

The salamandrid *Chelotriton paradoxus* from Enspel and Randeck Maars (Oligocene–Miocene, Germany)

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Abstract The late Paleogene to early Neogene salamander *Chelotriton paradoxus* is redescribed on the basis of new and excellent material from two deposits, the late Oligocene Enspel locality and the Miocene Randeck Maar. *C. paradoxus* is characterised by the following features: (1) skull outline broad and parabolic, (2) snout abbreviated, with nasal only half the length of the frontal, (3) quadratojugal with a series of 3–5 spikes on the lateral margin, and (4) osteoderms larger than in other genera. Like extant *Echinotriton*, its trunk ribs bear extensive spikes (epipleural processes), with an elongated one on the 3rd rib. The Enspel sample of *C. paradoxus* shows greater variation in the size and number of quadratojugal spikes, whereas the best-preserved Randeck specimen bears exceptionally tall tubercles on all dermal bones and osteoderms and has a larger quadratojugal. Based on preliminary taphonomical data, we suggest that *C. paradoxus* probably led a predominantly aquatic life.

F Frontal
Hb Hypobranchial
M Maxilla
N Nasal
P Parietal
Pm Premaxilla
Pra Prearticular
Prf Prefrontal
Ps Parasphenoid
pt Pterygoid
q Quadrate
qj Quadratojugal
sa Surangular
sq Squamosal
vo Vomer

Keywords Caudata · Morphology · Newts · Palaeoecology

Abbreviations

Ar Articular
Cb Ceratobranchial
D Dentary
Eo Exoccipital

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Introduction

Salamanders form abundant components in Cenozoic continental deposits, which in Europe are dominated by the family Salamandridae (Meyer 1860; Roček 1994; Böhme 1998, 2008; Venczel 2008; Roček and Wuttke 2010). In many extant ecosystems, they contribute substantially to biomass and to the flow of matter between aquatic and terrestrial habitats (Davic and Welsh 2004). Their presence and distribution have also been used to infer climatic properties in the Neogene (Böhme 2003).

The Cenozoic deposits of Central and Western Europe are rich in salamandrids, but in most deposits isolated bones dominate. Articulated specimens are more exceptional and have been reported especially from lake deposits, such as the volcanic crater lakes of Messel (Eocene), Enspel (Oligocene), and Randeck Maar (Miocene).

A rich collection of salamanders has accumulated from excavations at the Enspel locality in Rhineland-Palatinate, south-western Germany (Roček and Wuttke 2010). The Enspel crater-lake has produced vast number of pelobatid and palaeobatrachid anurans and salamandrids including *Chelotriton paradoxus*, a hyperossified newt-like salamandrid that closely resembles the extant genera *Tylotriton* and *Echinotriton*. These large salamanders form a clade with *Pleurodeles* (Pleurodelinae), sometimes referred to as “primitive newts” (Steinfarz et al. 2007; Zhang et al. 2008; Grosse 2011). They all share the massive and well-ornamented skull and the spike-like elongated ribs that are associated with skin glands.

Material collected over the past decade, including the exquisite type specimen of the newt *Ichthyosaura randeckensis* (Schoch and Rasser 2013), has drawn attention to the Randeck Maar in Baden Württemberg (southern Germany; Rasser et al. 2013). This site had already produced *Palaeopleurodeles hauffi*, an apparently neotenic salamandrid (Herre 1941; Westphal 1977), and four still undescribed specimens of *Chelotriton*, which we will propose to refer to *C. paradoxus*. The new Enspel and Randeck material forms the basis of this study, which reexamines *C. paradoxus*. The objective of the present paper is twofold: (1) to provide a description of the new Enspel and Randeck material, guided comparisons with the closest relatives, and (2) to assess the palaeoecological significance of *Chelotriton* for the Enspel and Randeck localities.

The material described herein is kept in the collections of the State Museum of Natural History Stuttgart (SMNS) and the Generaldirektion Kulturelles Erbe at Mainz (PW).

Systematic palaeontology

Order Caudata Scopoli, 1777

Family Salamandridae Goldfuss, 1820

Genus *Chelotriton* Pomel, 1853

Chelotriton paradoxus Pomel, 1853

Diagnosis: Large salamandrid with heavily ossified skull, a single row of rectangular osteoderms, and extensive tubercular ornamentation on dermal elements. (1) Skull outline broad and parabolic, (2) snout abbreviated, with nasal only half the length of the frontal, (3) quadratojugal with a series of 3–5 spines at lateral margin, and (4) osteoderms larger than in other genera.

Derived character-states shared with other salamandrids: (5) maxilla with posteromedial process nearing or suturing pterygoid (*Chelotriton*+*Echinotriton*), (6) quadratojugal long (*Chelotriton*+*Echinotriton*), (7) ossified carpal and tarsal elements (*Chelotriton*+*Echinotriton*), and (8) 1–3 epipleural processes on trunk ribs (*Chelotriton*+*Echinotriton*+*Tylotriton*).

Comment: Here, we treat *Chelotriton* as having only one species, *C. paradoxus*. The two referred species remain poorly known and are apparently substantially different from *C. paradoxus*. At present, we cannot see apomorphic features exclusive to the genus *Chelotriton* in either of them, which is why we restrict *Chelotriton* to the type species here.

Materials: Randeck sample (Fig. 1): SMNS 80210: partial skull in ventral view; SMNS 80672: complete skull exposed in dorsal and ventral view and anterior trunk vertebrae and ribs (17 mm); SMNS 86230: skull and trunk skeleton; SMNS 87847: braincase, parasphenoid and trunk skeleton.

Enspel sample (Fig. 2): There is a total of about 20 specimens from Enspel, the following ones being sufficiently well preserved to serve as a basis for this investigation: PW1995/5809-LS (skull roof, 16.5 mm, dorsal; see Roček and Wuttke 2010; Fig. 2b), PW1995/5810-LS (18 mm, dorsal; see Roček and Wuttke 2010; Fig. 2a), PW1995/5826-LS (postcranium; see Roček and Wuttke 2010; Fig. 2c), PW1996/5029-LS (16.5 mm, palate), PW1998/5030-LS (15 mm, palate), PW1998/5058-LS (17.5 mm, dorsal), PW1999/5000-LS (17.5 mm, dorsal), PW2001/5010-LS (16.5 mm, palate), PW2003/5006-LS (18 mm, palate), PW2006/5031-LS (19 mm, dorsal), PW2008/5181-LS (~15 mm, palate), PW2010/5000-LS (18 mm, palate), PW2010/5023-LS (complete skeleton, dorsal).

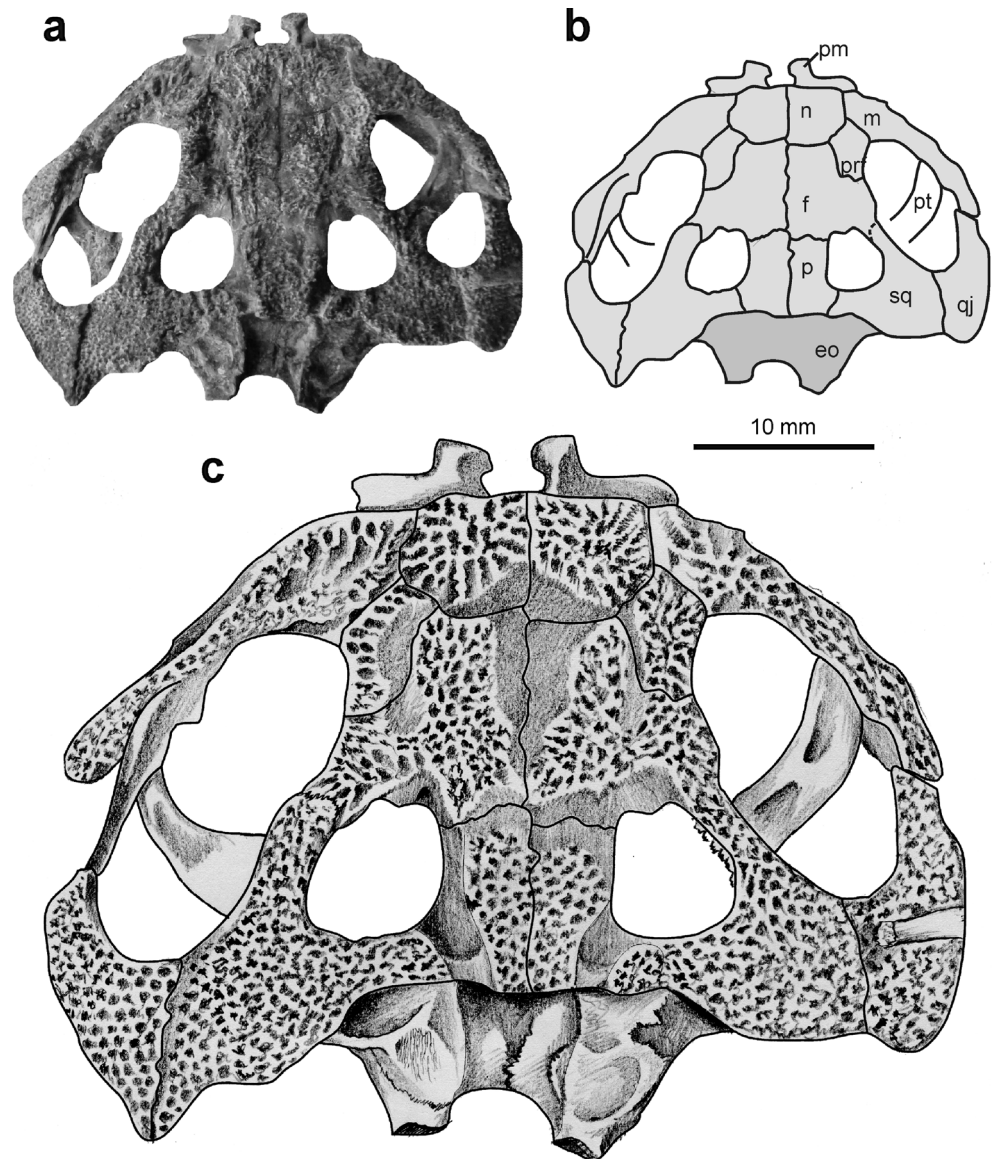
General remarks: In the following description, we refer to *Chelotriton paradoxus* as *Chelotriton*, and compare its features to the two best known of its closest extant relatives, *Echinotriton* (*E. andersoni*) and *Tylotriton* (*T. verrucosus*). We make use of the primary descriptions and figures provided by Bolkay (1928) and Herre (1935), and especially the distinction of *Echinotriton* and *Tylotriton* laid out by Nussbaum et al. (1982).

The skull of *Chelotriton* resembles most closely that of *Echinotriton* in the general outline (blunt-snouted and triangular, with straight lateral margins) and the large extent of ornamented areas. It differs from *Tylotriton* in not being rounded and in having fully ornamented medial areas on the frontal and parietal. However, compared to *Echinotriton*, the skull of *Chelotriton* has an abbreviated snout and is proportionately wider.

The dermal ornamentation, which covers the skull roof and osteoderms, consists of tall, densely set tubercles (Figs. 1, 2). In the Enspel sample, the ornamented field on the parietal is highly variable, ranging from triangular to rectangular in outline. While rather low in the Enspel specimens, the tubercles are exceptionally tall in the single well-preserved Randeck skull (Fig. 1). This difference also applies to the ornamentation of the osteoderms. The ornamentation varies both regionally and individually in the number and density of tubercles, as well as the distribution of reticulate ridges.

Skull roof: The premaxillae form the blunt anterior margin of the snout. The alary processes are straight and relatively wide,

Fig. 1 *Chelotriton paradoxus* from Randeck Maar. **a** SMNS 80672. **b** Interpretative drawing. **c** Detailed drawing showing ornamentation



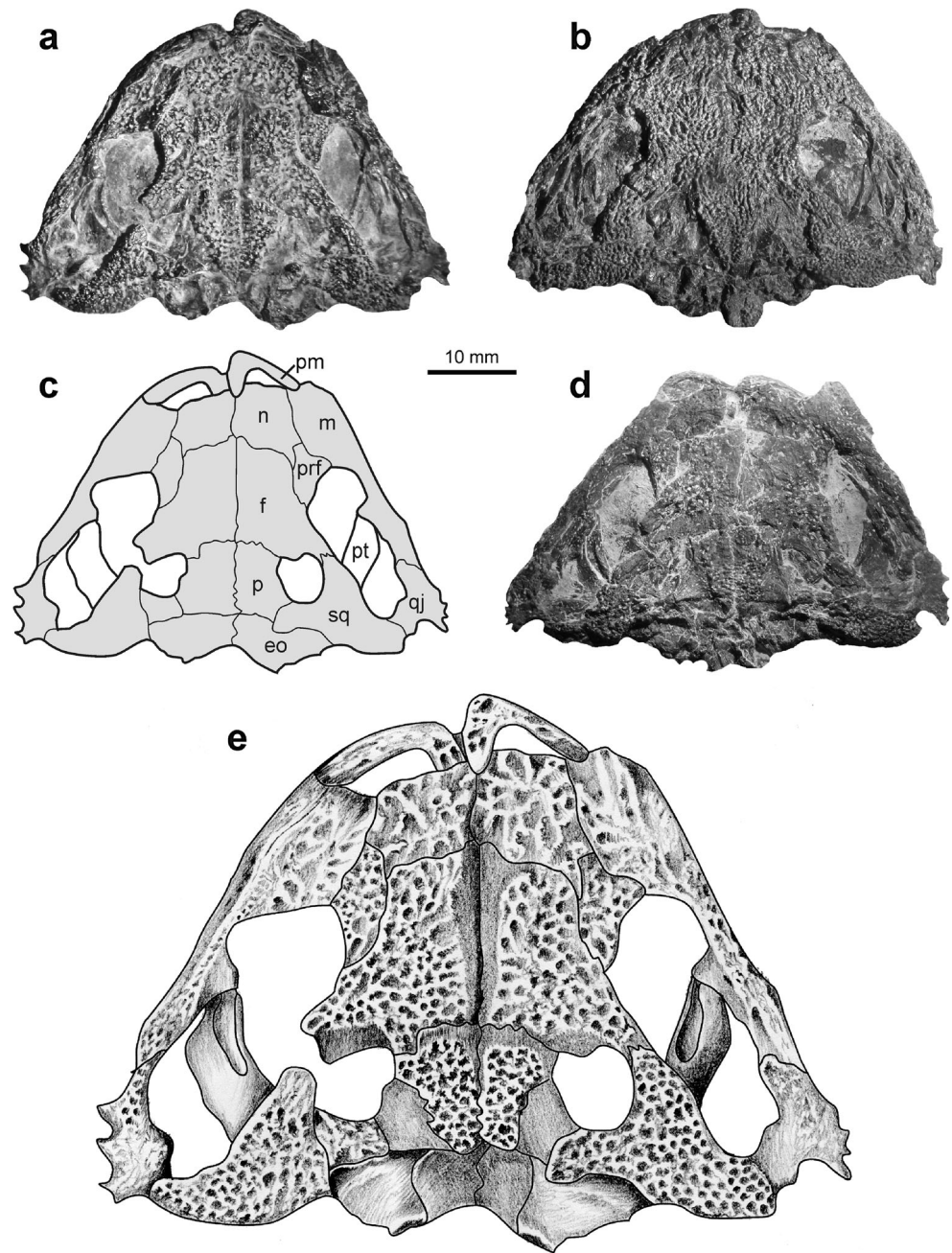
apparently not fully in contact at the midline, and completely overlapped by the rectangular nasals posteriorly. They are substantially shorter than the tooth-bearing ramus of the premaxilla, and their dorsal end is pointed. The premaxilla bore 20 or more teeth, which are of similar size and closely set. The teeth are not well preserved in any specimen, so it remains unclear whether they were pedicellate and what their cusps looked like.

The maxilla is very long, connecting the snout (prefrontal, nasal) with the palate (pterygoid) and cheek (quadratojugal). Unlike in most caudates, it is firmly integrated and bears an extended tooth arcade (Figs. 1, 2). Its tooth count is unknown, but must have exceeded 40. The anterior half is very wide, forming a rectangular, blade-like medial projection contacting the nasal and prefrontal. The posterior ramus is also heavily ornamented, with the exception of the posteromedial projection that is sutured to the pterygoid.

There is no separate lacrimal element, and no evidence of a septomaxilla either. The nasal is straight-edged and rather small. In contrast to *Echinotriton* and *Tylotriton*, the nasal forms a short, rectangular or pentagonal element (Fig. 3). It reaches only half the length of the frontal (Figs. 1, 2). The posterior half of the nasal and the frontal bear a continuous medial depression that is free of ornament or in which the ornament is less pronounced. In the Enspel sample, this depression is present only in some specimens, being narrower and posteriorly more extensive than in the Randeck specimen, where ornament is very weak in that region.

The fronto-squamosal bar is substantially wider than in *Tylotriton*, but somewhat less robust than in *Echinotriton*. The frontal is very wide, reaching almost twice the width of the parietal. It bears a parasagittal groove laterally that continues onto the prefrontal. The posterior end is sutured to the parietal medially and frames the fronto-squamosal fenestra

Fig. 2 *Chelotriton paradoxus* from Lake Enspel. **a** PW1998/5058-LS. **b** PW1995/5810-LS. **c** Interpretative drawing of PW1998/5058-LS. **d** PW1995/5809-LS. **e** Detailed drawing of ornamentation in PW1998/5058-LS



laterally by a smooth, unornamented flange. The prefrontal separates the maxilla from the frontal, and interposes between the posterior half of the nasal and maxilla. It has a pentagonal or hexagonal outline, anteriorly pointed and posteriorly blunt. The parietal is a rectangular element; whereas its central region is densely ornamented, the anterior and posterolateral portions are smooth. Posterolaterally, it was covered by the internal adductor muscles, which ran posterodorsally to attach on top of the first neural arches like in other salamandrids (Carroll and Holmes 1980).

The squamosal is not as elongated as in *Echinotriton*, with the posterior margin aligned transversely in most specimens

(Fig. 3). However, the length and posterior outline varies across the Enspel sample. In the Randeck specimen, the squamosal is much more massive and its ornamented area is posteriorly expanded, much like in *Echinotriton*.

As in other salamandrids, the ornamented areas of parietal and squamosal are broadly separated by a low and smooth portion of the parietal. This is consistent in the Enspel and Randeck specimens, resembling the condition in *Echinotriton*. The smooth gap between the squamosal and parietal ornamentation (formed by found on the parietal) is always wide.

The quadratojugal is longer than in *Tylotriton*, and in contrast to both *T.* and *Echinotriton* it bears a wide

Fig. 3 *Chelotriton* and other pleurodeline genera.

a *Echinotriton andersoni*

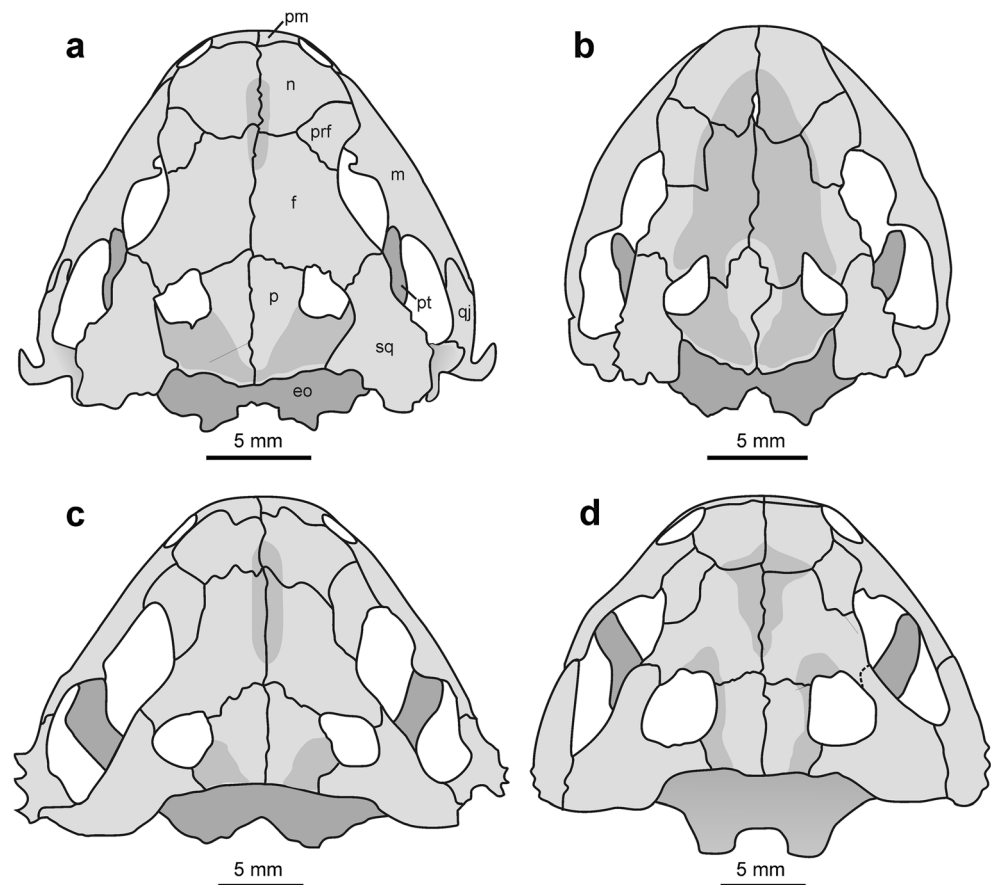
(Nussbaum et al. 1982).

b *Tylotriton verrucosus*

(Nussbaum et al. 1982).

c *Chelotriton paradoxus* from Enspel Maar.

d *C. paradoxus* from Randeck Maar.



ornamented plate (Fig. 3). Conversely, the maxilla, although it forms an elongate overlapping suture with the quadratojugal, is shorter than in *Tylotriton*. In the Enspel sample, the lateral margin of the quadratojugal bears a series of spines, whose orientation is relatively consistent across the sample. Although the number of these spines varies, the posteriormost one or two spines are usually aligned posterolaterally, whereas a larger anterior spine points anterolaterally. The length of the element and size of the ornamented area vary substantially within the Enspel sample, but both are still larger in the single completely preserved Randeck specimen.

Palate: The palate is dominated by the sword-shaped parasphenoid, which forms a wide, anteriorly tapering blade that covers the ventral floor of the braincase (Fig. 4). Its anterior end is rounded but obscured by elongate and curved vomerine processes. These are not quite as long as in *Pleurodeles* (Bolkay 1928), but their exact extent is difficult to assess because of crushing and damage. The ventral surface of the cultriform process bears a cross-shaped medial embossment, whose horizontal axis is level with the point where the basal plate begins. The plate is slightly narrower than the process, having markedly concave lateral margins, which are serrated in some specimens. The lateral portions of the plate house a depression which may contain an opening for the internal carotid artery. This is not present in all specimens, so

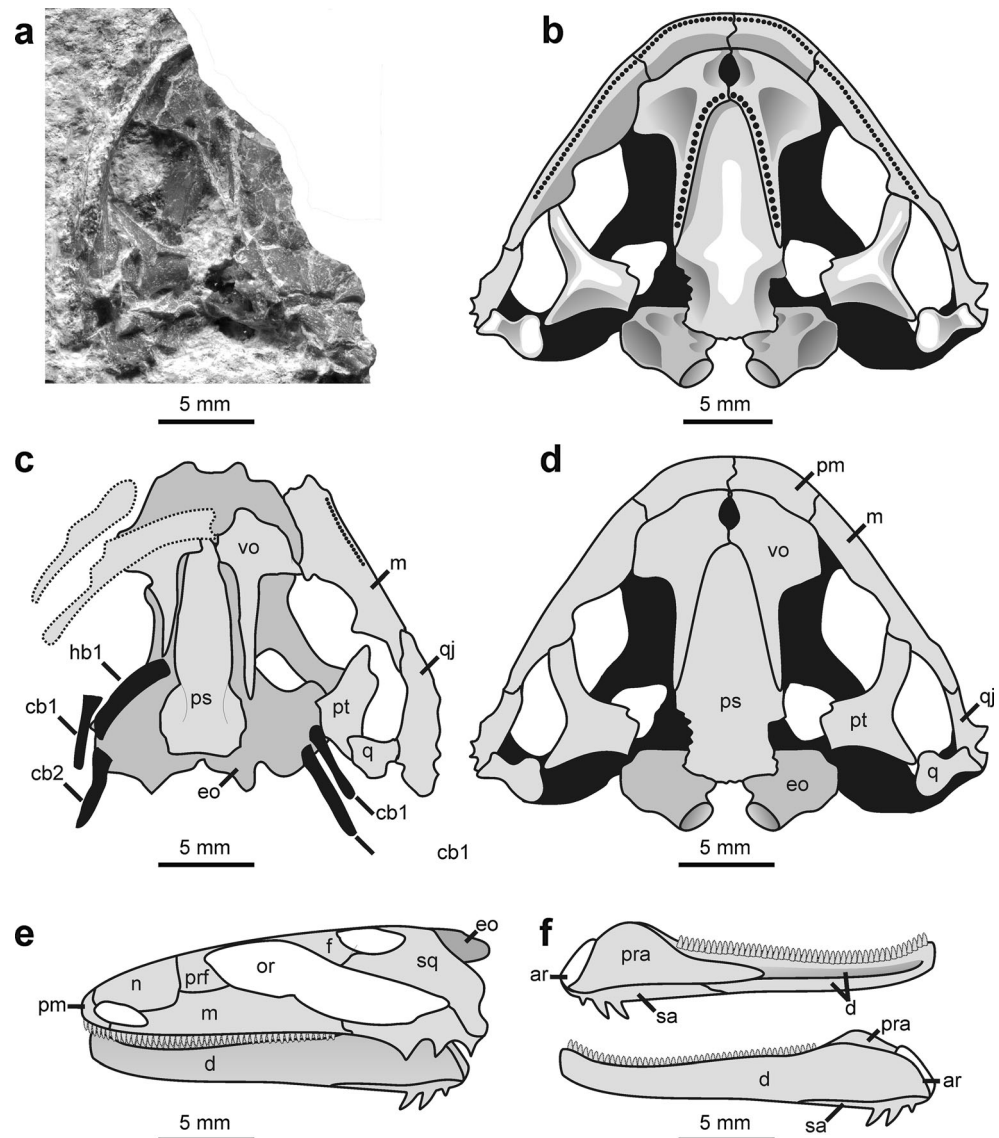
the course of the artery with respect to the parasphenoid must have varied.

The pterygoid is a small and thin triangular element. The shortest ramus is the quadrate process, which ends in a point (Fig. 4b). It has only a faint contact with the quadrate. The palatine process is broadly sutured to the tongue-like pterygoid process of the maxilla. In contrast, the basiptyergoid ramus is very wide but separated from the parasphenoid by a wide gap. Dorsally, the pterygoid bears a curved groove that received the pterygoid process of the palatoquadrate.

The vomer frames the entire lateral margin of the cultriform process. The posteromedial vomerine process bears a continuous row of teeth, much like in *Echinotriton* (Bolkay 1928). Only the medialmost margin of the choana is framed by the vomer; the remaining parts must have been continued by soft tissue as is usual in caudates. The midline suture of the vomers housed a large oval fenestra, set into a deep bowl-shaped depression. The vomers meet both anterior and posterior to this depression. The premaxilla and maxilla bear a continuous row of small, densely set teeth at the jaw margin, but the ventral shelves are much wider than the actual tooth arcade, forming a continuous suture with the vomer (premaxilla, anterior portion of maxilla).

The exoccipitals are well ossified and fail to meet in the midline. The condyles are clearly offset from the main body of

Fig. 4 *Chelotriton paradoxus* from Enspel and Randeck.
a Palate (SMNS 80210).
b, d Restoration of palate.
c Interpretative drawing of PW1996/5029-LS. **e** Restoration of skull in lateral view.
f Restoration of mandible in lingual (above) and labial view (below)



the element and well separated. The atlas is accordingly very broad and massive, projecting with a large odontoid peg between the exoccipital facets. The ventral surface of the exoccipital may be covered by dense pitting, much like the surface of the vertebral centra.

Mandible: The lower jaw is relatively robust when compared with other salamandrids. The dentary is relatively deep, also in the symphyseal region. It bears a series of grooves and pits on the ventral side. The tooth count in the dentary must have been around 50. The angular and surangular are broad and heavily ornamented, both along the flanks and ventrally. The surangular bears a set of 2–3 spikes resembling those of the quadratojugal in arrangement and size.

Hyobranchium: The hyobranchial apparatus of *Echinotriton* and *Tylotriton* was described by Wake and Özeti (1969). In *Chelotriton*, apparently only four elements were ossified, the basibranchial (copula), hypobranchial 1, and ceratobranchials 1

and 2. The basibranchial was short, apparently with elongate anterior and posterior continuations in cartilage. The hypobranchial is the largest bone, forming a stout and markedly curved rod with slightly expanded ends. Its extent of ossification varies between specimens in the Enspel sample, resulting in different length and proportions. The ceratobranchials are simpler than the hypobranchial, with a wide proximal end, a long and thin shaft, and an unexpanded distal end. The overall morphology of the preserved elements is consistent with that of *Tylotriton* and *Echinotriton* (Wake and Özeti 1969).

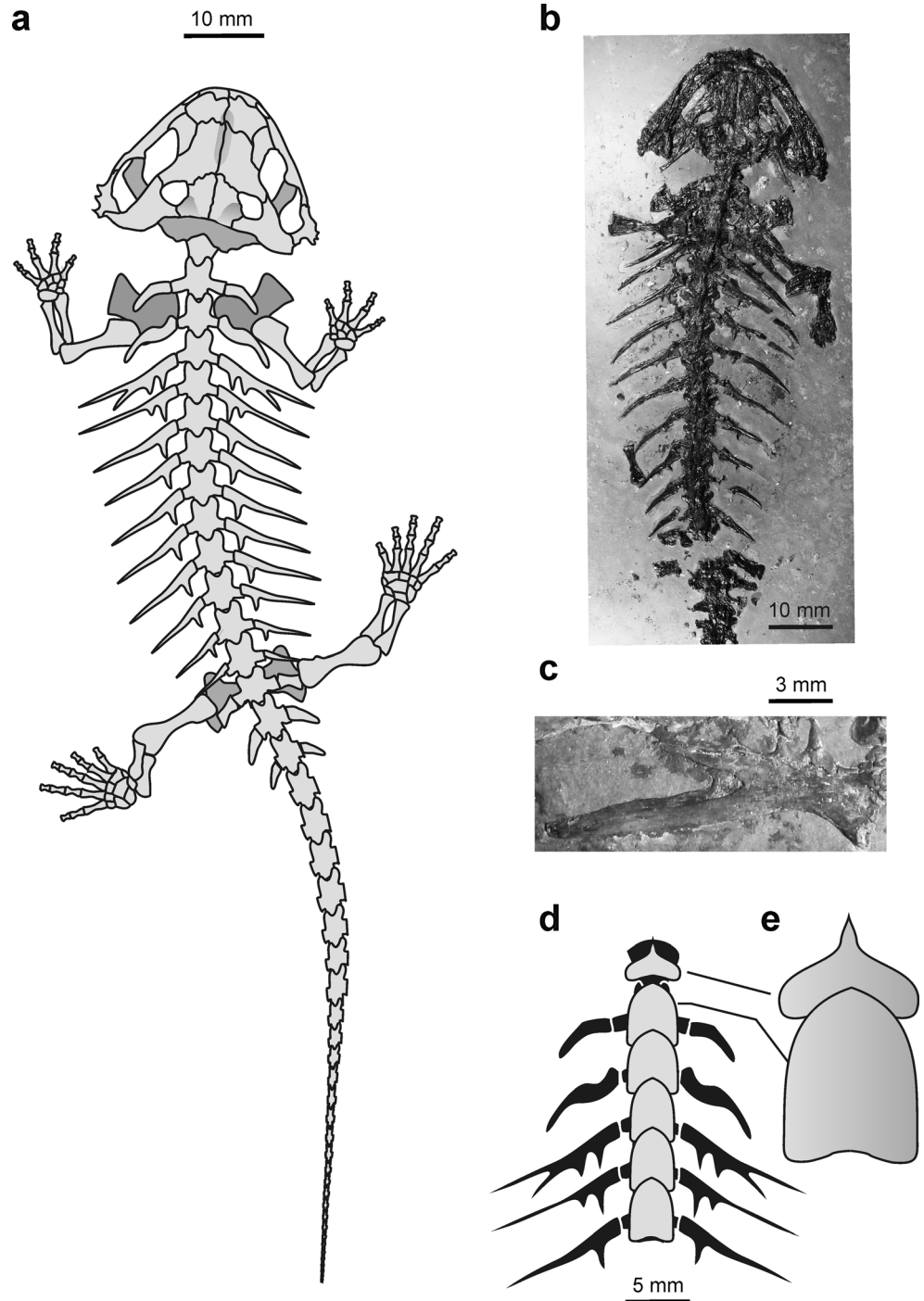
Axial skeleton: Consistently across the sample, 13 presacral vertebrae are present in the trunk. There are 37 caudal vertebrae, the last 20 being very small. The dorsal vertebrae are much more massive and broader than in other newts, closely resembling those of *Pleurodeles* (Haller-Probst and Schleich 1994). They are covered with densely pitted ornamentation both dorsally and especially ventrally.

The ribs are highly distinctive, but not always preserved well enough to show the presence, number, or outline of bifurcations and additional epipleural processes (spikes). The ribs of the second and third vertebra are simple without bifurcations, whereas the following trunk ribs are bifurcated or bear more or less distinct spikes. The 4th rib is the largest and most distinctive, bearing one or two spikes proximally that point dorsally, and a much longer posterodorsal spike that is nearly as wide as the

distal end of the rib itself. A very similar morphology was described by Nussbaum et al. (1982) in *Echinotriton*. The following ribs each bear one or two smaller spikes in the proximal half of the rib, variable in size and position. This morphology is consistent from the 5th through the 12th presacral rib. The caudal ribs are shorter and stouter and lack spikes.

Osteoderms: A single, median row of osteoderms covers all vertebrae from the atlas through to the 5th caudal (Fig. 5).

Fig. 5 *Chelotriton paradoxus* from Lake Enspel. **a** Restoration of skeleton. **b** PW2010/5000-LS. **c** Forked 4th rib of PW2001/5010-LS. **d** Restoration of anterior trunk with associated osteoderms. **e** Atlantal and axial osteoderms in articulation



Their length corresponds closely to that of the associated vertebra, whereas their width decreases continuously caudally. The anterior trunk osteoderms are substantially wider than in *Tylotriton* and *Echinotriton*. Their ornamentation closely resembles that of the dermal skull, with the Randeck specimen having higher tubercles than the Enspel sample. The first (atlantal) osteoderm differs from subsequent ones in being shorter and having a spike-like anterior projection. The axial and following osteoderms are anteriorly convex, overlapping the concave posterior margin of the preceding plate. The second and third osteoderm are the widest.

Girdles and limbs: The appendages are well ossified, with the ends of long bones fully formed and the carpal and tarsal elements largely complete. The pectoral girdle consists of a massive scapulocoracoid, which reaches about half the length of the humerus. It is more differentiated than in *Salamandra* (Francis 1934). The humerus is somewhat stouter than in *Salamandra* and has fully ossified proximal and distal ends. It bears a prominent deltoid process that is markedly offset from the shaft. In the carpus, the medial elements are poorly ossified or absent. The radius has a slightly asymmetrical, markedly broadened distal end, whereas the ulna is slightly curved and has a widened proximal head but no olecranon. The manus is much smaller than the pes, its phalangeal formula is: 2–3–3–3. The pelvic girdle is usually crushed and poorly preserved, apparently consistent with that of *Salamandra*. The femur bears a prominent fourth trochanter. It is substantially longer than tibia and fibula. The gently curved fibula is slightly longer than the straight and stout tibia. A full complement of tarsals is ossified, consistent in number and arrangement with those of *Salamandra* (Francis 1934). The foot is large, consisting of slender metatarsals and phalanges (2–3–4–4–3).

Discussion

Evolutionary history

The long evolutionary history of the Pleurodelinae (*Pleurodeles-Chelotriton-Tylotriton-Echinotriton*) has been highlighted by Noble (1928), Herre (1935), and Nussbaum et al. (1982). The available evidence suggests three evolutionary implications of different importance, each of which requires further work, both on neglected fossils and a more detailed morphology of the two extant genera *Tylotriton* and *Echinotriton*.

Westphal (1980) described a specimen from the Eocene Messel lake deposit, Germany, which he assigned to a new species, *Chelotriton robustus*. If this is in fact an early representative of *Chelotriton*—either an ancient species or population of *C. paradoxus*—then the genus would span a geological time of at least 31 Ma. The Enspel and Randeck localities alone extend over ~7 Ma.

The variation found in the present study—both between the Randeck and Enspel sample and within the Enspel sample—is considerable. One may rightly ask whether all the material belongs to the same species. However, the present paper forms only the first step in elucidating the morphological variation among *Chelotriton* across stratigraphy and between localities; any comprehensive analysis of variation would require inclusion of the many isolated elements available from *Chelotriton*, as well.

A second evolutionary implication that needs to be elucidated in detail is the question whether *Chelotriton* represents a lineage or clade separated from *Tylotriton* and *Echinotriton*, or whether it forms a grade towards both, or one of them. Nussbaum et al. (1982) have already raised this question, but their answer was shaped by incomplete knowledge of the morphology of *Chelotriton*. In particular, they emphasised differences between *Echinotriton* and *Chelotriton* that demonstrably do not exist, such as the supposedly unossified carpals and tarsals of *C. paradoxus*, which were, in fact, ossified.

Finally, knowledge of the interrelationships of the pleurodelines as a whole might be decisively influenced by the study of the various samples of *Chelotriton* and other genera falling into this clade.

Chelotriton, extant salamandrids, and palaeoecology

C. paradoxus appears to have been a common salamander in the periphery of the Randeck and Enspel lakes. Its presence in lake sediments does not necessarily mean that adults lived in the lake; they may have been washed in from peripheral habitats. However, the large number and the preservation of many more or less completely preserved adult specimens in Lake Enspel suggest a predominantly aquatic lifestyle. The apparently reversed reciprocal distribution of *Chelotriton* and fishes in the Enspel sequence furthermore supports this assumption, which had also been put forward by Roček and Wuttke (2010) based on their interpretation of the hyobranchial apparatus of *Chelotriton*. On the other hand, the presence of a supposed regurgitate (PW2001/5036-LS), possibly of bird origin (see Smith and Wuttke 2015, this issue) and containing *Chelotriton* bones, indicates that *Chelotriton* either populated shallow lake margins or was capable of excursions onto land where it fell victim to some unknown predator.

C. paradoxus is characterised by a strongly ossified skull and elongated ribs. Striking morphological similarities in these features identify *C. paradoxus* as a close relative to the extant Asian salamandrid genera *Tylotriton* and *Echinotriton* (see also Nussbaum et al. 1982).

Currently *Tylotriton* contains 19 nominal species, many of which are widely distributed across South Asia (e.g. Nussbaum et al. 1995, Stuart et al. 2010), whereas the two species of *Echinotriton* have highly restricted distribution areas in China (*Echinotriton chinhaiensis*, known from the type locality east of the city of Ningbo and two nearby valleys:

Xie et al. 2000) and Japan (*E. andersoni*, known from Okinawa and Anami, Ryukyu Islands: Kaneko and Matsui 2004).

Although the breeding biology of many *Tylotriton* species is still unknown, these salamanders apparently breed mostly in lotic waters (e.g. Roy and Mushahidunnabi 2001) or on land (Sparreboom et al. 2001). Typically, *Tylotriton* species have a biphasic amphibian life-cycle with an aquatic larval stage (Ziegler et al. 2008). In contrast, adults of both *Echinotriton* species are fully terrestrial and mate on land (Sparreboom et al. 2001). Females deposit large terrestrial eggs in close proximity to lentic water bodies (Xie et al. 2000). The larvae are washed out of the clutches during heavy rains into the nearby waters where they lead an aquatic life until metamorphosis.

The elongated ribs and epipleural processes known from fossil *Chelotriton paradoxus* shared with both living genera *Tylotriton* and *Echinotriton* have an adaptive significance. They are important morphological features of antipredator behaviours (Brodie et al. 1984). In *Tylotriton*, knob-like epipleural processes aid the ribs to elevate warts producing toxic mucous the animal assumes a rigid antipredator posture (Brodie et al. 1984), whereas the sharp tips and epipleural processes observed in *Echinotriton* penetrate through the skin (Brodie et al. 1984). Concluding from the shared features of anterior trunk ribs, a similar mechanism must have existed in *Chelotriton*. The hook-like spike in the cheek region of *Echinotriton* is associated with a bright-coloured gland, whereas *Chelotriton* bore a series of spikes, indicating the existence of a set of smaller glands rather than a large one as in *Echinotriton*. At any rate, the defence mechanisms shared by *Chelotriton* and the extant species also suggest similar defence behaviour in the extinct genus.

It may further be fruitful to study the morphological variation in the context of environmental parameters. To that end, the mode of distribution of morphotypes (random or clustered) would have to be analysed within the *Chelotriton* sample, and study how these might correlate with palaeoecological traits.

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