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# Taxonomic status of the enigmatic salamander *Cryptotriton adelos* (Amphibia: Plethodontidae) from northern Oaxaca, Mexico, with observations on its skull and postcranial skeleton

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Papenfuss and Wake (1987) described a new species of plethodontid salamander from northern Oaxaca, Mexico, which they named *Nototriton adelos*. The species was assigned to *Nototriton* primarily on the basis of its similarity to members of that widespread genus, which as then constituted ranged from Oaxaca, Mexico, to east-central Costa Rica. At that time, *Nototriton* had no unique synapomorphies but rather included diminutive species that could be excluded from membership in all other genera. Wake and Elias (1983), who erected *Nototriton*, acknowledged that the genus might eventually be shown to be paraphyletic, but they were unable to further resolve the phylogeny with information then available. The original description of *N. adelos* was based on the holotype and three paratypes; in the subsequent 25 years, despite many futile attempts, only one additional specimen of this species has been discovered: UTAVC A-3956, the largest known specimen, a female, 25.6 mm snout-vent length, from near the type locality.

From the start, assignment of the species to *Nototriton* was problematic on zoogeographic grounds: it was the only member of its genus from west of the Isthmus of Tehuantepec in southeastern Mexico. Later, when DNA sequence data demonstrated conclusively the paraphyly of *Nototriton*, *N. adelos* was transferred to the newly erected genus *Cryptotriton* (García-París & Wake 2000), but in the absence of sequence data for this species. Once again, however, *C. adelos* was the only member of its genus from west of the Isthmus of Tehuantepec.

Hanken's (1983) study of allozymic variation in the endemic Mexican plethodontid genus *Thorius* included a single specimen of *Cryptotriton adelos*, but Papenfuss and Wake (1987) subsequently argued that this specimen, and the species to which it belongs, was not a member of *Thorius*. *Cryptotriton adelos* lacks the unique subocular groove (orbitolabial groove; Taylor 1944), which intercepts the upper lip and gives a characteristic and distinctive lateral profile to the head in all known species of *Thorius* (Taylor 1940, Plate XLVII; Gehlbach 1959, Fig. 1).

All efforts to collect more specimens of *C. adelos* have been fruitless, thereby precluding additional molecular analyses that might help resolve the species' generic assignment. We therefore decided to examine the osteology of the species by using high-resolution X-ray computed tomography (CT) in an attempt to discover skeletal features that might be phylogenetically informative. Digital scans of a single adult specimen (MVZ 208582, a male, 23.8 mm snout-vent length; www.digimorph.org/specimens/Thorius_adelos) reveal a combination of characters, which while unusual for *Thorius* in some respects includes features that otherwise are unique to that genus. Furthermore, the osteology of *C. adelos* excludes it from membership in any other clade of tropical plethodontids. Accordingly, we reassign the species as follows:

***Thorius adelos* (Papenfuss & Wake 1987)**

*Nototriton adelos* Papenfuss & Wake 1987, p. 7
*Cryptotriton adelos* (Papenfuss & Wake 1987), García-París & Wake 2000, p. 58

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## Osteology

The skull of *T. adelos* is substantially more robust and more extensively ossified than all other known *Thorius* (Fig. 1A–C). Nevertheless, as is typical for *Thorius* but unlike other bolitoglossines (Wake & Elias 1983), *T. adelos* has a prominent dorsal fontanelle between the parietal bones and to a lesser extent between the frontals (cf. Hanken 1984, Fig. 1; Wake 1991, Fig. 9). The fontanelle is larger in most other *Thorius*, although it is relatively small in *T. aureus*, which has the most robust skull among the remaining species (Hanken & Wake 1994). The skull of *T. adelos* is relatively shorter and more compact than those of other *Thorius*, such as *T. narisovalis*, a substantially larger species from Cerro San Felipe, Oaxaca (cf. Figs. 1C and D; www.digimorph.org/specimens/Thorius_narisovalis). Using radiographs, Papenfuss and Wake (1987) were unable to identify in *T. adelos* a posteriorly directed columnar process or "spur" on the posterior margin of the squamosal bone, a process present in only two plethodontid genera, *Thorius* and *Oedipina* (Wake 1966). This spur is the origin of a ligament that inserts on the posterior end of the ceratohyal, but the functional basis for a spur rather than a simpler origin of the ligament from the squamosal is not understood. *Thorius adelos* clearly has such a process, although it is less distinct and less columnar than the one in *T. narisovalis* (cf. Figs. 1C and D). Individual CT slices of *T. adelos* reveal that this process is cylindrical, as in other *Thorius*. One minute septomaxillary bone is present, on the right side (Fig. 1B, C). This typically paired bone is absent in *Nototriton* and *Cryptotriton* (Wake & Elias 1983) but variably present in several species of *Thorius* (e.g., Hanken 1984). Nasal bones are large and well developed compared to other *Thorius*, as are the relatively stout maxillary and dentary bones. This specimen has more maxillary teeth (26) and they are larger than maxillary teeth in any other *Thorius*. Paired frontal processes of the unpaired premaxillary bone are fused at their base and postorbital vomerine processes are lacking; these character states were used previously to assign the species to *Nototriton* (Papenfuss & Wake 1987), but they apply equally to *Thorius.* Unlike all other *Cryptotriton*, the nasal bone in *T. adelos* is not pierced by the nasolacrimal duct, which had been inferred incorrectly from earlier radiographic data (Papenfuss & Wake 1987).

Ossification of certain skeletal elements that remain cartilaginous in nearly all other tropical salamanders, such as the ends of long bones, vertebral condyles and mesopodial cartilages, is characteristic of adult *Thorius* (Hanken 1982). The specimen of *T. adelos* has ossified condyles on both the humerus and the anterior ends of the centra of the trunk vertebrae (Fig. 1A, C). Intervertebral cartilage is ossified in such a way that the centrum is opisthoceolous with a stout anterior condyle (Wake 1970), but the condyle is less evident and less well developed than is typical for most species of *Thorius* (cf. Figs. 1C and D). In contrast to many other *Thorius*, however, cartilaginous ends of the more distal long bones remain unmineralized, as do mesopodial elements (Fig. 1A).

## Discussion

These osteological features, in combination with earlier allozyme data (Hanken 1983), support the inclusion of *T. adelos* within *Thorius* but not within either *Nototriton* or *Cryptotrition*. This taxonomic reassignment resolves one of the most puzzling zoogeographic patterns in tropical salamanders. All other species of *Cryptotriton*, *Nototriton* and *Dendrotriton* (all of which are small to miniaturized salamanders that may resemble *Thorius* superficially) are restricted to mid-elevation cloud forests in Central America to the east and south of the Isthmus of Tehuantepec. The presence of a single species west of the Isthmus requires either a much larger ancestral distribution of *Cryptotriton* or *Nototriton* or a dispersal event from Central America, across the Isthmus, to northern Oaxaca. Yet, neither scenario appears likely given the small size (and likely low dispersal capabilities) of these salamanders and their restriction to cloud forest habitats. By contrast, *Thorius* is most speciose in Oaxaca, and particularly in the Sierra de Juárez where *T. adelos* is found.

This reassignment brings to 24 the total number of species of *Thorius* currently recognized (AmphibiaWeb 2012). Locally, *T. adelos* is part of a multispecies assemblage of plethodontid salamanders that are distributed along an elevational transect that extends from the peak of Cerro Pelón (3000 m) to the village of Valle Nacional (ca. 500 m), about 30 km to the northeast (Wake *et al.* 1992). Eighteen species are found along this transect, including seven *Thorius*; an eighth species of *Thorius* is found elsewhere in the Sierra de Juárez (Hanken & Wake 2001). Syntopic with *T. adelos* are *T. insperatus* and possibly *T. smithi*, the latter extending to elevations as low as 800 m.

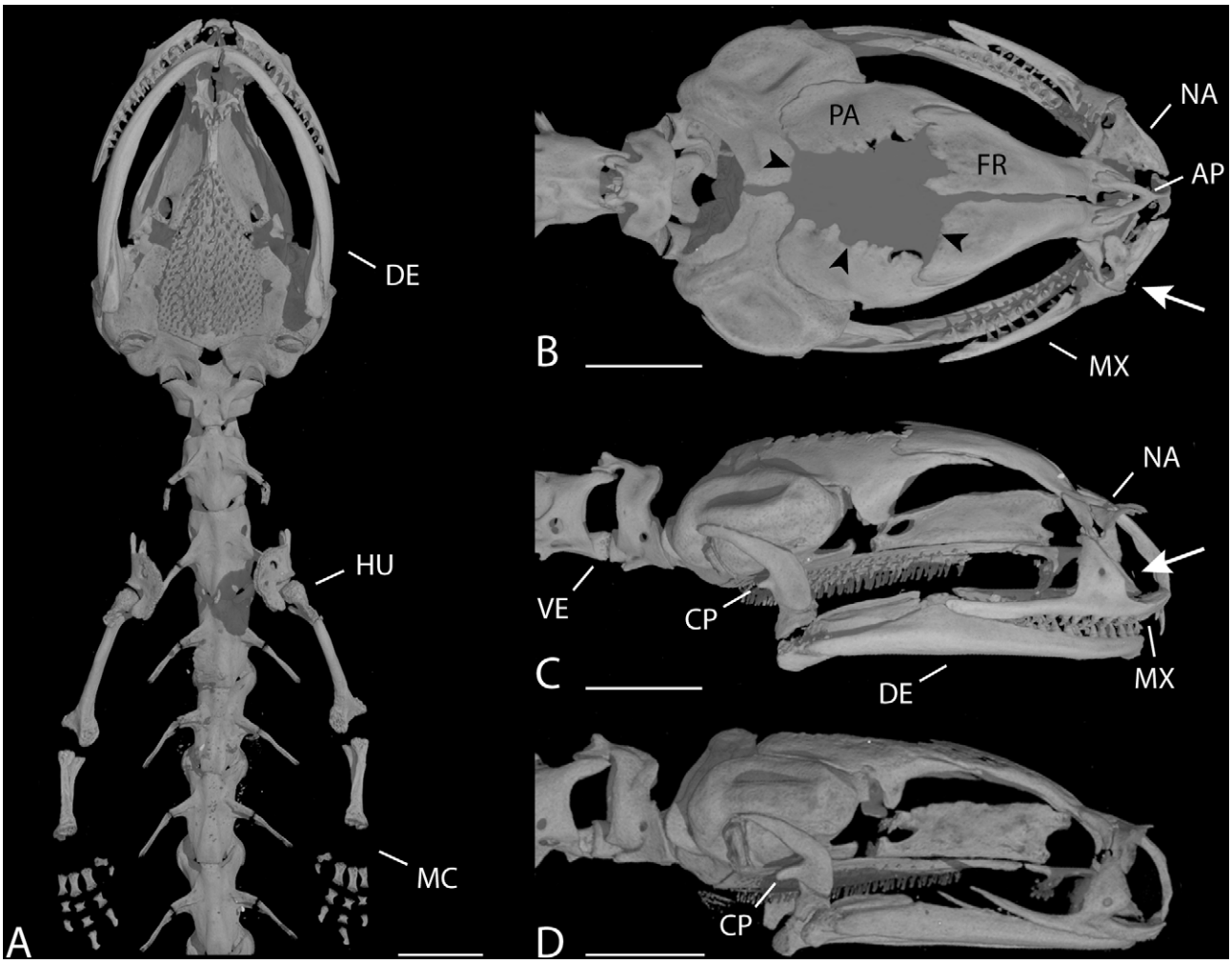


**FIGURE 1.** A–C: Three-dimensional reconstructions of X-ray CT scans of the anterior skeleton and skull of MVZ 208582, an adult male *Thorius adelos*, seen in ventral, dorsal and lateral views, respectively (www.digimorph.org/specimens/Thorius_adelos). D: Three-dimensional reconstruction of X-ray CT scan of the skull of MVZ 162257, an adult female *T. narisovalis*; lateral view (www.digimorph.org/specimens/Thorius_narisovalis). Maxillary teeth are present in *T. adelos* but absent in *T. narisovalis*. Abbreviations: AP, ascending processes of the premaxilla; CP, columnar process on the squamosal; DE, dentary; FR, frontal; HU, ossified condyle on the humerus; MC, unmineralized mesopodial (carpal) cartilages; MX, maxilla; NA, nasal; PA, parietal; VE, anterior condyle on second trunk vertebra. Arrow: septomaxilla (right side only); arrowheads: dorsal fontanelle. Scale bar, 1 mm.

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