

A NEW SALAMANDRID FROM THE MIOCENE RANDECK MAAR, GERMANY

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ABSTRACT—A new species of salamandrid is named and described from the Miocene of Randeck Maar, a long-term volcanic lake deposit in southern Germany. Based on a fully articulated specimen, *Ichthyosaura randeckensis* is named and described as a 3–4 cm long newt with a robust posterolateral process of the frontal, a heavily ornamented skull roof, and a premaxilla with spike-like, parallel alary processes framing a slender fontanelle posteriorly. In a phylogenetic analysis of 14 salamandrid taxa and 38 morphological characters, *I. randeckensis* is found to nest with *I. alpestris*, with which it shares apomorphic character states in the morphology of premaxilla and nasal. The present analysis employed more morphological characters than hitherto considered, highlighting the need to conduct more osteological studies of extant salamanders. Its results are largely consistent with recent molecular phylogenetic studies: *Tylotriton* and *Pleurodeles* form a clade, with *Notophthalmus* and *Euproctus* falling within unresolved trichotomies, followed by *Cynops* and *Ommatotriton* as successive crownward clades, then *Triturus* sensu stricto (*T. marmoratus* and *T. cristatus*), and finally *Lissotriton* and *Ichthyosaura* as terminal sister taxa.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The Salamandridae, which constitutes the second-most diverse clade of extant salamanders, has an evolutionary history that dates back into the Late Cretaceous (Zhang et al., 2008). The 89 living species and 22 genera fall into three subclades: (1) the spectacled salamander *Salamandrina* (Salamandrininae: two species), (2) the 16 species of ‘true salamanders’ (Salamandrinae: *Salamandra*, *Chioglossa*, *Lyciasalamandra*, *Mertensiella*), and (3) the more aquatic ‘newts’ (Pleurodelinae: 17 genera, 71 species). Most salamandrids are characterized by keratinized skin, a frontosquamosal bar, and fused premaxillary bones. Evolutionary biologists find them fascinating because of their diverse life histories (Reilly, 1987), courtship behavior (Houck and Arnold, 2003), and feeding morphology (Wake and Özeti, 1969). Milner (1983) and Zhang et al. (2008) reported paleontological and molecular evidence for a European origin of this Northern Hemisphere taxon. The evolutionary history of salamandrids is documented by numerous fossils, including both articulated and microvertebrate material (Meyer, 1860; Roček, 1994; Böhme, 1998, 2003; Venczel, 2008; Roček and Wuttke, 2010). Among these, articulated material from volcanic crater lake deposits are significant in terms of preservation quality and anatomical information, such as those from the Eocene Messel lake, the Oligocene Enspel locality, and the Miocene Randeck Maar deposit in southwestern Germany (Herre, 1941; Westphal, 1963, 1977, 1980; Roček and Wuttke, 2010).

Here, we report a new salamandrid taxon, based on articulated material that was discovered by new excavations within the Randeck Maar deposit. The complete articulation and excellent preservation render the new finds a potential keystone taxon for the analysis of salamandrid intrarelationships. The objective is (1) to describe the new form in comparison with its closest extant relatives, (2) conduct a phylogenetic analysis of salamandrids with

the focus on the relationships of the new taxon, and (3) elucidate the autecological features of this newt.

MATERIALS AND METHODS

The material is housed in the Staatliches Museum für Naturkunde Stuttgart (SMNS), which includes the following specimens: SMNS 95461 (the holotype specimen of new taxon described herein), and four fragmentary or larval newt specimens that cannot be safely referred to any pleurodeline genus at present (SMNS 58653, 87000, 95462, 95959).

The following taxa were studied first hand for comparison: *Palaeopleurodeles hauffi* (SMNS 50168), *Chelotriton robustus* (SMNS 80210), *Cynops pyrrhogaster* (SMNS-O 7696), *Ichthyosaura alpestris* (SMNS-O 10992-11018), *Lissotriton vulgaris* (SMNS-O 10492, 11019), *L. helveticus* (SMNS-O 11020, 54532), *Palaeopleurodeles hauffi* (SMNS 50168), *Pleurodeles waltl* (SMNS-O 2268), *Salamandra salamandra* (SMNS-O 10518), and *Triturus marmoratus* (SMNS-O 75452).

Anatomical Abbreviations—**a-p**, alary process of premaxilla; **d**, dentary; **eo-op**, exoccipital and opisthotic; **f**, frontal; **f-p**, frontal process; **m**, maxilla; **n**, nasal; **p**, parietal; **pm**, premaxilla; **prf**, prefrontal; **pt**, pterygoid; **sq**, squamosal.

GEOLOGICAL SETTING

The Randeck Maar is situated southeast of the city of Kirchheim unter Teck at the northern margin of the Swabian Alb mountain range, southern Germany (Fig. 1). It forms part of the Urach-Kirchheim Volcanic Field that comprises more than 350 diatremes (Mäussnest, 1978). The Randeck Maar formed in a phreatomagmatic explosion when magma came into contact with groundwater. The result was a maar lake with steep margins and a diameter of about 1.2 km. Today, less than 60 m of maar sediments are preserved.

These lake sediments comprise massive freshwater limestones, calcareous to marly laminites, and bituminous laminites

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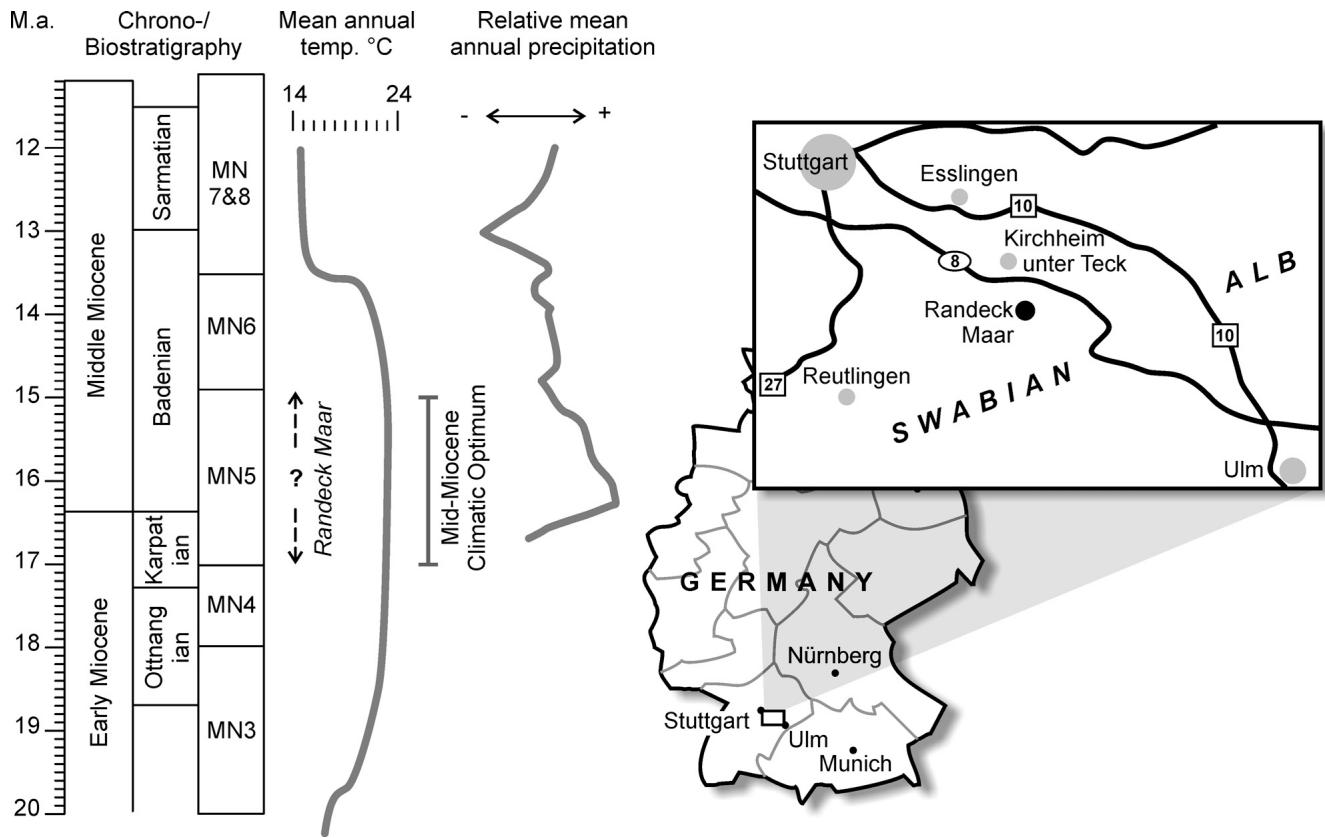


FIGURE 1. Stratigraphic correlation of Randeck Maar sediments and location of Randeck Maar in southern Germany. The exact position within MN 5 is unknown. Mean annual temperature after Böhme (2003); precipitation after Böhme et al. (2011).

(Jankowski, 1981). These rocks are well known for their high-quality preservation of fossils, especially insects and plants (summarized by Schweigert, 1998; Schweigert and Bechly, 2001). Rare mammal fossils allowed for the correlation with Mammal Neogene Zone MN 5 (Heizmann, 1983), which is late Karpatian to early Badenian in age (Fig. 1). A more precise dating within MN 5 is not possible, and reliable absolute ages from volcanic rocks are not available.

Although excavations started in the 19th century, well-documented scientific excavations remained the exception (e.g., Westphal, 1963). Consequently, little is known about the environmental lake history and fossil biocoenoses. Therefore, the SMNS and the University of Tübingen are now conducting long-term scientific excavations, which started in 2009. The newt fossil described herein was found in that year and comes from an undisturbed deeper-water succession of finely laminated calcareous sediments. Detailed information about the excavations and paleoenvironments will be published elsewhere.

SYSTEMATIC PALEONTOLOGY

- LISSAMPHIBIA Haeckel, 1866
- CAUDATA Scopoli, 1777
- SALAMANDROIDEA Noble, 1931
- SALAMANDRIDAE Goldfuss, 1820
- PLEURODELINAE Dubois and Raffaëlli, 2009
- ICHTHYOSAURA Sonnini and Latreille, 1801

Diagnosis—(1) Alary processes of premaxilla thin, spike-like, aligned in parallel; (2) nasal with posterolateral indentation to accommodate frontal.

ICHTHYOSAURA RANDECKENSIS, sp. nov.
(Fig. 2)

Type Locality—Randeck Maar (Baden-Württemberg, southwestern Germany).

Type Horizon—Limnic deposits of Randeck Maar (MN5 Unit, late Burdigalian, early Miocene).

Type Specimen—SMNS 95461. Complete specimen in dorsal view, skull length 7 mm, 48 mm total body length (Fig. 2A–E).

Diagnosis—(1) Posterolateral process of frontal long and broad, ending bluntly; (2) pit-and-ridge ornament covering most of skull roof, especially the nasal, frontal, and parietal; (3) muscle attachment areas on parietal divided by transverse ridge; (4) fusion of premaxilla reaching almost mid-level of alary processes. Characters shared with other pleurodelines and especially newts are the convex lateral margin of the frontal-parietal, a substantial premaxillary fontanelle, and the toothed portion of the maxilla being foreshortened.

Comment—A partial specimen (SMNS 58653) generally resembling this taxon was described as *Triturus* sp. by Roček (1996). However, the absence of the skull and anterior trunk in that specimen does not permit definitive assignment to *I. randeckensis* or even to *Ichthyosaura*.

Identification—*I. randeckensis* is clearly distinct from the two other salamandrids known from Randeck Maar, *Chelotriton* sp. and *Palaeopleurodeles hauffi* (Herre, 1941; Westphal, 1977; Löffler and Westphal, 1982). In contrast to these two *Tylotriton*-like taxa, *I. randeckensis* has a typical *Ichthyosaura*-like skull morphology (no closed frontosquamosal bar, different ornament, fused premaxillae with elongate posterior alary processes framing an elongate fenestra), substantially shorter ribs, an elongated

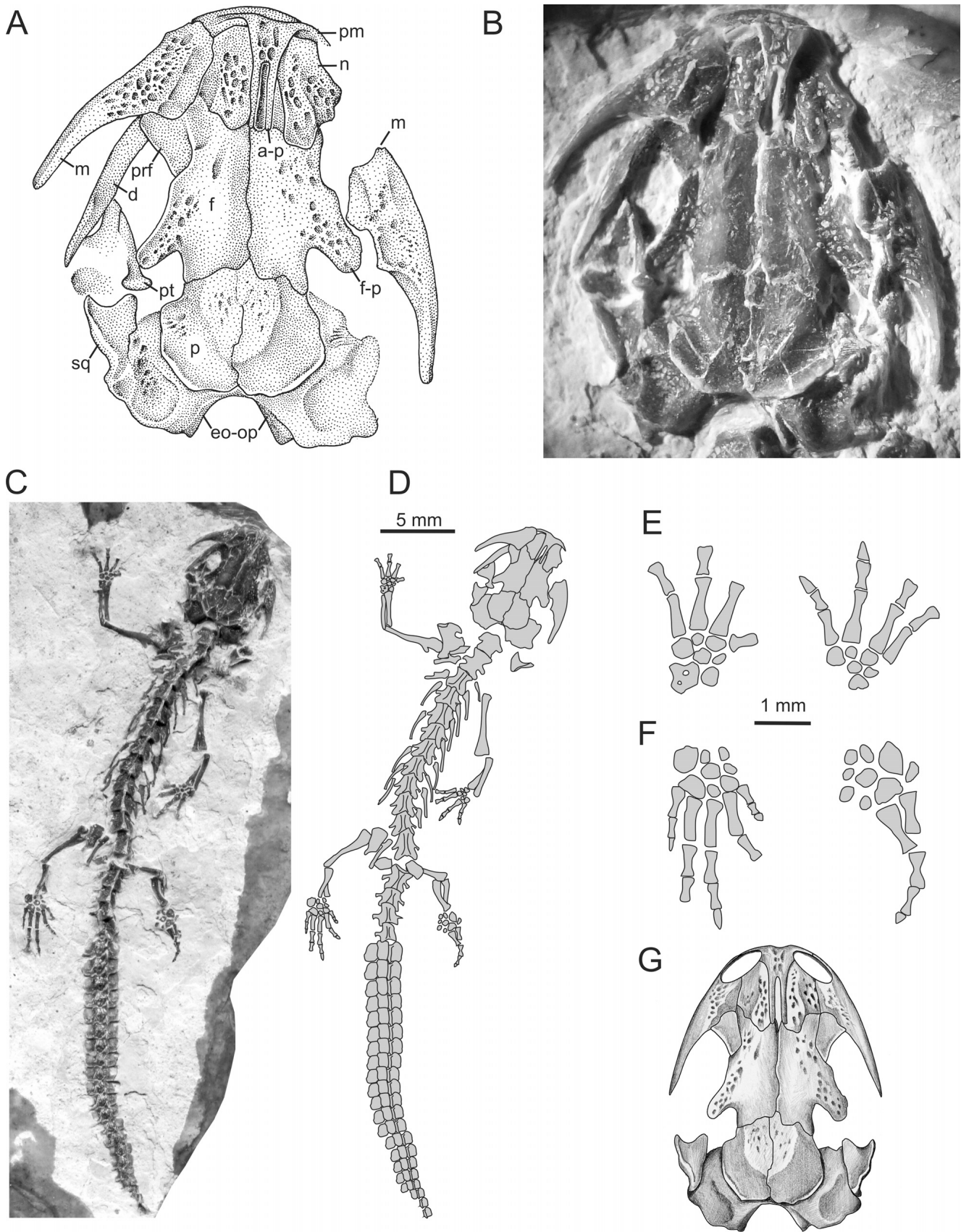


FIGURE 2. *Ichthyosaura randeckensis*, sp. nov. Type specimen (SMNS 95461). **A**, drawing of skull roof (dorsal view); **B**, photo of skull; **C**, photo of complete specimen; **D**, drawing of skeleton; **E**, left and right carpus and manus; **F**, left and right tarsus and pes; **G**, reconstruction of skull.

ilium, high-crested neural arches, and fully ossified carpi and tarsi. It is also substantially smaller and at the same time has more fully ossified limbs than any *Tylostrotion*-clade taxa. In addition, there are only three tarsals in the distal tarsus, a feature shared with newts (*Cynops*, *Ommatotriton*, *Triturus*, *Neurergus*, *Lissotriton*, and *Ichthyosaura*). Distinguishing the new taxon from others occurring at the type locality does not, therefore, pose any problems.

Nomenclature—We follow Dubois and Raffaëlli (2009) in using the generic name *Ichthyosaura* Sonnini and Latreille, 1801, rather than *Mesotriton* Bolkay, 1928 (see also Schmidtler, 2009, for a detailed nomenclatural history of *I. alpestris*); this name was accepted by the most recent authors (Speybroek et al., 2010; Pyron and Wiens, 2011).

DESCRIPTION

General

The following description is based exclusively on the type and only diagnostic specimen of *Ichthyosaura randeckensis*. SMNS 95461 includes the whole specimen in dorsal exposure, with the left arm turned anterior and the right one held posterior (Fig. 2C, D). The skull is excellently preserved but several elements have been displaced. On the right-hand side, the maxilla lies close to the cheek, whereas the left maxilla is only rotated outwards. However, the three-dimensional structure of most skull bones is still well preserved, such as the dome-shaped arrangement of median roof elements and the structure of the premaxillae.

Skull Roof

The ornamentation is more pronounced than in most salamandrids, notably the European and Asian newts. In using this informal name we follow Zhang et al. (2008) who applied to it all those monophyletic taxa formerly attributed to *Triturus*, today falling into *Ichthyosaura*, *Lissotriton*, *Ommatotriton*, and *Neurergus*. The whole skull is relatively wide and more robust than that of most other European and Asian newts (Fig. 2A, B) and retains a wide gap between the frontal and squamosal elements. The derived features of the premaxilla (fontanelle, alary processes) clearly differ from the condition in *Tylostrotion* and *Pleurodeles*.

The median elements of the skull roof are relatively wide and more consistent with the skull of *Tylostrotion* than with the European and Asian newts. The interorbital width/skull length ratio is 0.36, measured at the narrowest level of the frontals. The premaxillae are fused in the tooth-bearing ventral part and the anterior-most region of the dorsal portion, as revealed by the type. Despite this fusion, the premaxillary fenestra is elongate but very narrow, with the thin, spike-like alary processes forming straight sagittal margins. This feature is significant at generic level, because *Lissotriton* has posteriorly diverging alary processes that frame a posterolaterally expanded fenestra. The anterodorsal portions of the premaxillae are heavily ornamented, whereas the alary processes are smooth. The maxilla is longer than in most European newts, with the free posterior end (dental shelf) constituting half of the length of the element. It has an extensive alary process that is also completely covered by radial pits and ridges. It sutures with the relatively wide nasal, which has a stepped posterolateral margin much like that in *Ichthyosaura alpestris*. The nasal is extensively ornamented by pits and bears a gently curved, medial ridge. In contrast, the prefrontal appears to be entirely smooth. The frontal is wider than in most other European newts and has a more robust posterolateral process. The lateral margin of this process is markedly upturned and thickened. Despite its large size, this process is well separated from the squamosal by a wide gap. The lateral part of the frontal, including the process, is ornamented with numerous pits, whereas the medial region is smooth. The parietal bears fine grooves in its medial portion, which has a

rounded outline, and has deep lateral and posterior troughs to accommodate the internal adductor muscles. The opisthotics are large, widely separating the squamosal and parietal bones. As is typical of newts, the dorsal surface of the ear capsule reflects the roof of the semicircular canals. The squamosal is smaller than in *M. alpestris*, especially its medial portion is shorter and posteriorly pointed.

Palate and Mandible

Only the pterygoid is partially exposed in SMNS 95461 (Fig. 2A). It has the typical abbreviated shape of European newts, with the slender palatine ramus somewhat shorter than in *M. alpestris*. The dentary is exposed only in small parts on either side, with three small newt-like teeth on the right side.

Axial Skeleton

The vertebrae are well exposed and almost fully articulated, but considerably crushed. Therefore, the height of the crested neural spines cannot be measured and compared exactly. The atlas is substantially shorter than the axis. The atlas has a small posterodorsal spine, in the second vertebra the spine is longer but highest in the posterior half, and from the third vertebra on, the spines extend along the entire dorsal margin of the vertebra and are of equal height. The thin-crested neural arches are consistent with those of *Ichthyosaura alpestris*, *Lissotriton*, and the Asian newts (Haller-Probst and Schleich, 1994). The transverse processes are relatively longer than in *Pleurodeles*, and are more consistent with vertebrae of *Salamandra* or the more advanced newts. The ribs are throughout short, much smaller and more delicate than in *Pleurodeles* and *Tylostrotion*, and as in *Ichthyosaura* and *Lissotriton*, only the ribs of the axis and third vertebra bear uncinuate spines.

Appendicular Skeleton

The girdles and limbs are articulated and almost completely preserved (Fig. 2C, D). The scapula is crushed but apparently very similar to that of other newts in outline. The very slender humerus has an elongated, finger-like deltopectoral process the base of which is clearly offset from the shaft. Compared with the more robust humerus of adult *Ichthyosaura alpestris*, the process in *I. randeckensis* is proportionately longer. The radius and ulna are not much different in length, and the ulna has only a short olecranon. The distal end of the radius is markedly widened. The carpus consists of seven fully ossified elements, consistent with *Ichthyosaura alpestris* and *Lissotriton*. The phalangeal formula of the hand cannot be ascertained, because the second digits lack distal phalanges.

In the pelvis, the ilium is elongated and has a narrow shaft. The femur is also comparably delicate and as in other salamandrids slightly shorter than the humerus. In contrast to *Salamandra* and more pronounced than in *Pleurodeles*, the fibula bears a long posterior crest. As in other well-ossified newts (e.g., *Cynops*), this crest is continuous and tall. Like all salamandrids, the tibia has a hook-like dorsal process on the proximal end, connecting to the femur. There are at least eight elements in the tarsus, but the number of distal tarsals is definitely reduced to three like in all other newts.

PHYLOGENETIC ANALYSIS

Previous Work

The crucial anatomical foundations for subsequent phylogenetic studies were formed by Wiedersheim (1877), Bolkay (1928), and Francis (1934) who described salamandrid osteology, ontogeny, and structural diversity in great detail. Later, the survey of Haller-Probst and Schleich (1994) complemented the existing descriptions of salamandrid species, focusing on cranial and

vertebral characters, and Estes (1981) and Milner (2000) have provided useful synopses of fossil material. Descriptions of fossil taxa, such as *Archaeotriton* (Meyer, 1860; Böhme, 1998), *Brachycormus* (Roček, 1996), *Chelotriton* (Westphal, 1980; Roček and Wuttke, 2010), and *Palaeopleurodeles* (Herre, 1941; Westphal, 1977) have added to the knowledge of salamandrid diversity, as have studies on fossil representatives of extant lineages (Westphal, 1978).

Venczel (2008) has recently conducted a cladistic analysis with inclusion of various fossil taxa known only from disarticulated material. Here, we take a different approach, focusing on extant taxa whose ontogeny, adult osteology, and individual variation are well known, in order to elucidate the position of the new taxon from Randeck Maar. The present analysis employs characters listed by previous authors (Bolkay, 1928; Haller-Probst and Schleich, 1994) as well as new characters obtained from the first-hand study of rich skeletal material (see Appendix 1). At the present, inadequate knowledge of critical anatomical regions in most fossil taxa, and the still relatively poor comparative osteological basis for extant salamandrids, precluded the inclusion of most fossil taxa in this analysis. Future analyses will focus on a larger set of taxa, including restudied fossil ones.

Various analyses of extant salamandrids have been published since the 1990s, starting with Titus and Larsen (1990) and MacGregor et al. (1990) who considered molecular data. García-Paris et al. (2004) partitioned the *Triturus* clade into several monophyletic genera: *Lissotriton*, *Ichthyosaura* (= *Mesotriton*), and *Triturus sensu stricto*. Recently, Steinfartz et al. (2007) and Zhang et al. (2008) have published new trees of the Salamandridae based on molecular data.

Analysis

We performed a cladistic analysis employing the software package PAUP 3.1 (Swofford, 1991). A total of 38 morphological characters and 14 taxa were analyzed (see Appendices 1 and 2, references for characters given there). The analysis was run in the Branch-and-Bound mode, with all multistate characters unordered. The analysis found two most parsimonious trees, with tree length of 74 steps (consistency index [CI] = 0.649; retention index [RI] = 0.720; rescaled consistency index [RC] = 0.467). Bremer support and bootstrap values were also calculated in PAUP (see next section). In a further step, the 38 osteological characters of the present analysis were optimized on the topology of Zhang et al. (2008). This constrained tree required 77 steps (CI = 0.62, RI = 0.69, RC = 0.43).

Results

The resulting topology (Fig. 3A) was not completely resolved but is generally consistent with recent findings (Titus and Larson, 1990; Frost et al., 2006; Steinfartz et al., 2007; Zhang et al., 2008). The focus of the present analysis, the position of *Ichthyosaura randeckensis*, gave an unequivocal result: it nests with *I. alpestris* within a clade spanned by *Lissotriton* and *Ichthyosaura*. The nodes found in the present analysis are as follows.

- (1) Unresolved trichotomy *Salamandra* (outgroup), *Euproctus*, and all other ingroup taxa. A clade formed by *Euproctus* and all other newts is supported by five synapomorphies and one homoplasy, but a low bootstrap value (<50%). The position of *Euproctus* at this basal node is not consistent with recent molecular findings (Steinfartz et al., 2007; Zhang et al., 2008) and is probably caused by convergences in skull morphology (patrietals, frontosquamosal bar) shared by *Euproctus*, *Notophthalmus*, and *Typhlonectes*, as well as by the uniquely modified posterior skull region of *Euproctus*, which has masked features indicating a relationship with higher pleurodeles.

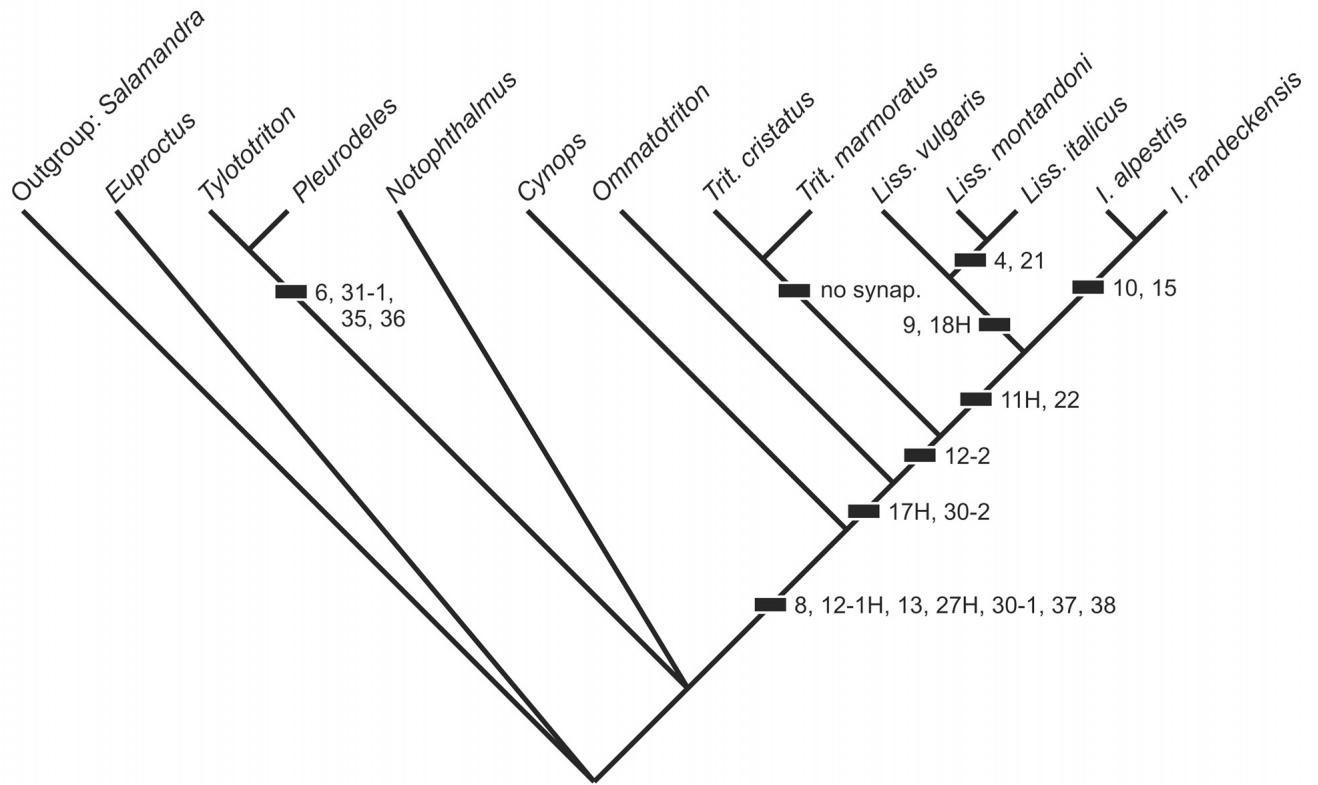
- (2) Unresolved trichotomy of 'primitive newts' (*Tylototriton*, *Pleurodeles*), *Notophthalmus* (North American newts), and the Eurasian newts. This node is found by PAUP, but not supported by unambiguous synapomorphies (one step Bremer, 56% bootstrap).
- (3) *Tylototriton* and *Pleurodeles*. Supported by four synapomorphies (three steps Bremer, 92% bootstrap). This robust node represents the clade referred to as 'primitive newts' (Zhang et al., 2008) and which has been found by many recent analyses (Steinfartz et al., 2007; Grosse, 2011).
- (4) European and Asian newts. This clade includes *Cynops*, *Ommatotriton*, *Triturus*, *Lissotriton*, and *Ichthyosaura*. It is supported by four synapomorphies and two homoplasies (one step Bremer, 61% bootstrap). This group was also found to be monophyletic by Zhang et al. (2008). Steinfartz et al. (2007) found a similar clade including *Euproctus*, however.
- (5) Modern European newts. Includes *Ommatotriton*, *Triturus*, *Lissotriton*, and *Ichthyosaura*. It is supported by one synapomorphy and one homoplasy (two steps Bremer, 65% bootstrap). The monophyly of modern European newts was found by Zhang et al. (2008).
- (6) A clade consisting of *Triturus* plus (*Lissotriton* and *Ichthyosaura*) is supported by only one potential synapomorphy (character 12-2) (two steps Bremer, 60% bootstrap).
- (7) *Triturus marmoratus* and *T. cristatus*. Although representing a clade found by recent molecular analyses, this group is not supported by synapomorphies or homoplasies here, but was nevertheless found as a clade by PAUP (one step Bremer, 50% bootstrap).
- (8) *Lissotriton* and *Ichthyosaura*. This clade is supported by only one potential synapomorphy (character 12-2) (two steps Bremer, 60% bootstrap). Zhang et al. (2008) also found *Lissotriton* and *Ichthyosaura* to form sister taxa, whereas Steinfartz et al. (2007) found *Ichthyosaura* to nest with *Cynops*.
- (9) Here, the genus *Lissotriton* is a clade represented by three species with one synapomorphy and one homoplasy (two steps Bremer, 63% bootstrap).
- (10) Within *Lissotriton*, *L. italicus* and *L. montandoni* are here found to be sister taxa with two synapomorphies (four steps Bremer, 88% bootstrap).
- (11) *Ichthyosaura alpestris* and the new taxon from Randeck Maar are found to be sister taxa on the basis of two synapomorphies (two steps Bremer, 70% bootstrap). On this basis, the new taxon is referred to *Ichthyosaura*.

Discussion

The significance of the present results are twofold. (1) The well-preserved material of *Ichthyosaura randeckensis* can be placed unequivocally within the clade of modern European newts (*Triturus*, *Ommatotriton*, *Lissotriton*, *Ichthyosaura*). (2) Although the morphological characters include a large number of homoplasies, some newly recognized characters add to the stability of morphology-based cladistics of the Salamandridae. The most interesting region is the snout (Fig. 3B), especially the divergent morphological patterns in the premaxilla, premaxillary fenestra, and the nasal-frontal region. In contrast to the homoplasy-laden frontosquamosal arch and palate, the snout region shows apomorphic features. Future studies should follow this line of research in exploring further skeletal regions (pelvis, limbs, vertebrae) and additional salamandrid taxa.

The present result that *Ichthyosaura* and *Lissotriton* form sister taxa corroborates the results of Zhang et al. (2008), which found this topology by analyzing molecular data. Optimizing the 38 characters of the present analysis on the topology obtained by

A



B

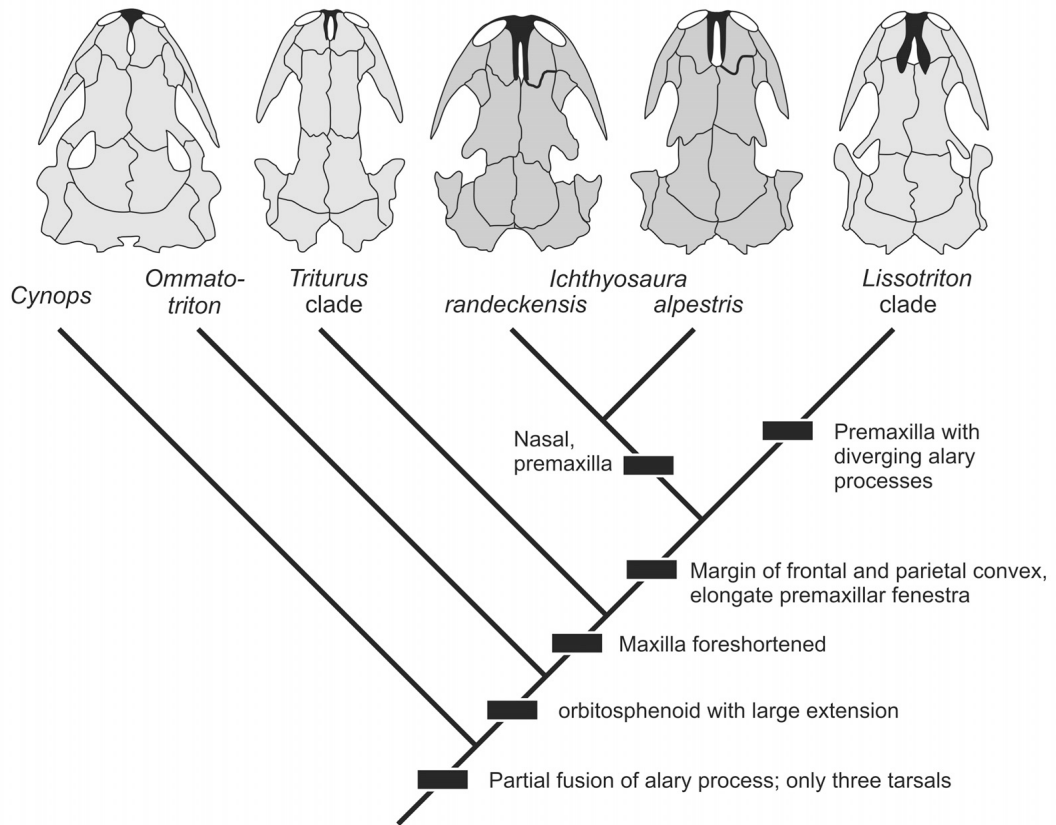


FIGURE 3. Cladistic analysis. **A**, topology of cladogram as found by PAUP analysis; **B**, close-up of relationships amongst European newts, with the most important morphological characters mapped.

Zhang et al. (2008) revealed two likely osteological homoplasies that obscure relationships between salamandrids when analyzed in isolation: character 2-1 is shared by *Typhlonectes*, *Pleurodeles*, and *Notophthalmus*, whereas character 24-1 occurs in both *Notophthalmus* and *Euproctus*. In turn, characters 5, 7, and 28 all rank as synapomorphies in Zhang et al.'s (2008) topology, contrasting their homoplastic status in the topology found in our morphological data set. In sum, the more basal position of *Euproctus* found by our analysis is likely to result from homoplasies rather than reflecting its true relationships.

Our results are also generally similar to, but somewhat less consistent with, the results of Venzel (2008), who obtained *Triturus cristatus* as still more closely related to *Ichthyosaura* than *Lissotriton*. Future analyses should focus on the inclusion of more fossil taxa (e.g., *Chelotriton*, *Palaeopleurodeles*, *Brachycormus*, *Archaeotriton*), but this requires revision of some of these taxa and also an intensified search for additional morphological characters in order to establish a broader platform for phylogenetic analysis. The present study has shown that additional characters can be found when comparative data are assembled, but many character states can only be identified in well-preserved or articulated material, which is not common in most fossil deposits yielding salamander fossils. Consideration of incompletely known taxa is very much needed, but requires knowledge of variation of preserved features in order to elucidate their phylogenetic reliability (e.g., vertebral or certain cranial elements).

PALEOENVIRONMENT AND PALEOECOLOGY

The closest relative of *Ichthyosaura randeckensis*, the alpine newt *I. alpestris*, is known to inhabit larger and more stable water bodies than *Lissotriton* spp. (Engelmann et al., 1985). It is also reported to prefer forests with good access to water in uplands and to be absent in forest-poor areas. By contrast, the different species of *Lissotriton* appear to be more flexible in that they also breed in tiny ponds and ephemeral water bodies and some species can survive drought-periods (Grosse, 2011).

Considering the climatic conditions of the Randeck Maar time interval, some approximations can be made about the paleoecological requirements of *I. randeckensis*. The lake sediments are correlated with Mammal Neogene Zone MN 5 (Heizmann, 1983). This period widely corresponds to the so-called middle Miocene climatic optimum (Fig. 1), which was the warmest period in the Neogene, with a low Antarctic ice volume (Zachos et al., 2001). The climatic conditions in central Europe included high annual temperatures, high rates of precipitation in general, and periods of particularly high seasonality in precipitation (Fig. 1; Böhme, 2003; Böhme et al., 2011). Böhme et al. (2007) suggested a mean annual temperature of 17.4–20.5°C for southern Germany during this time interval, contrasting with 9–10°C today.

The lake itself was a classical volcanic crater (maar) lake with steep slopes as well as a large and stable water body, which is expressed in regularly laminated sediments (Jankowski, 1981; Schweigert, 1998). Due to steep slopes, the lake comprised only a narrow lakeshore with a reed belt. Fossil macrofloral remains are particularly abundant in the Randeck Maar lake sediments and provide useful paleoecological proxies. They show that the forests surrounding the lake were characterized amongst others by the oak *Quercus mediterranea* and the legume *Podocarpium podocarpum*, which allows the reconstruction of a subhumid, sclerophyllous forest. This indicates at least temporal (seasonal) droughts (Kovar-Eder and Kvacek, 2007).

In summary, *I. randeckensis* thrived during a time of high mean temperatures, in (and close to) a lake with a large and stable, non-ephemeral water body that was surrounded by a subhumid, subtropical forest affected by temporal droughts. With its closest

relative, *M. alpestris*, the new species had in common a preference for larger and stable water bodies with adjacent forests.

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APPENDIX 1. Morphological characters.

- (1) Ornament. Dermal skull roof smooth (0), or with pitted ornament on nasals and anterior frontals (1), or throughout ornamented throughout (2).
- (2) Ornament. Nasals, frontals, and parietals smooth or pitted (0), or covered with numerous ridges (1).
- (3) Ornament. Squamosal smooth (0), or ornamented (1).
- (4) Snout. Outline of preorbital region rounded (0), or markedly stepped (1).
- (5) Premaxilla. Toothed portion paired (0), or unpaired (= fused along midline) (1). (Wake and Özeti, 1969).
- (6) Premaxilla. Dorsally exposed (0), or completely overplated by nasals (1).
- (7) Premaxilla. Medially sutured (0), or separated by fontanelle (1).
- (8) Premaxilla. Alary processes free (0), or fused for at least 50% of their length (1).
- (9) Premaxilla. Alary processes parallel (0), or diverging to form deltoid fontanelle (1).
- (10) Premaxilla. Alary processes variable but always broad (0), or spike-like (1).
- (11) Premaxillary fontanelle. Absent (0), or short (1), or enlarged to long slit (2).
- (12) Maxilla. Toothed portion extends to quadrate (0), or extend beyond the eye but falls short of quadrate (1), or falls short of posterior margin of eye (2). (Wake and Özeti, 1969).
- (13) Maxilla and pterygoid. Nearing or in contact (0), or widely separated (1).
- (14) Nasal. Nasals fail to contact one another (0), or at least in partial contact (1). (Wake and Özeti, 1969).
- (15) Nasal. Suture with frontal transversely straight (0), or stepped with anterolateral projection of frontal (1).
- (16) Frontal. Interorbital width/skull length 0.25–0.3 (0), or 0.32–0.35 (1), or 0.37–0.49 (2).
- (17) Frontal. Posterolateral process absent (0), or faint and pointed (1), or robust (2).
- (18) Frontal. Frontal planar (0), or with anterior depression framing enlarged fontanelle (1).
- (19) Frontosquamosal arch. Absent (wide gap between bones) (0), or partial (squamosal and frontal nearing) (1), or closed (2). (Wake and Özeti, 1969).
- (20) Frontal and prefrontal. Lateral ridge absent (0), or present (1).
- (21) Frontal and prefrontal. Smooth or with dorsally rounded ridge (0), or bearing ridge with longitudinal groove (1).

- (22) Frontal and parietal. Lateral margin straight to gently convex (0), or markedly convex (1).
- (23) Frontal and parietal. Medial suture straight (0), or sigmoidally curved (1).
- (24) Frontal and parietal. Attachment of adductors only marginal (0), or extending medially, leaving large parts of parietal unornamented (1).
- (25) Parasphenoid. Basal plate offset (0), or continuous with cultriform process (1).
- (26) Parasphenoid. Posterior ventral crest absent (0), or present (1).
- (27) Pterygoid. Triradiate (0), or with quadrate ramus reduced to a stub (1).
- (28) Vomer. Fontanelle large (0), or tiny (1).
- (29) Vomer. Dentigerous posterior processes 'S'-shaped (0), or of deltoid outline (1).
- (30) Orbitosphenoid. Without posterodorsal extension (0), or with small extension (1), or with large extension (2).
- (31) Jaw articulation. Near posterior margin of parasphenoid (0), or level with carotid openings (1), or anterior to basipterygoid ramus (2).
- (32) Mandible. Prearticular and angular not fused with articular (0), or fused (1). (Venczel, 2008).
- (33) Operculum. Ossified (0), or cartilaginous (1). (Wake and Özeti, 1969).
- (34) Atlas. Centrum not shorter than trunk vertebrae (0), or substantially shorter (1). (Wang and Evans 2000).
- (35) Ribs. Trunk ribs form short rods (0), or as long as three vertebral centra (1).
- (36) Ilium. Slender with elongated shaft (0), or stout with short and broadened shaft (1).
- (37) Neural spines. Low, posterodorsally ascending (0), or elevated with thin crest forming straight horizontal dorsal margin (1).
- (38) Tarsals. More than three distal tarsals in the ankle (0), or just three (1).

APPENDIX 2. Character-taxon matrix. **Abbreviations:** A, polymorphic states (0, 1).

	10	20	30	38
<i>Salamandra</i>	0000000000	0000000000	0000000000	00100000
<i>Tylototriton</i>	2110110000	1000022021	0000110010	11011100
<i>Pleurodeles</i>	2110101000	0001022121	0010110010	11011100
<i>Notophthalmus</i>	2110111000	1001022121	0001111110	21110000
<i>Euproctus</i>	0000101000	2100002021	0001110110	01110000
<i>Cynops</i>	1010110100	0111022021	001A111111	21010011
<i>Ommatotriton</i>	0000101100	1110011021	0000111112	21110011
<i>Trit. marmor</i>	0000101100	1210001001	0000111112	21110011
<i>Trit. cristatus</i>	0000101100	1211001001	0000111112	21110011
<i>Lissotr. vulgar</i>	0000101110	2210011101	0110111112	21110011
<i>Lissotr. mont</i>	0001101110	2210021111	1110111112	21110011
<i>Lissotr. italicus</i>	0001101110	2210021121	1100111112	21110011
<i>Ichth. alpestris</i>	0000101101	2210111001	01A 0111112	21110011
<i>Ichth. rand.</i>	1000101101	1210122001	011011111?	21110011