best seen in UOMNH F-59813 (Fig. 14; 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 and the premaxilla is fused (Fig. 14-15). 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 prevomerine tooth row reveals a V-shape, similar to what is seen in *T. granulosa*.

Discussion: 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 Raffaëlli (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 labelling 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 less than 40 individual 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 vertebral caps represented an ontogenetic feature for one taxon, or a true difference between two taxa, though the existence of *T. miocenica*, which was similar in size to *T. lindoei* but possessed less extensive dermal caps than *T. oligocenica*, was enough for Estes to maintain them as separate species. With the additional specimens now available, I 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 appear 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 of death and preservation is therefore unlikely. This solidly places *T. lindoei* within the *Taricha* genus. The long accessory rib processes resemble those seen in *T. oligocenica*, best seen in (Naylor, 1979). Interestingly, the shape of the prevomerine tooth row revealed in one specimen of *T. lindoei* (UOMNH F-30616; Fig. 15 B; Fig. 16) bears a V-shape similar to that seen in extant *Taricha granulosa*. The anteriorly-directed narrowing of the skull is consistently present in *T. lindoei* and is not exhibited 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 3), while the vertebrae of fully adult *T. miocenica* are around the same size as adult *T. lindoei* (Estes, 1981). The fact that salamandrids are known to be variable in size (Duellman and Trueb, 1986; Estes, 1981; 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.

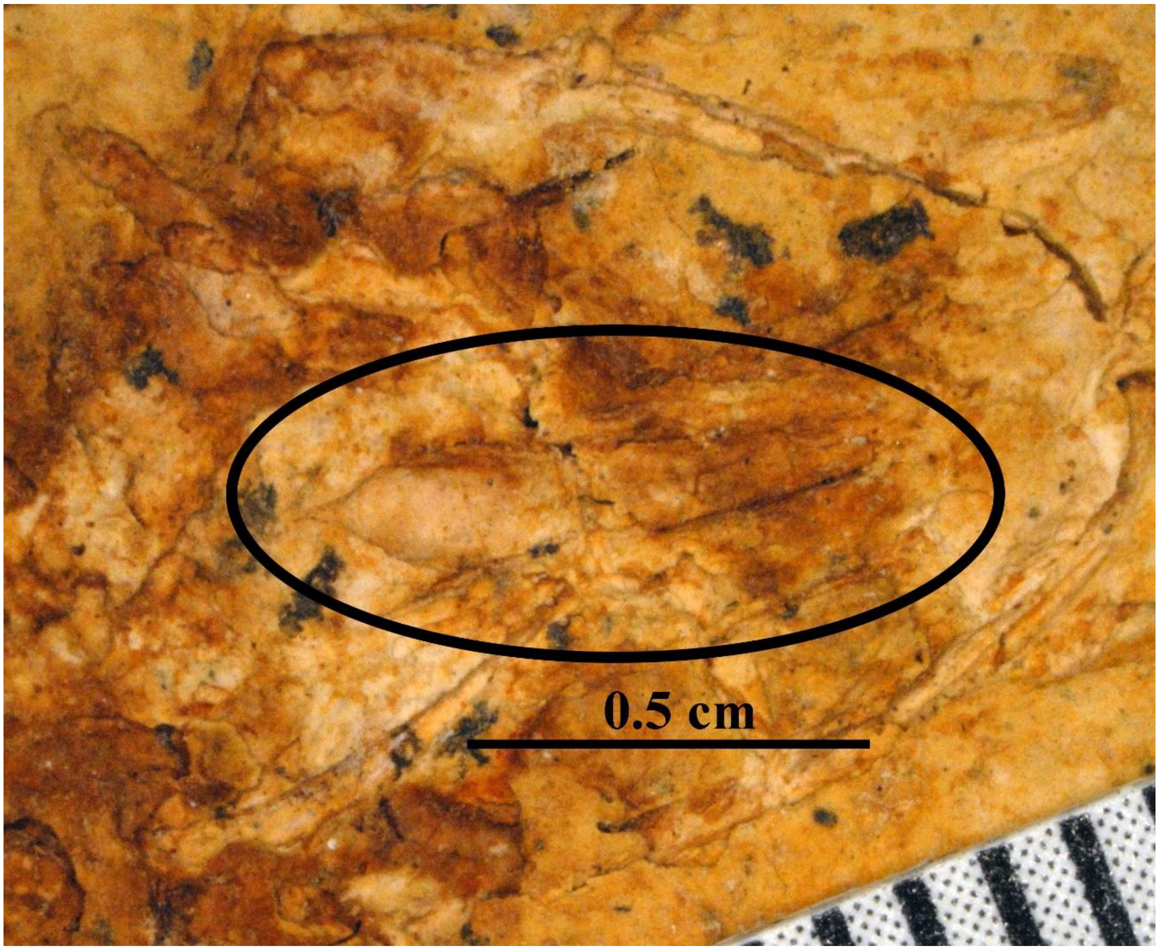


Figure 16. Skull impression of UOMNH F-30616 showing V-shaped prevomerine tooth row. Anterior to the right; prevomerine tooth row circled; V-shape points anteriorly and opens up posteriorly.

CHAPTER IV

PHYLOGENETIC ANALYSES

Description of Characters

1. Premaxilla: Paired (0), or fused (1) (Wake and Özeti, 1969 [1]). The degree of fusion along the length of premaxillae. In state 0, the premaxillary bones exist as two separate bones as in early tetrapods and early salamanders. In state 1, the premaxillary bones completely fuse medially into a single premaxilla.

2. Premaxilla: alary processes free (0), or fused together for at least 50% of their length (1) (Venczel 2008 [2]; Schoch and Rasser, 2013 [8]). In state 0, the alary processes are free of each other, and extend dorsally towards the nasals. In state 1, the alary processes are fused medially for a significant portion of their length.

3. Dermal skull roof: smooth (0), with pitted ornament on nasals and anterior frontals (1), or ornamented throughout (2) (Schoch and Rasser, 2013 [1]). The dermal skull roof may be relatively smooth in the nasal and anterior frontal regions, in state 0. In state 1, the ornamentation appears as a number of divots of variable depth, size, and spacing to form a somewhat irregular surface, but is not extensive enough to effect the overall shape of the distal nasals and anterior frontals, but in state 2, the pitting dominates the vast majority of the distal nasals and anterior frontals causing an irregular pit-and-ridge ornamentation that alters the overall shape of the skull and gives the ornamented regions a pustular appearance.

4. Nasals, frontals, and parietals: smooth or pitted (0) or covered with ridges (1) (Schoch and Rasser, 2013 [2]). The nasals, frontals, and parietals may each be smooth or with

radial pits, as in state 0, but they may also bear laterally directed grooves on each bone, as in state 1.

5. Squamosal: smooth (0), or ornamented (1) (Schoch and Rasser, 2013 [3]). The squamosals may be smooth (state 0), or the anterior dorsal surface of the squamosals may be pitted.

6. Frontal: Posterolateral process absent (0), or faint and pointed (1), or robust (2). The posterolateral process of the frontal in newts often (but not always) connects with a similar anterior process of the squamosal to compose the frontosquamosal arch (Schoch and Rasser, 2013 [17]). There may be a complete absence of this process (state 0), or there may be only a small, pointed process that does not form a bony arch (though cartilage may bridge the gap extending posterolaterally from the posterior end of the frontal (state 1), or there may be a robust process that in connects with a similar, anteromedially extending squamosal process related to the completion of a bony frontosquamosal arch.

7. Frontal and prefrontal: Lateral ridge absent (0), or present (1) (Schoch and Rasser, 2013 [20]).

8. Frontal and parietal: Medial suture straight (0), or sigmoidally curved (1) (Schoch and Rasser, 2013 [23]).

9. Frontal and parietal: Attachment of adductors only marginal (0), or extending medially, leaving large parts of parietal unornamented (1) (Schoch and Rasser, 2013 [24]). The attachment of adductor muscles to the frontal and parietal tend to leave less room for ornamentation the further they extend medially on those elements (state 1),

while marginal attachment allows for more pitting on the surface of the frontal and parietal bones.

10. Frontosquamosal arch: absent (0), partial (1), or closed (2). (Wake and Özeti (1969) [2]; modified in Naylor, 1978b, Estes, 1981, Titus and Larson, 1995, and Schoch and Rasser, 2013 [19]). Frontosquamosal arches are found only in the Family Salamandridae. This structure projects posteriorly from the frontals and anteriorly from the squamosals to form a bar. In state 0, this structure is absent; in state 1, the projections from the frontal and the squamosal do not meet and fuse to form a complete structure; in state 2, these projections meet and fuse to form the completed structure.

11. Maxilla: toothed portion extends to the quadrate (0), extends beyond the eye but falls short of the quadrate (1), or falls short of the posterior margin of the eye (2) (Wake and Özeti, 1969 [3]). State 0 indicates that the toothed maxillary bones reach and possibly fuse to the quadrate. In state 1, the maxillae still extend beyond the eye, but do not meet and fuse with the quadrate. The maxillae of state 2 are significantly shorter, and stop far short of the posterior margin of the eyes.

12. Nasals: fail to contact one another (0), narrowly contact one another (1), or broadly contact one another (2) (Wake and Özeti, 1969 [4]; modified in Naylor, 1978b). For state 0, the nasals do not contact each other along their length; for state 1, there is distinct, but narrow contact medially; for state 2, the nasals are in broad median contact over the extent of the bones.

13. Orbitosphenoid: without posterodorsal extension (0), with small extension (1), or with large extension (2) (Venczel, 2008 [12]). In state 0, the morphology of the orbitosphenoid is simple, with no dorsal and medial extension in the posterior region of

the element; in state 1, there is a posteromedial extension facing posterodorsally, but it does not project further than other extensions of the orbitosphenoid and is not very differentiated from the rest of the element, forming only a small ridge; in state 2, this projection is long, distinct, extending further posterodorsally than any other part of the orbitosphenoid and clearly differentiated from the rest of the orbitosphenoid.

14. Parasphenoid: basal plate offset (0), or continuous with cultriform process (1) (Schoch and Rasser, 2013 [25]).

15. Parasphenoid: crest absent (0) or present (1) (Schoch and Rasser, 2013 [26]). In state 0, the parasphenoid has no crest; in state 1, the parasphenoid possesses a ventrally-directed crest on the posterior end of the parasphenoid's basal plate.

16. Operculum: Ossified or mineralized (0), or unmineralized cartilage (1) (Wake and Özeti, 1969 [5]; Titus and Larson 1995 [6]).

17. Caudosacral ribs: present (0), or absent (1) (Wake and Özeti, 1969 [6]).

18. Fifth toe: present (0), or absent (1) (Wake and Özeti, 1969 [7]). The fifth (outermost; digit V) toe and fifth distal tarsus may be present, as in state 0, or lost, as in state 1.

19. Second basibranchial: present (0), rudimentary (1), or completely absent (2) (Wake and Özeti, 1969 [13]). In salamanders, three states are possible for the second basibranchial: it may be complete and well-developed, like in state 0; in state 1, a reduced, incomplete second basibranchial only occasionally remains as a cartilaginous element; the second basibranchial is completely absent in state 2.

20. Epibranchial: present (0), or fused or lost (1) (Wake and Özeti, 1969 [14]).

21. Radii of the hyobranchial apparatus: two pairs (0), or anterior pair lost (1) (Wake and Özeti, 1969 [15]). The anterior pair of radii may be present as a remnant of the hypohyals, as in state 0, or completely absent, as in state 1.

22. Interradial cartilage absent (0), very well developed (1), intermediate (2), or secondarily lost (3). This functionally significant structure is found only when the first pair of hyobranchial radii are absent (Wake and Özeti, 1969 [16]). This cartilage may be absent, with the first pair of hyobranchial radii present, well developed (state 1), somewhat reduced (state 2), or significantly reduced or lost despite absence of the anterior radii (state 3).

23. First basibranchial: ossified (0), cartilaginous but mineralized (1), or unmineralized cartilage (2) (Wake and Özeti, 1969 [17]). In state 0, the first basibranchial is a completely ossified bony element; in state 1, this element is cartilaginous, but is mineralized throughout; in state 2, the element is still cartilaginous, but bears no evidence of mineralization.

24. First ceratobranchial: bony (0), or cartilaginous (1) (Wake and Özeti, 1969 [18].

25. Epibranchial/ceratobranchial ratio: E<C (0), or E>C (1). Lengthening of the epibranchial is associated with derivative features of tongue protrusion (Wake and Özeti, 1969 [39]).

26. Maxilla and pterygoid: joint absent (0), or present (1) Wake and Özeti (1969 [40]). In state 0, there are no joints present between the maxilla and pterygoid, but in state 1, these elements meet to form a joint.

27. Pterygoid: Triradiate (0), or with quadrate ramus reduced to a stub (1) (Schoch and Rasser, 2013 [27]). In state 0, the pterygoid is prominently triradiate, with a ramus

extending anteriorly towards the maxilla, another medially towards the otic capsule, and a third extending posterolaterally towards the jaw articulation. In state 1, the pterygoid is no longer truly triradiate, as the quadrate (posterior) ramus is no longer prominent, and is reduced to a slender stub.

28. Jaw articulation. Near posterior margin of parasphenoid (0), level with carotid openings (1), or anterior to basipterygoid ramus (2) (Schoch and Rasser, 2013 [31]).

29. Mandible: Prearticular and angular not fused with articular (0), or fused with the articular (1) (Schoch and Rasser, 2013 [32]).

30. Lung reduction: well-developed lungs (0), or reduced or absent (1) (Wake and Özeti, 1969 [8]; Titus and Larson, 1995 [8]).

31. Skin texture: smooth (0), or rough or keratinized (1) (Wake and Özeti, 1969 [9]). Naylor (1979b) pointed out that other salamander families, along with basal salamandrids like *Salamandra*, lack rough skin.

32. Rib protrusion: trunk ribs form short rods (0), or are as long as three vertebral centra and distally sharpened (1) (Schoch and Rasser, 2013 [35]).

33. Accessory (uncinate or epipleural) rib processes absent to short (0), or elongate (1). In both states, the size of the rib processes (if present) decreases posteriorly. In state 1, the largest (anteriormost) processes (if any are present) are small blunt bumps extending ≤1mm dorsally and posteriorly from the rib. In state 2, the anteriormost, bluntly-tipped processes distinctly branch away from the main rib by several millimeters, or about a third of the rib's total length.

34. Neural spines. Low, posterodorsally ascending (0), or elevated with thin crest forming straight horizontal dorsal margin (1) (Schoch and Rasser, 2013 [37]).

35. Expanded, capped neural spines of trunk vertebrae absent (0), or present (1). In some salamanders, the neural spine is laterally expanded, with dermal bone caps that may or may not extend anteriorly and posteriorly to abut one another (state 1). State 0 represents a vertebral column lacking these flat caps of bone.

36. Scapular portion of scapulocoracoid short and wide (0), or long and thin (1). In state 0, newts like extant *Taricha* have a scapular region is short and shaped somewhat like an anvil. In state 1, this region is longer and thinner, somewhat like an uneven hourglass.

37. Atlas: Centrum not shorter than trunk vertebrae (0), or shorter than trunk vertebrae (1) (Schoch and Rasser, 2013 [34]). In state 0, the centrum of the atlas is either longer than or equal to the length of the subsequent vertebrae. In state 1, the centrum of the atlas is shorter than seen in subsequent vertebrae.

38. Atlas: Robust neural crest slopes anteriorly (0), or extends horizontally and anteriorly before dropping straight down at the anterior end of the atlas (1).

39. Inter-prezygapophyseal neural arch margins: concave (0), or linear to convex (1) (Boardman and Schubert, 2011). The inter-prezygapophyseal margins of the neural arch may be further ventral than the prezygapophyses, as in state 0, or may extend anteriorly to be linear with or anterior to the prezygapophyses, as in state 1. This comparison has only been used for distinguishing North American taxa in the literature (Boardman and Schubert, 2011), so no data for other taxa is available at this time.

40. Prevomerine tooth row: V-shaped (0), or Y-shaped (1).

41. Iris: yellow or partially yellow (0), or black (1).

42. Radioglossus and hyoglossus: single, undifferentiated and unpaired (0), differentiated, hyoglossus developed, but radioglossus particularly well developed (1),

differentiated with single hyoglossus and paired but poorly developed radioglossals (2), or greatly reduced (3) (Wake and Özeti, 1969 [35]).

43. Courtship pattern: no capture (0), ventral capture (1), dorsal capture (2), or caudal capture (3) (Titus and Larson, 1995 [14]). In state 0, males do not attempt to capture females as a part of courtship. In states 1-3, capture is a part of the male courtship pattern, but the method of capture occurs either ventrally (state 1), dorsally (state 2), or caudally (state 3) relative to the female salamandrid.

44. Egg size: large number of small eggs (0), intermediate size and number of eggs (1), or small number of large eggs (2) (Wake and Özeti, 1969 [10]).

45. Reproductive pattern: oviparous (0), or ovoviviparous (1) (Wake and Özeti, 1969 [12]).

46. Male dorsal glands: unbifurcated (0), or bifurcated (1) (Titus and Larson, 1995 [16]).

47. Ciliated epithelium in anterior female cloacal tube: absent (0), or present (1) (Titus and Larson, 1995 [17]).

48. Epidermis: epidermal lining in anterior half of female cloacal chamber present (0), or absent (1) (Titus and Larson, 1995 [18]).

49. Pseudopenis in male cloacal chamber: absent (0), or present (1) (Titus and Larson, 1995 [19]).

50. Female anterior ventral glands: present (0), or absent (1) (Titus and Larson, 1995 [20]).

51. Other female cloacal glands: absent (0), or present (1) (Titus and Larson, 1995 [21]).

52. Male posterior ventral glands: present (0), or absent (1) (Titus and Larson, 1995 [22]).

53. Ceratohyal: partially ossified (0), or completely unmineralized (1) (Wake and Özeti, 1969 [20]).

54. Second Ceratobranchial: ossified (0), mineralized cartilage (1), or unmineralized cartilage (2) (Wake and Özeti, 1968 [19]). This element may be a fully ossified bony element (state 0), a cartilaginous, but mineralized element (state 1) or a completely unmineralized cartilaginous element (state 2).

55. Insertion of rectus cervicus profundus: single (0), or multiple (1) (Wake and Özeti, 1969 [23], modified in Titus and Larson 1995 [34]).

56. Myocommata in rectus cervicus profundus: three (0), one (1), or none (2) (Wake and Özeti, 1969 [24]. In state 0, there are three myocommata between the sternum and insertion, in state 1, there is only one in the same location, and in state two, myocommata are completely absent from the rectus cervicus profundus.

57. Hebosteoypsiloideus: more differentiated (0), or less differentiated (1) (Wake and Özeti, 1969 [25]). The hebosteoypsiloideus is a narrow muscle that originates posteriorly to the second basibranchial. It may be clearly differentiated from the rectus cervicus profundus (where it inserts), to assist in the general retractor system in state 0, or may act merely as part of the rectus cervicus profundus in state 1.

58. Inter-oss-quadrata: muscle fibers fall short of raphe (0), a few fibers extend to the raphe (1), or the muscle is well developed and extends completely to the raphe (2) (Wake and Özeti, 1969 [26], modified by Titus and Larson, 1995 [37]).

59. Tongue: well-developed tongue pad without free posterior flap (0), lack of differentiated tongue pad (1), tongue pad free at posterior margins (2), or tongue pad with a large, free posterior flap (3) (Wake and Özeti, 1969 [27]).

60. Basiradialis: small and weak to well developed (0), or well developed and strong (1) (Wake and Özeti, 1969 [28]).

61. Rectus abdominus profundus: differentiated and separate from rectus abdominus superficialis (0), or the two muscles are not distinct (1) (Wake and Özeti, 1969 [30]; modified in Titus and Larson, 1995 [40]).

62. Genioglossus: superficial fibers extensive, with medial fibers inserting in the vicinity of the tips of the ceratohyals (0), or medial fibers are absent and lateral fibers are well developed (1) (Wake and Özeti, 1969 [31]).

63. Geniohyoideus and genioglossus: unconnected (0), attached by dense beds of tissue at anterior ends of ceratohyals (1), or connection present but genioglossus undifferentiated (2) (Wake and Özeti, 1969 [32], modified by Titus and Larson, 1995 [42]).

64. Rectus cervicus superficialis: inserts primarily in the vicinity of first ceratobranchial-first basibranchial attachment (0), or a well-developed slip extends anteriorly to insert near the tip of the first basibranchial (1) (Wake and Özeti, 1969 [33]).

65. Rectus cervicus profundus: insertion of slips absent from first basibranchial and radii (0), are present on posterior part of first basibranchial (1), or are present on the first basibranchial and radii (2) (Wake and Özeti, 1969 [34]).

66. Depressor mandibulae: exhibits skeletal head and cutaneous head (0), two skeletal heads (1), or a single part (2) (Wake and Özeti, 1969 [36]).

67. Subhyoideus: lacks attachment to the mandibulae (0), attaches to mandible by muscle fibers (1), or attaches to mandible by a tendon (2) (Wake and Özeti, 1969 [37]).

68. Interradialis: muscle is present but poorly developed (0), or present and well developed (1), or absent (2) (Wake and Özeti, 1969 [38]).

69. Dorsal aposematism: absent (0), or present (1) (Duellman and Trueb, 1986). In state 1, bright warning coloration is present as a dorsal stripe down the back. In state 0, there is no special coloration.

70. Ventral aposematism: absent (0), or present (1) (Duellman and Trueb, 1986). In state zero, colors of the belly and ventral side of the head, limbs, and tail are similarly colored to the rest of the body. In state 1, the underside of the salamander exhibits bright warning coloration.

71. Ventral aposematism: yellow to orange in color (0), or red (1).

72. Egg deposition: singly or in a spherical mass of 7-39 eggs (0), or in a flattened mass of 6-16 eggs (1) (Dubois, A and J. Raffaëlli (2009).

73. Shape of rostrum (snout): remains broad throughout (0), or tapers anteriorly (1).

Results

The phylogenetic analysis using only the 41 osteological characters produced 19 most parsimonious trees, with a retention index of 0.685 and a consistency index of 0.754. The strict consensus tree with bootstrap support values for this analysis are illustrated in Fig. 17 A. Bootstrap support for this tree was high (≥50%) for the Pleurodelinae (all taxa in the analysis except outgroup *Salamandra*), Pleurodelini (*Tylototriton* and *Pleurodeles*), and Tarichina (*Notophthalmus* and *Taricha*) but low (<50%) for the Molgini (*Triturus*, *Cynops*, *Euproctus*, *Notophthalmus*, and *Taricha*). The members of the Pleurodelini form a well-supported dichotomy, but there is an unresolved trichotomy within the Molgina (*Triturus, Cynops,* and *Euproctus*) and poorly resolved polytomy for the North American Tarichina.

The second analysis, which used all 73 characters (including soft tissue characters) produced 9 most parsimonious trees (Appendix), with a retention index of 0.693 and a consistency index of 0.795. The full matrix of characters can be viewed in Table 4. The bootstrap support for the strict consensus tree (Fig. 17 B) was high for the Pleurodelinae, the Pleurodelini, and the Molgini. Bootstrap support was low for the separation of the modern European and modern Asian newt clades (*Triturus* and *Cynops*) from the Corsica-Sardinia newt clade (*Euproctus*) within the Molgina, the Tarichina, *Taricha* (all extant species of genus *Taricha*, plus *T. lindoei* and *T. oligocenica*, and without *Notophthalmus*), and a "*Palaeotaricha*" branch within the genus *Taricha* that contained both fossil taxa. In this tree, the Pleurodelini resolve into a dichotomy just as in the first analysis, while there is a trichotomy with *Euproctus,* modern Eurasian newts, and North American newts.

Table 4. Distribution of character states for 12 salamandrid taxa. Dagger symbol (†) indicates fossil taxa.

Character	10	20	30	40	50	60	70	73
Salamandra	0000000000	0000011001	0021?00000	0000001???	?312110100	0012021020	0102123211	???
Pleurodeles	0021121102	0201100020	0020200110	1100001???	?310000000	1002010200	0011133000	???
Tylototriton	0021121102	0201100010	0010200110	1100101???	?010000000	1102100200	0011233011	???
Euproctus	1000021012	2001111010	1100211011	1000001???	?332000110	0000100200	1011333011	???
Triturus	1100011001	2021111020	1100211210	1001001???	?201001011	0002100200	1011332011	???
Cynops	11100211?2	2211101020	1100201210	1001101???	?302000011	0000100200	1011332011	???
Notophthalmus	1021121012	1101111020	1310101210	1000101?2?	?221000000	0001100200	?011333011	???
Taricha granulosa	1010121012	0001101020	1210101210	1000001011	0321000010	0001100200	?011333001	000
Taricha torosa	1010121012	0001101020	1210101210	1000001012	0321000010	0001100200	?011333001	000
Taricha rivularis	1010121012	0001101020	1210101210	1000001012	1321000010	0001100200	?011333001	110
Taricha oligocenica †	1010121012	0001101020	1?1010121?	?010111111	??????????	??0???????	??????????	??0
Taricha lindoei †	1010121012	0001101020	1?1010121?	?010001011	??????????	??0???????	??????????	??1

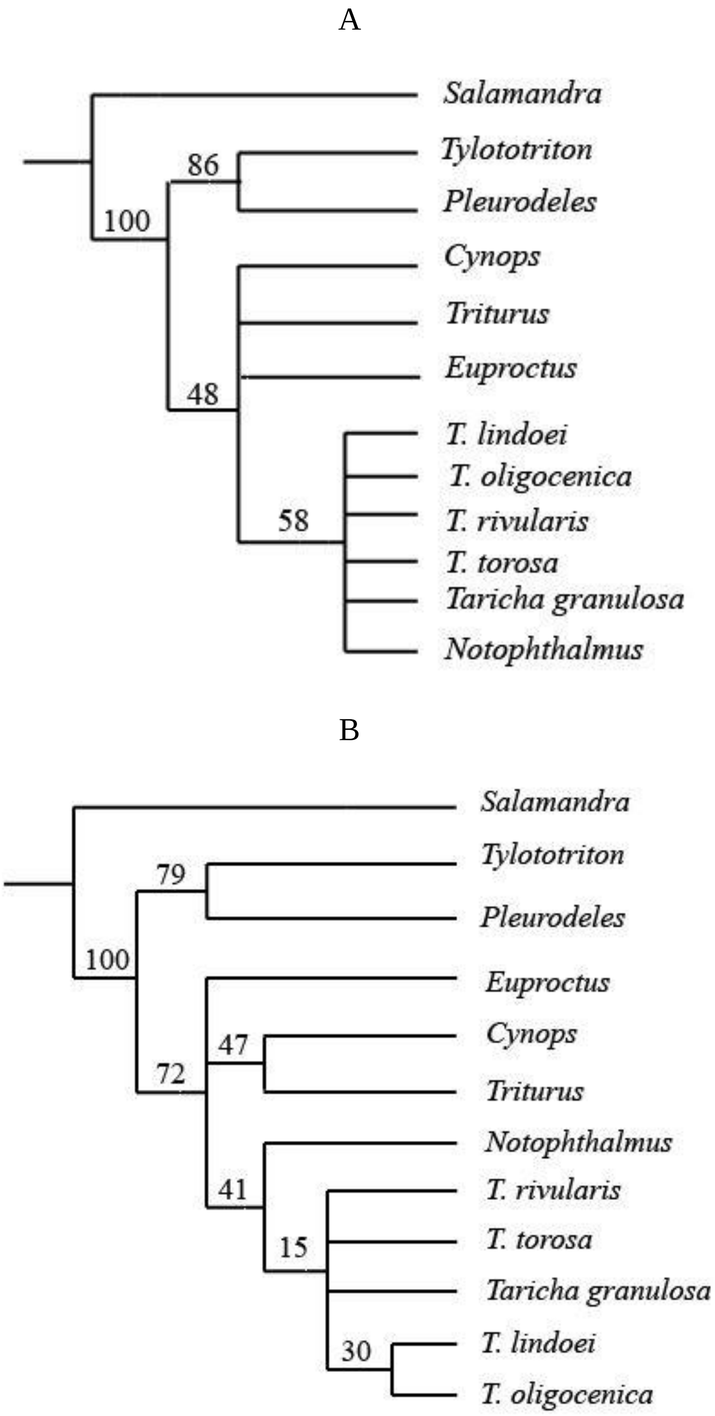


Figure 17. Strict consensus trees for simple parsimony analyses with bootstrap support values. A, the consensus tree for the 41 osteological characters only; B, the strict consensus tree using all 73 morphological characters.

Discussion

The osteological phylogenetic analysis (Fig. 17 A) produces a few important insights: (1) The current state of osteological characters in the Salamandridae can accurately, and with good support, distinguish the Salamandrinae (true salamanders) from the Pleurodelinae (newts) and the Pleurodelini (primitive Asian newts) from the Molgini (modern Eurasian and North American newts), just as in the latest molecular phylogenies (Weisrock et al., 2006, Zhang et al., 2008). (2) The resolution within the Molgina and Tarichina is poor when using only osteological characters, but the Molgina and Tarichina still diverge as in molecular phylogenies like Weisrock et al. (2006) and Zhang et al. (2008). As stated in Schoch and Rasser (2013), future studies need to explore skeletal regions (skull, pelvis, limbs, vertebrae) in greater detail, and with additional salamandrid taxa (both extant and fossil), to determine if there are additional apomorphic and synapomorphic characters. Increasing the data on apomorphies in this group will help determine if there are truly enough osteological characters to accurately understand the relationships of fossil (and even just extant) newts, and then use these relationships to help classify newts at the generic and specific levels (Bell et al., 2009). While this may not be as important in analyses including only extant taxa, because of the availability of molecular data, only osteological characters can be used to describe the relationships of fossil taxa to each other and to living groups. (3) While there appears to be a soft polytomy within the North American salamandrids, both fossil taxa, *T. oligocenica* and *T. lindoei*, are placed within the North American newts in all 19 most parsimonious trees. Given that the North American taxa are distinguished by at least 7 characters, it is probable that the placement of *T. oligocenica* and *T. lindoei* within this clade is correct.

The use of all 73 characters (Fig. 17 B) provides better resolution for the separation of Molgina and Tarichina, with 9 most parsimonious trees resulting from the analysis (Appendix). Within these trees, there are three different arrangements of *Euproctus* relative to *Triturus* and *Cynops*; *Euproctus* may branch off between the Pleurodelini and the *Triturus*/*Cynops* clade, between the *Triturus*/*Cynops* clade and the North American clade, or form a dichotomy with a *Triturus*/*Cynops* clade. Of these three arrangements, it is the third that is best supported by molecular data (Zhang et al., 2008), but the consensus tree in this analysis instead forms a trichotomy between *Euproctus*, the modern European and modern Asian clades, and the North American clade (Fig. 17 B). According to Schoch and Rasser (2013), *Euproctus* is somewhat problematic in its skull morphology, with the parietals and frontosquamosal bar convergent with Notophthalmus, and a modified posterior skull region that may have masked osteological features indicative of a closer relationship to salamandrids like *Triturus* and *Cynops*. Future research on Euproctus should focus on searching for additional, probably postcranial, characters to solve the issues with skull morphology.

In the North America clade (Tarichina), *Notophthalmus* is placed consistently outside of all members of *Taricha* and both fossil taxa when all 73 characters are used (Fig. 17 B; Appendix). While the bootstrap support is low, previously done morphological (Wake and Özeti, 1969; Titus and Larson, 1995) and molecular (Titus and Larson, 1995; Weisrock et al. 2006; Zhang et al., 2008) analyses support this divergence. Within the genus *Taricha*, however, the relationships are unresolved, with five different arrangements of the taxa (Appendix): (1) *T. torosa* and *T. rivularis* are sister taxa and form a sister group with the other taxa, with *T. granulosa* forming a dichotomy with the paired fossil taxa. (2) A stepwise branching off of taxa, starting with *Notophthalmus*, then sequentially *T. torosa*, *T. rivularis*, *T. granulosa*, *T. lindoei*, and T. *oligocenica*. (3) The fossil taxa form a sister group to all extant *Taricha*, with *T. granulosa* forming a dichotomy with *T. torosa* and *T. rivularis*. (4) *T. granulosa* diverges first, followed by the paired fossil taxa, then the paired *T. torosa* and *T. rivularis*. (5) A similar arrangement to the second arrangement, only *T. rivularis* diverges before *T. torosa*. Finally, the strict consensus tree exhibits an unresolved polytomy of *T. torosa*, *T. rivularis*, *T. granulosa*, and the paired *T. oligocenica* and *T. lindoei*.

The only constant of these arrangements and the strict consensus tree is the pairing of fossil taxa *T. oligocenica* and *T. lindoei*; however, even this has poor bootstrap support (30%) and is held up by a single character (long accessory processes on the ribs). There may be a number of reasons behind the poor resolution the species of *Taricha*. First, many of the morphological characters used in this analysis are muscular or reproductive in nature, and therefore do not help place fossil taxa within the tree. Second, there may be a lack of species-level character data for both extant and fossil *Taricha*. Third, the species may be cryptic, with few morphological differences, in which case morphology alone may not effectively discriminate taxa. The differences that do exist between *Notophthalmus* and *Taricha*, and among species of *Taricha*, are limited, and often in the soft tissue. Osteological characters seem to be of limited utility because of a high degree of homoplasy (such as in the presence or absence of an expanded dermal cap on the neural spine of the vertebrae), further enhancing the difficulty of resolving species relationships within *Taricha*.

General clade relationships agree with the latest molecular phylogenies (Weisrock et al., 2006; Zhang et al., 2008) in both analyses, allocating the selected taxa into the following groups: outgroup ("true" salamander *Salamandra*), primitive Asian newts (*Tylototriton*, *Pleurodeles*), modern European (*Triturus*) and modern Asian (*Cynops*) newts, Corsica-Sardinia newts (*Euproctus*), and North American newts (*Taricha*, *Notophthalmus*), although the osteological analysis struggled to resolve the relationships of *Euproctus* and the species within *Taricha*. The relationships of all Old World taxa agree in both trees, and in the North American clade, *Notophthalmus* shares a common ancestor with all of *Taricha*, including *T. oligocenica* and *T. lindoei*.

These analyses clearly support the classification of *T. oligocenica* and *T. lindoei* as members of the North American salamandrid clade. Once all 73 characters are used, the polytomy of *Notophthalmus* and all species of *Taricha* is resolved, and the fossil taxa are nested within the genus *Taricha*. Interestingly, the larger analysis also suggests a deep origin for the genus *Taricha* of at least 33-32 million years (Early Oligocene).

Future studies should include extant taxa *N. perstriatus* and *N. meridionalis*, and fossil taxa such as *T. miocenica*, *N. robustus*, and *N. crassus*, with more characters able to differentiate between *Notophthalmus* and *Taricha* and the species within those genera. These actions may help better resolve the relationships of the North American newts. Currently, this study can only support the classification of *T. lindoei* and *T. oligocenica* as part of the North American clade of newts, nested within a deeply rooted genus *Taricha.*

CHAPTER V

FUNCTIONAL MORPHOLOGY AND CONSERVATION BIOLOGY

Functional Morphology

The overall impression of *Taricha oligocenica* is that of a sturdy or robust, moderate-to-large-sized newt with a mosaic of defensive adaptions present in the Salamandridae. Fig. 18 is an artist's reconstruction of *T. oligocenica*, taking into consideration the morphology unique to *T. oligocenica* and the morphologies of newts with similar characteristics to the fossil taxa. First, the frontosquamosal arch, which consists of an anteromedial projection from the squamosal and a posterolateral projection from the frontal, 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; this structure also increases the difficulty of swallowing for predators similar to *Thamnophis*, which attempt to swallow their prey headfirst (Brodie, 1968a; Naylor, 1978a; Brodie, 1983; Duellman and Trueb, 1986), or predators such as *Rana* and some fishes, which attempt to swallow their prey whole (Brodie, 1968a; Naylor 1978a). Though not all salamandrids possess a complete, bony arch (some are partially or completely cartilaginous, reduced, or absent) 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 such as bullfrogs and snakes (Naylor, 1978a). Additionally, the

Figure 18. Artist's reconstruction of *Taricha oligocenica*. Reconstruction based on morphological characteristics of the fossil taxa as well as the morphologies of extant salamandrids with similar characters. Artwork by Elizabeth White (University of Oregon), scientific consultation provided by John J. Jacisin III (University of Oregon).

paired arches can form a protective shelf over the eyes of newts, as seen when swallowing or taking a defensive posture (Brodie, 1977). As mentioned above, the skull and frontosquamosal arches of *T. oligocenica* are more extensively pitted than seen in living members of *Taricha*, but less than in *Echinotriton* or *Tylototriton*.

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 the dermal caps on the vertebral neurals crests (examples include *Notophthalmus*, *Cynops*, and *Tylototriton*; Brodie, 1983; Duellman and Trueb, 1986)), though not all newts with bony arches possess these vertebral plates, such as extant *Taricha* (Naylor, 1978a; Naylor, 1978b; Brodie, 1983). These plates have been recognized as defensive in nature (Naylor, 1978a; Brodie, 1983; Duellman and Trueb, 1986), as they have no muscle attachments and form interlocking series along the usually vulnerable spine of these salamanders. The amount of protection provided by these plates likely differs by how extensively they cover the spine (Van Frank, 1955). *Taricha oligocenica* stands out in that its dermal plates are as extensive as extant *Tylototriton*, perhaps even more so, as the caps of *Tylototriton* decrease in width anteriorly (Van Frank, 1955, Estes, 1981).

The elongate accessory rib processes of *T. oligocenica* and *T. lindoei* are hereproposed to provide defensive and respiratory roles analogous to the uncinate processes of early tetrapods like *Eryops* (Codd et al., 2008), birds (Tickle et al., 2007), and some reptiles (Codd et al., 2008). These processes can provide enhanced protection of the trunk region, as they extend caudally towards each successive rib and provide attachment locations for trunk musculature, effectively strengthening the rib cage and improving respiration (Tickle et al., 2007 Codd et al. 2008). It is also notable that the uncinate processes in birds increase in length as the birds become more specialized toward an aquatic lifestyle, namely, diving birds have longer processes than walking birds, and non-specialist birds show intermediate lengths (Tickle et al., 2007). Given the appearance of similar structures in a variety of organisms, this thesis suggests that the appearance of these homoplastic structures in *T. oligocenica* are further proof of a semi-aquatic lifestyle. Additionally, the utilization of ribs defensively is not unheard of in salamandrids, as *Echinotriton andersoni* and *Pleurodeles waltl* both have free rib tips that pierce the skin to stab and poison potential predators (Nussbaum and Brodie, 1982; Duellman and Trueb, 1986; Heiss, 2010). As the tips of the rib processes appear to be blunt, they are unlikely to have been skin-piercing (Heiss, 2010), but the increased muscle attachment and overall robustness of the structures could have provided extra resistance against crushing forces when attacked. Unfortunately, testing this hypothesis, along with the function of a longer scapular portion of the scapulocoracoid in a newt, would involve a significant biomechanical study, which is beyond the scope of this thesis.

The skin of all newts is highly toxic and sometimes fatal to potential predators; it is especially potent in the genus *Taricha* (Wakely et al., 1966; Brodie, 1968a; Brodie, 1968b; Brodie et al., 1974; Hanifin, et al., 2004). Given that *T. oligocenica* and *T. lindoei* are phylogenetically bracketed with other toxic newt species, as shown in Chapter IV, it is probable that the fossil species were also highly toxic, though 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 (*Rana catesbeiana*) voluntarily ate an individual of *T. granulosa* (Brodie, 1968a). The defensive advantages of a robust, hardy body, combined with toxic skin secretions, were perfectly embodied 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; Naylor, 1979, Brodie, 1983).

Fossil Newts and Conservation Biology

The fossil record of North American salamandrids does not currently permit a detailed investigation of their evolution through time. The presence of *Taricha oligocenica* can, however, be used comparatively with extant *Taricha* to examine what changes likely took place. This can be used to postulate why these changes took place, then predict what further changes may occur in the face of climate change.

Given the fossil flora found with *T. lindoei* and *T. oligocenica* in the Big Basin Member of the John Day Formation (Meyer and Manchester, 1997) and the Mehama Formation, respectively (Retallack et al., 2004), and the preference of extant *Taricha* for similar redwood forests and oak woodland forests with abundant precipitation (Duellman, 1999; Jones et al., 2005; Lannoo et al., 2005), it appears that the genus *Taricha* has preferred hardwood-dominated or redwood forests for at least 32 million years. This, along with the aquatic requirements of newts (Duellman and Trueb, 1986; Jones et al., 2005), sets a precedent for habitat preference in the future. As the threats of climate change, human activity, and infection continue to push amphibians into global decline (Lannoo et al., 2005; Pyron and Wiens, 2011; Denoël), the genus *Taricha* will be forced to either adapt, track habitat, or face extinction. The fossil record of North American newts seems to suggest an attempt to track habitat, rather than adapt to a new one; *T. lindoei* (eastern Oregon), *T. miocenica* (Montana), and *N. crassus* (South Dakota) disappeared from the areas they occurred in once their preferred forest habitats vanished in that area. While species like *T. granulosa* have a wide distribution along the Pacific Coast and have shown an ability to also live in Douglas-fir forests (Duellman, 1999; Jones et al., 2005), species like *T. rivularis* are endemic and relatively isolated, as are all *Notophthalmus* species outside of *N. viridescens* (Duellman, 1999; Lannoo et al., 2005). A map of the current distributions for all North American newts in the United States of America can be viewed in Fig. 19. These endemic species are at greater risk of disappearing in the future should their habitat change than species with wide distributions (Duellman, 1999; Lannoo et al., 2005). The ability of newts like *Taricha* and *Notophthalmus* to track preferred habitat or adapt to climate change will surely affect individual populations of all species in the future, and may play a deciding role in the fate of North American newts, especially those with limited geographic distributions.

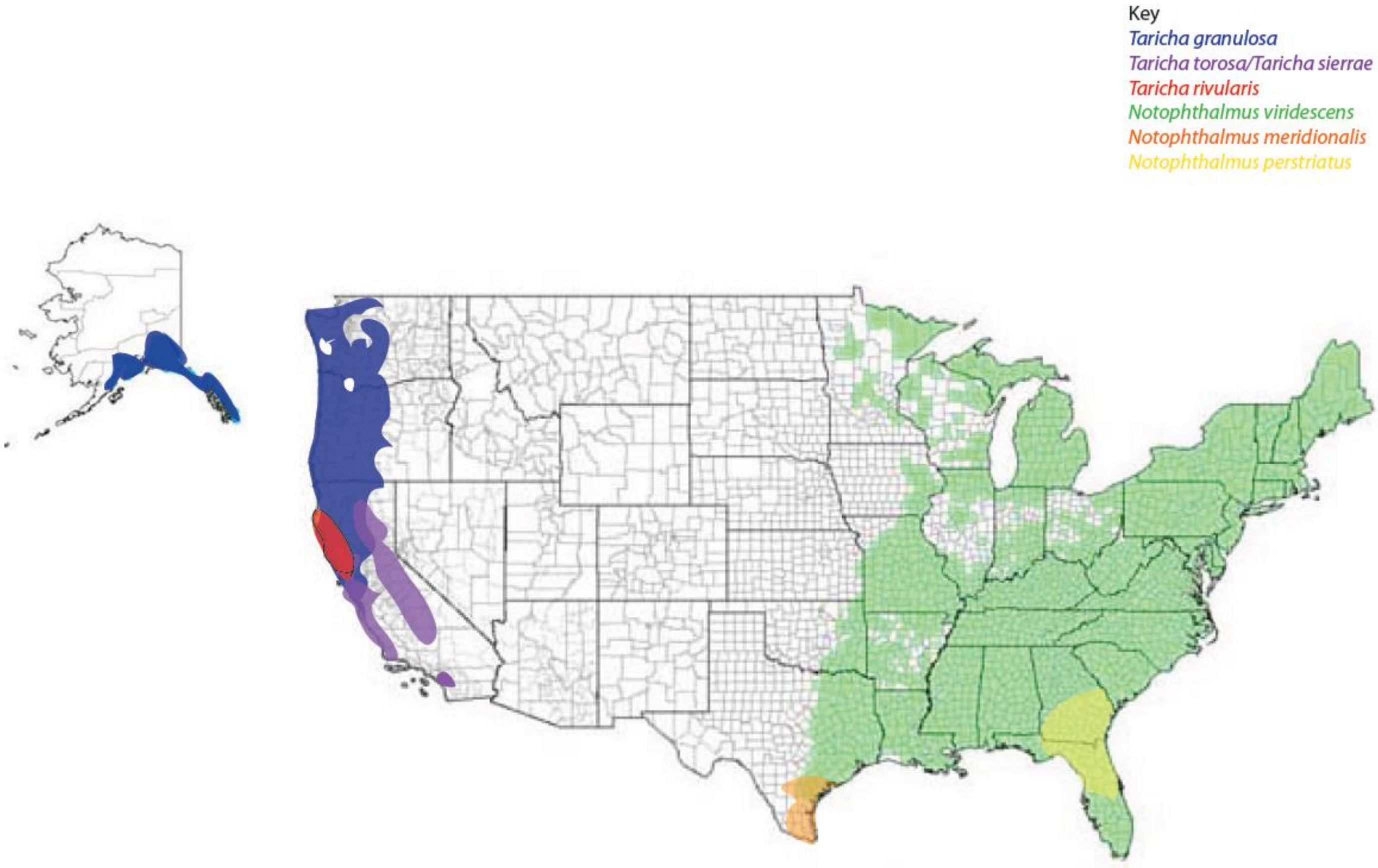


Figure 19. Map of current salamandrid distributions within the United States of America. Base layer modified from Duellman and Trueb, 1986. Note the small distributions of *T. rivularis* (red), *N. meridionalis* (orange), and *N. perstriatus* (yellow).

CHAPTER VI

CONCLUSIONS

Simple Parsimony Analyses

The two simple parsimony analyses of salamandrids provided mixed results when compared to the recent molecular phylogenies of Weisrock et al. (2006) and Zhang et al. (2008), yet consistently nested *Taricha oligocenica* and *Taricha lindoei* within the North American clade of newts. The analysis using all 73 characters, including soft tissue characters, provided better resolution for North American newts than using only the 41 osteological characters. The larger analysis consistently placed the fossil taxa within the *Taricha* lineage, and paired *T. oligocenica* and *T. lindoei* as closely related taxa. Unfortunately, the morphological characters in this analysis were unable to further resolve the positions of the fossil taxa relative to extant species of the genus, so their classification within the genus is uncertain. The phylogenetic analyses in this study do not necessarily support a direct ancestral relationship between the fossil taxa and the extant taxa, as previously assumed in Tihen (1974) and Naylor (1979), but do suggest that *Taricha* as a genus has a deeply rooted origin into at least the Early Oligocene. 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.

Detailed morphological study of the specimens supports their classification as separate species. As in the phylogenetic analysis, this conclusion suggests that the genus *Taricha* has deep roots in the Oligocene, where ancestors to living species may have diverged 33-32 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.

Fossil Collection, Preparatory Work, and Micro CT

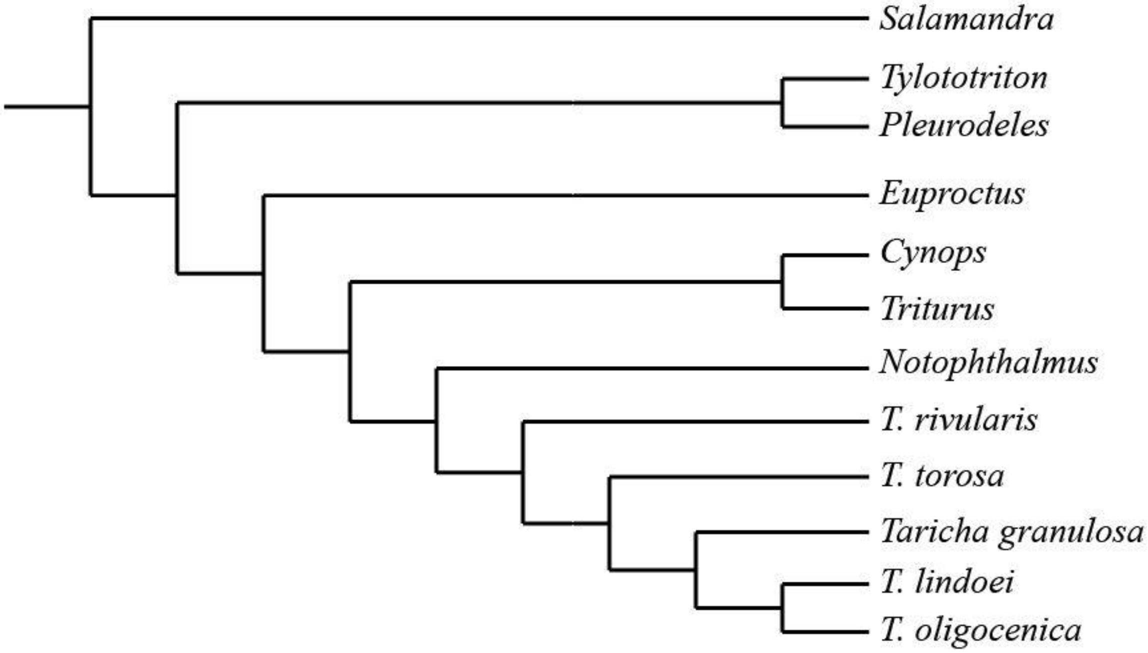
As this study shows, additional collection in fossiliferous areas of the Mehama Formation and the Big Basin Member of the John Day Formation is key to gaining further knowledge on the fascinating evolution and paleoecology of North American salamandrids. Some of the fossils used in this study can be further prepared through removal of extraneous rock, allowing a few of the larger and better preserved specimens to be scanned using Micro CT, then made into detailed three-dimensional models for improved morphological study and comparison.

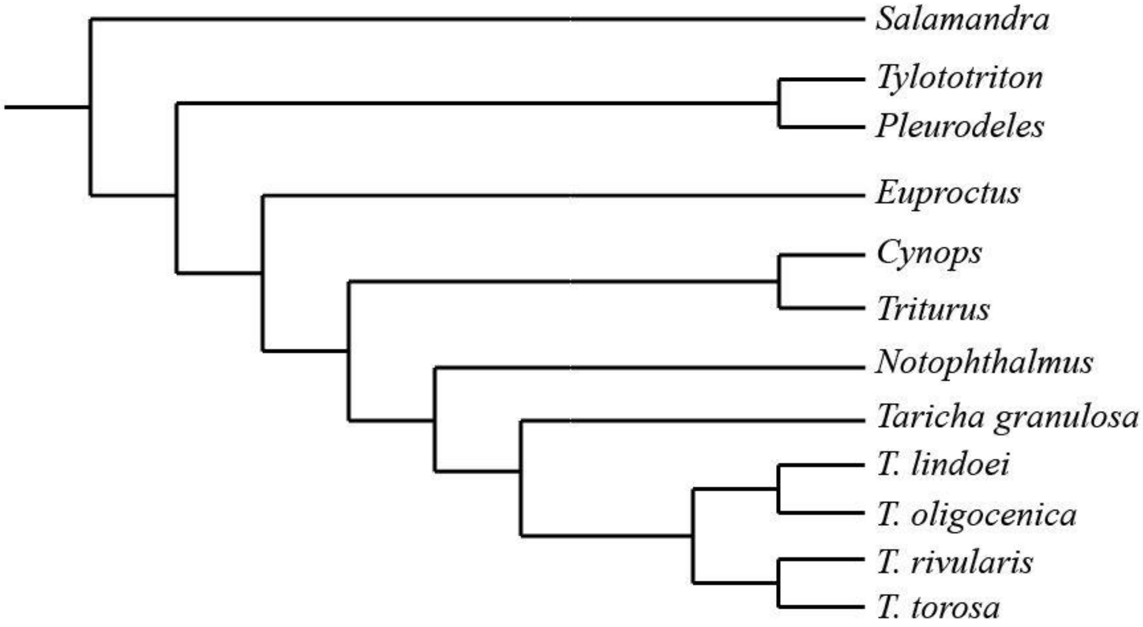
Future Research and *Taricha miocenica*

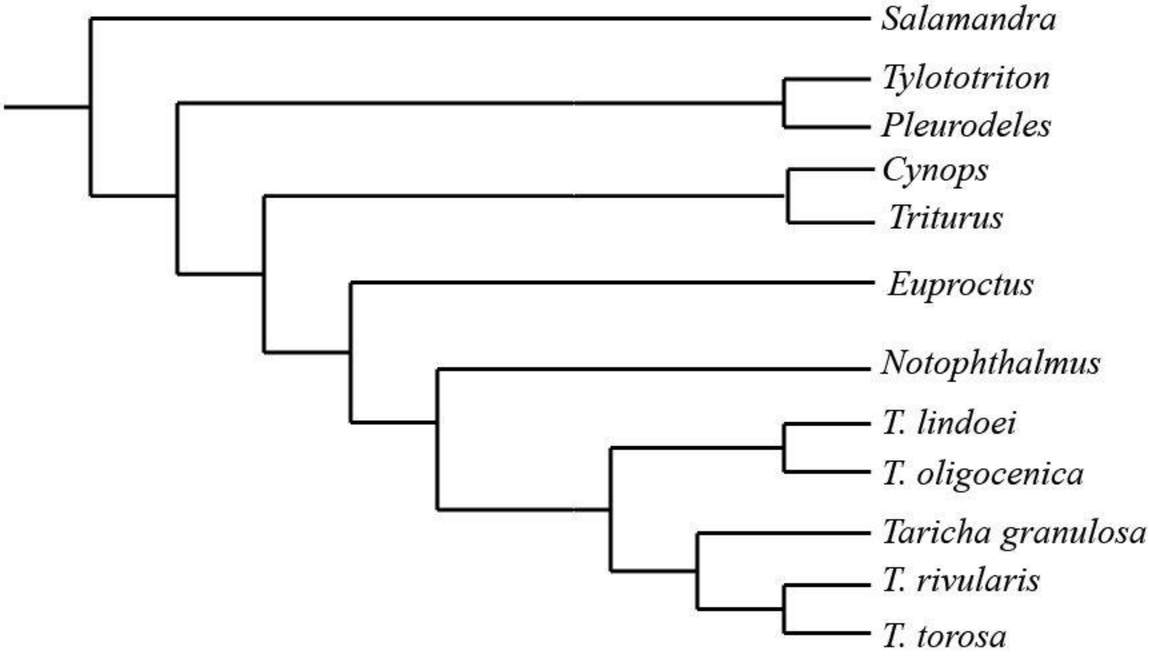
Future research should also include any additional specimens of fossil *Taricha* from the Oligocene not covered in this study. Because no specimens of *Taricha miocenica* were viewed outside of published literature (Tihen, 1974; Estes, 1981; Holman, 2006) in this study, it is of particular importance to examine and compare these fossils in greater detail with the fossils of *Taricha* and perhaps *Notophthalmus*, along with skeletons of extant members of these genera, to determine what exactly their evolutionary relationships with modern North American salamandrids. The difficulty of such determinations is enhanced by the fact that *T. miocenica* (and all fossils of *Notophthalmus*) are only preserved as isolated bones, usually vertebrae, as opposed to the partial to near complete skeletons studied in this thesis (Tihen, 1974; Estes, 1981). Despite the complications, only by performing such studies can we hope to draw concrete conclusions on the phylogenetic positions of *T. oligocenica* and *T. miocenica* relative to each other and to North American salamandrids both past and present.

APPENDIX

THE 9 MOST PARSIMONIOUS TREES FROM THE 73 CHARACTER SIMPLE PARSIMONY ANALYSIS



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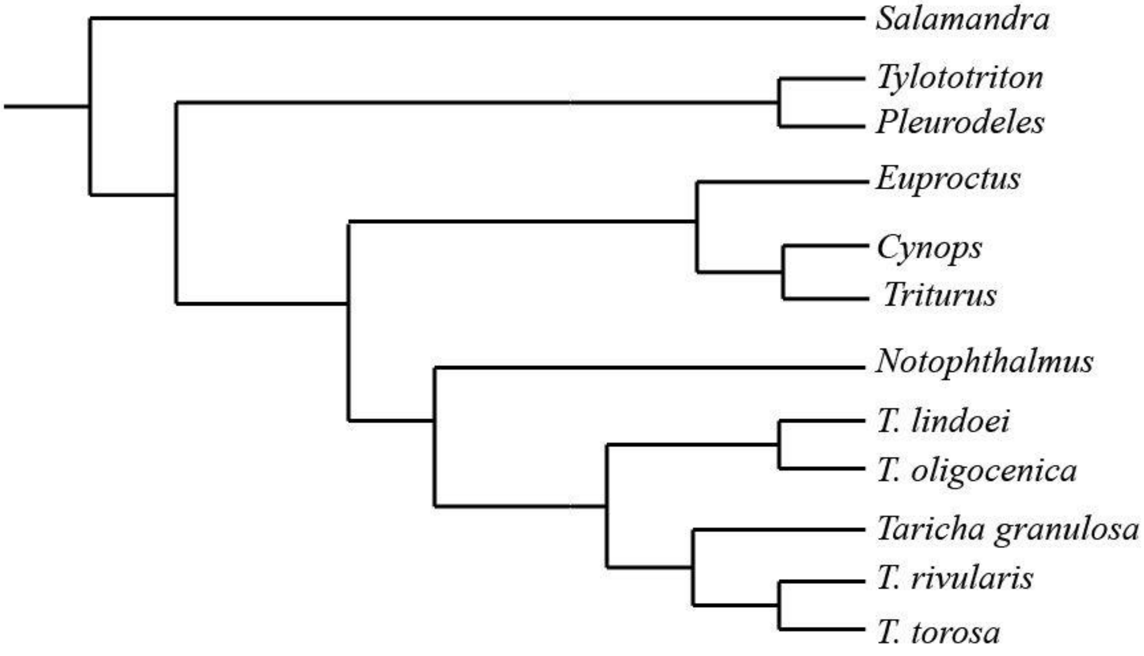
T. rivularis
T. torosa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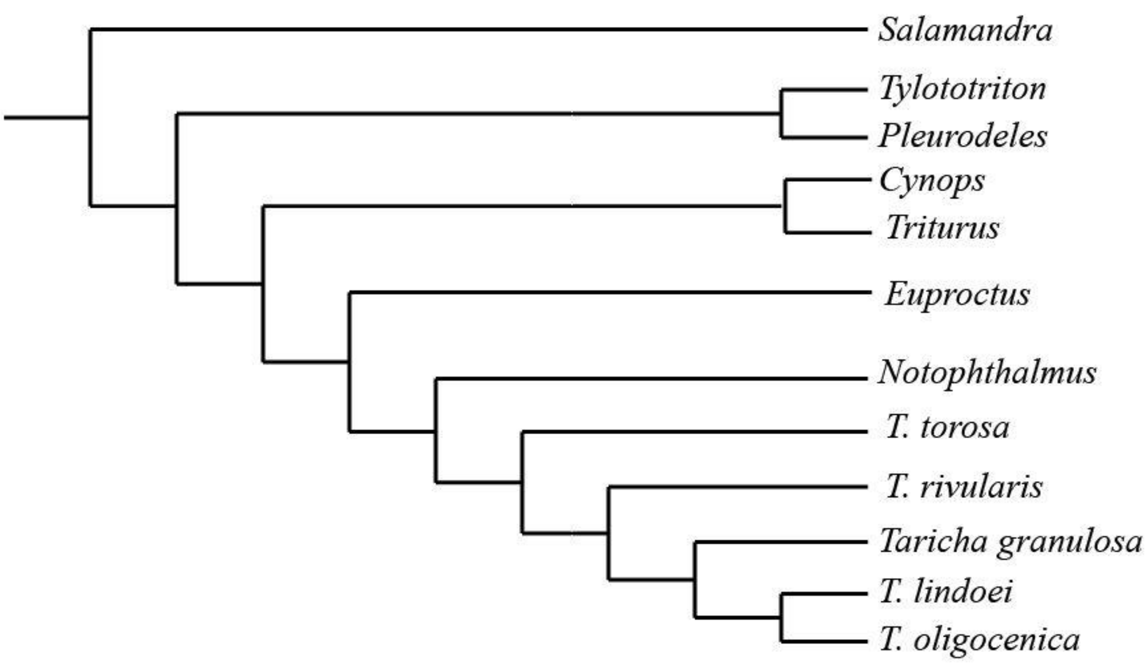
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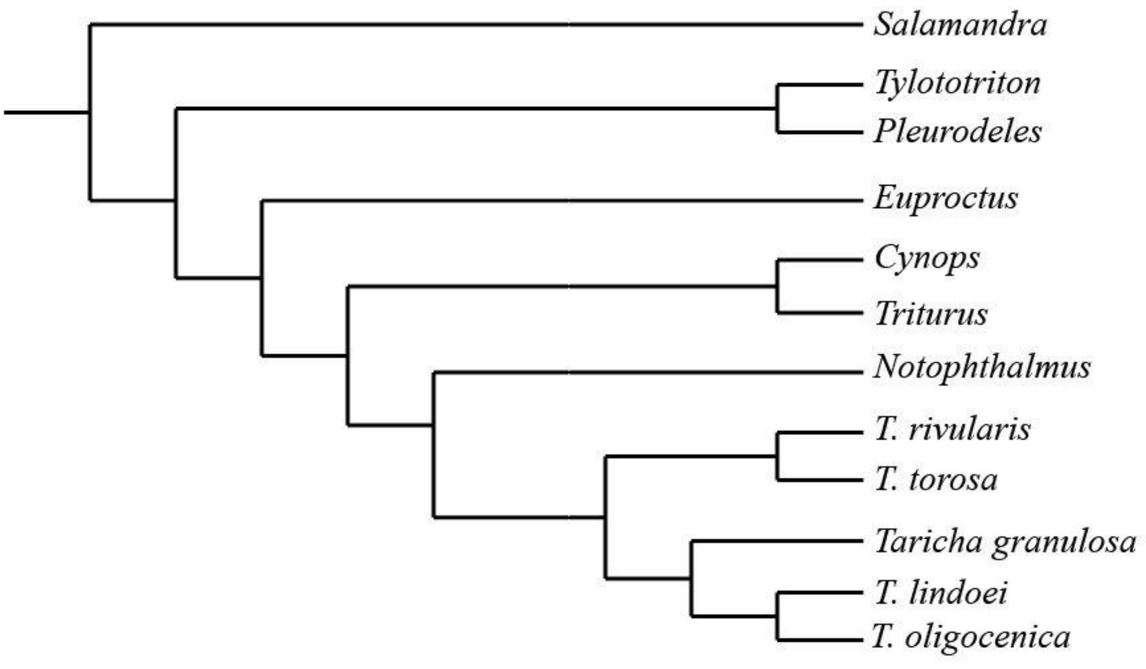
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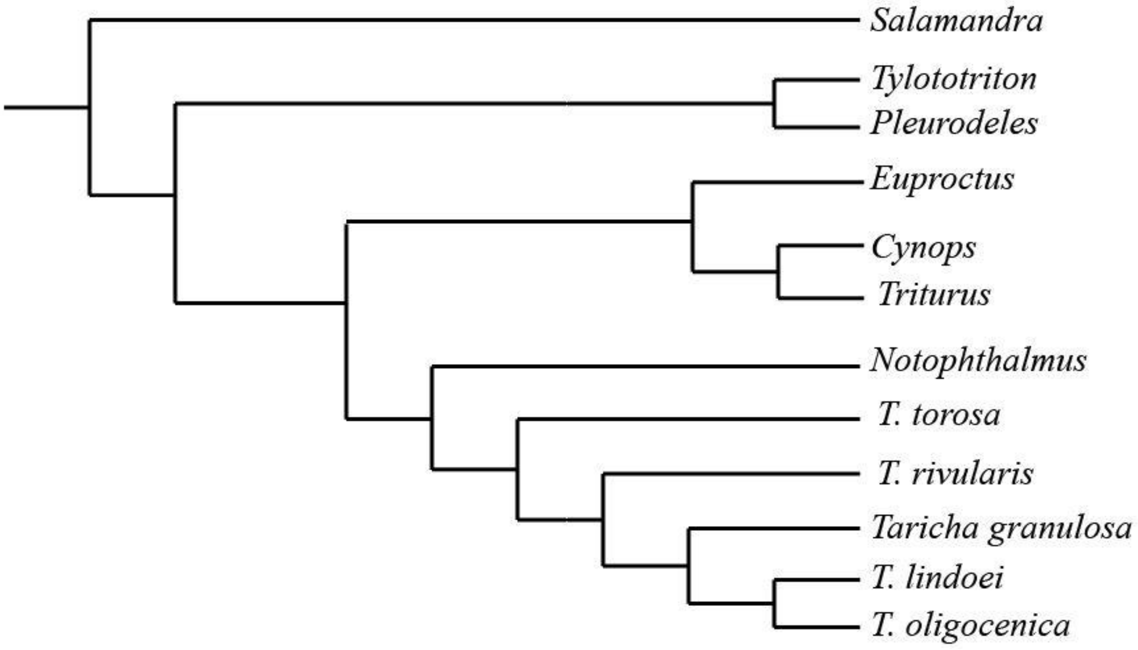
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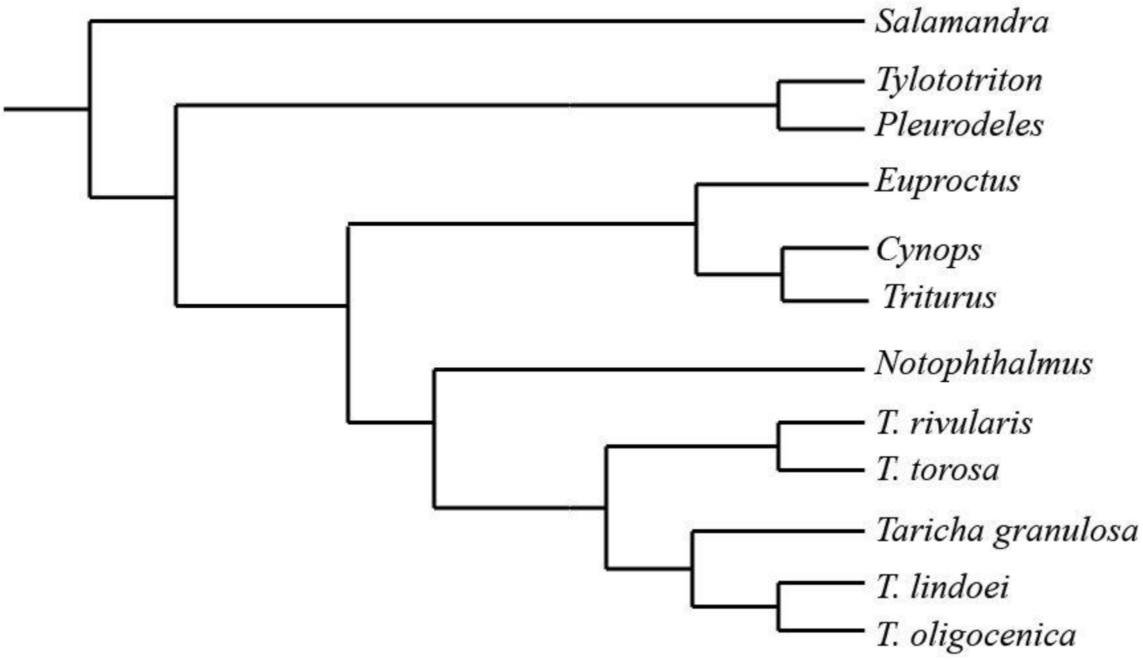
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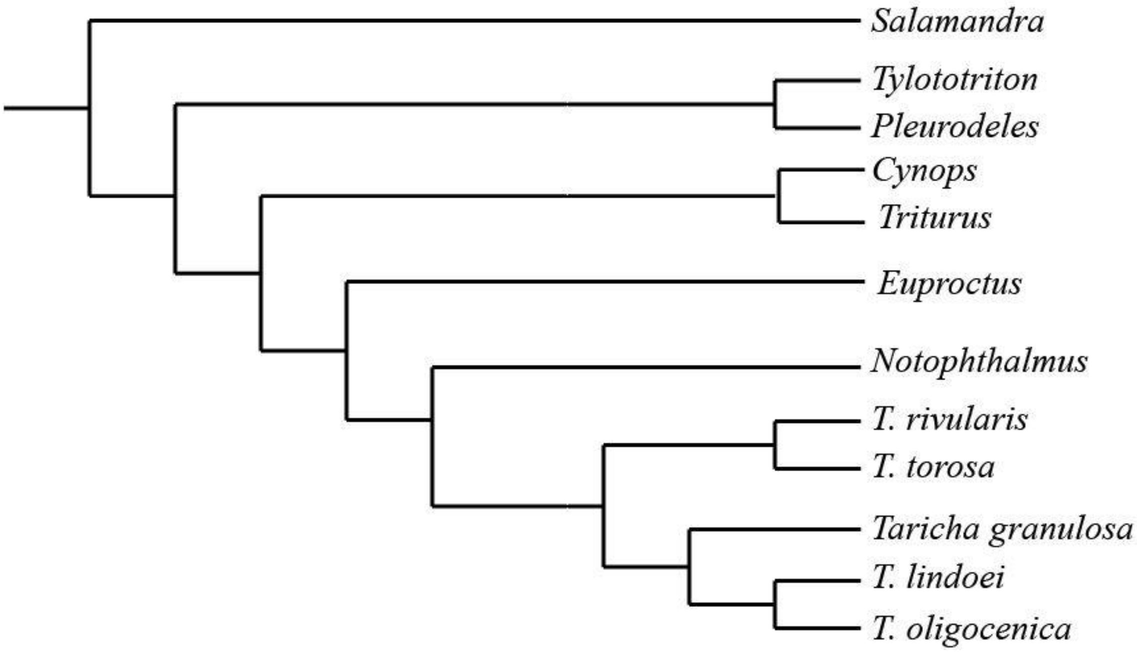
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T. oligocenica

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