Notes on the cranium of the paedomorphic *Eurycea rathbuni* (Stejneger, 1896) (Urodela: Plethodontidae) with special regard to the dentition

Günter Clemen [1], David M. Sever [2] & Hartmut Greven [3]

[1] Doornbeckeweg 17, D-48161 Münster, Germany
gclemen(at)web.de

[2] Department of Biological Sciences, Southeastern Louisiana University, Hammond, LA 70402
dsever(at)selu.edu

[3] Institut für Zoomorphologie und Zellbiologie der Heinrich-Heine-Universität Düsseldorf, Universitätsstr.1,
D-40225 Düsseldorf, Germany
grevenh(at)uni-duesseldorf.de (corresponding author)

> ## Abstract

We illustrate the skull, the lower jaw, and especially the dentition of the highly specialized troglobitic salamander *Eurycea rathbuni* using cleared and stained specimens, scanning electron microscopy, and a few histological sections. Arrangement of the skeletal elements corresponds to earlier descriptions. Dentigerous bones are the fused premaxillae, the vomeres, the palatinal portions of the palatopterygoid in the upper jaw and palate, and the dentaries and coronoids in the lower jaw. Each bone bears a single row of teeth, which are especially numerous and small on the premaxillae and dentaries. Generally, teeth are monocuspid and most are recurved. The dividing zones are unrecognisable to slightly distinct, but do not reach the fully transformed state. Absence or only traces of pedicellation, monocuspidity and an enlarged base are typical for urodele teeth in a relative early stage of development.

> ## Kurzfassung

Wir stellen Schädel, Unterkiefer und vor allem die Bezahnung des pädomorphen, troglobionten Schwanzlurches *Eurycea rathbuni* anhand von Aufhellungspräparaten, Rasterelektronenmikroskopie und einigen histologischen Schnitten dar. Die Anordnung der einzelnen Skelettelemente entspricht früheren Beschreibungen. Zahntragende, mit einer einzigen Zahnzeile bestückte Knochen sind im Oberkiefer und Gaumen die mittig fusionierten Prämaxillaria, die beiden Vomeres sowie die beiden palatinalen Abschnitte der Pterygopalatina und im Unterkiefer die beiden Dentalia sowie die beiden Coronoide. Prämaxillaria, und Dentalia sind mit auffallend vielen kleinen Zähnen besetzt. Alle Zähne sind monocuspid und homodont. Eine Ringnaht, die den Zahnsockel von der Krone trennt, ist entweder nicht zu erkennen oder mehr oder weniger angedeutet, erreicht aber nirgends das Aussehen von Ringnähten „metamorphosierter" Zähne. Die Verankerung der Zähne ist je nach zahntragendem Knochen leicht pleurodont oder akrodont. Einspitzige Zähne mit breiter Basis, denen die Ringnaht fehlt oder bei denen sie nur angedeutet ist, sind für relativ frühe Larvenstadien von Urodelen charakteristisch.

Introduction

During amphibian metamorphosis, which is considered as a heterochronic process and a period of temporal concentrated development (e.g., Alberch, 1989), the cranial skeletal tissues undergo a wide range of morphogenetic responses. The variation in the temporal sequence of metamorphic events may be caused by a differential sensitivity of tissues to and their response at different concentration of thyroxin. Further, response specifity may also be directly conferred by epigenetic interactions (see Rose, 2003, and references therein). Remarkable changes are known in the tooth systems of Urodela, i.e., the various dentigerous

bones, their accompanying dental laminae and their dentition and include here the complete loss of larval elements (e.g., the palatal and coronoid systems), the *de novo* condensation and differentiation of adult elements (e.g., vomer and vomerine bar in salamandrids), and changes in the shape, size and/or positions of elements (e.g., tooth bearing bones and dentition) (e.g., Clemen 1979 a, b; Clemen & Greven, 1994; Davit-Béal *et al.*, 2006, 2007).

With respect to the dentition, one of the most apparent changes is the sudden shift from monocuspid teeth in larvae to basically bicuspid teeth in transformed specimens and the progressive development of an annular dividing zone, which finally separates the dentine crown from the basal pedicel in transformed specimens ("pedicellate condition"; for further dentitional modifications see Davit-Béal *et al.*, 2006, 2007, and references therein). At least the sudden change from monocuspid to bicuspid teeth is correlated with metamorphosis and directly or indirectly dependent on thyroxin (Greven & Clemen, 1990).

However, several paedomorphic Urodela (for definition of paedomorphosis see Gould, 1977; Duellman & Trueb, 1986), tend to acquire metamorphic traits leading to a "partial" metamorphosis. They may retain non-pedicellate, monocuspid teeth (e.g., Sirenidae: *Siren lacertina; Pseudobranchus striatus*: Clemen & Greven, 1988), monocuspid teeth with an incipient dividing zone (e.g., Proteidae: *Necturus maculosus*: Greven & Clemen, 1979; Plethodontidae: *Eurycea neotenes*: Clemen & Greven, 2000) suggesting "interruption" of the normal developmental sequence of the teeth at different levels or may develop bicuspid, i.e., "transformed" teeth (e.g., Cryptobranchidae: *Andrias* spp.: Greven & Clemen, 1980; *Cryptobranchus alleganensis*: Greven & Clemen, 2009; Amphiumidae: *Amphiuma means*: Clemen & Greven, 1980) or depending on the tooth system even monocuspid and bicuspid teeth (Ambystomatidae: *Ambystoma mexicanum*: Clemen & Greven, 1977; Bolte & Clemen, 1991), which suggests differential sensitivity to thyroxin.

Several species of *Eurycea*, a genus widely distributed in eastern and south-central North America, are either facultatively or obligatorily paedomorphic and some may respond to thyroxin application (Kezer, 1952; for further readings see Sweet, 1997). Precocious maturation (=progenesis) has been suggested as the principal heterochronic process leading to paedomorphosis in *E. neotenes* (Bruce, 1976). *E. rathbuni* from the Edwards Plateau in central Texas is a troglobitic blind member of a clade formerly named *Typhlomolge* (e.g., Hillis *et al.*, 2001; Larson *et al.*, 2003), with the conservation status of "vulnerable" (IUCN Red list 2008). It is considered as an extreme case of paedomorphosis and cave adaptation (Duellman &

Trueb, 1985). A response of *E. rathbuni* to thyroxin application has been reported by Dundee (1957; see, however, Gorbman, 1957).

The general anatomy including the skull and the lower jaw of *E. rathbuni* was described by Emerson (1905), and some of her results were discussed by Hilton (1945). Wake (1966) gave a detailed description of the osteology of "*Typhlomolge*" spp. on the basis of a single female (and three females of the related *T. tridentifera*), but did not add specific drawings. Potter & Sweet (1981) presented new data on skull morphology (e.g., innervation pattern, deformation grids of the skull and teeth numbers). However, a more detailed analysis of the tooth systems of *E. rathbuni* is missing.

In this note we present some new drawings of the cranium, but omit the hyobranchium, which was incomplete in our material, and then focus on the various tooth systems and the detailed description of the teeth of *E. rathbuni*.

Material and methods

The *Eurycea rathbuni* were collected at various dates at San Marcos, Hays County, Texas, and were used in a previous study by Sever (1985). Specimens varied from 50.1–54.5 mm snout-vent length, fixed *in toto* in 10% neutral buffered formalin, rinsed in water, and stored in 65% ethanol prior to dissection. Material included skulls and lower jaws of a male (no. 5929) and a female (no. 5031), the skull of a female (no. 5031), and serial sections (7 µm thick) of the skull of a further female (no. 5932) stained with Azan, PAS, AB pH 1.0 and AB (pH 2.5)-PAS. We used the DIC (Nomarski) technique for visualizing the relevant structures due to the poor staining.

First, the skulls were stained *in toto* with Alizarin-Red S in 50% ethanol to visualize the teeth. Then, skulls were photographed, fixed again in buffered formalin after Lillie (Romeis, 1989) for several days, cleared and stained with Alcian blue and Alizarin-Red (Park & Kim, 1984) and stored in glycerol. The resulting preparations were drawn to scale. Thereafter the dentigerous bones were excised and transferred into an enzyme solution of 30 ml saturated aqueous sodium borate, 70 ml distilled water and 1 g pancreatin for several days to remove the soft tissue. This was not fully successful in all cases due to the long store in ethanol. The isolated delicate bones were dehydrated, critical point dried sputter-coated with gold and viewed in a SEM (Hitachi S-539).

Table 1. Number of tooth loci on the dentigerous bones on the right and left side of three specimen of *Eurycea rathbuni*; co coronoid; d dentary; pl palatinum; pm premaxilla; v vomer.

	right: v/pl	left: v/pl	right: d/co	left: d/co	right: pm	left : pm
5929 ♂	16/15	16/14	42/15	42/15	25	24
5930 ♀	16/14	16/15				
5931 ♀	16/14	16/14	43/14	43/13	23	24

Results

Skull morphology

Fig. 1 a–d

Our drawings of the skull and the lower jaw of male 5929 (Fig. 1 a–c) and female 5931 (Fig. 1 d–f) correspond to a large extent to the detailed description of EMERSON (1905; see also WAKE 1966). The slight differences between the male and the female primarily concern size. Therefore, and because the drawings are largely self-explaining, we give only a very short account primarily on the tooth bearing elements.

In both sexes the anterior portion of the skull is extremely broad and depressed.

The dorsal aspect (Fig. 1 a, d) shows primarily some chondrocranial elements (the cartilaginous *solum nasale*, tectum synoticum, and otic process of the palatoquadrate and the osseous the occipito-otic complex and quadrate) and from anterior to posterior the ossified elements of the dermatocranium (the premaxillae with their broad dorsal processes separated for their entire length, the frontals, the parietals, the squamosal and the pterygoid).

The ventral aspect (Fig. 1 b, e) shows chondrocranial elements (*solum nasale*, the otic process of the palatoquadrate, occipito-otic complex, quadrate) and the dermatocranial elements, i.e., premaxillae (maxillae are absent) fused to a single element, which bears a slightly curved *pars dentalis* with a single tooth row, and the large adjacent parasphenoid with its bilobed anterior region. Laterally of the parasphenoid project the vomeres, the palatopterygoids and squamosal. The vomeres form broad *partes palatinae* and exhibit anterior processes attaching them to the premaxillae. Vomeres approach anteriorly, but do not touch each other and are separated widely from each other posteriorly. Their lateral (labial) and anterior margins bear a single row of teeth.

The relatively large palatopterygoids abut posteriorly on the anterior border of the otic process of the palatoquadrate and articulates mediodorsally with the parasphenoid and anteriorly with the vomer. The anterior expanded portion of the palatopteygoids, the palatine, bears labially a single row of teeth, which is continuous with the row of vomerine teeth. The narrower posterior part, the pterygoid, is edentulous. The latter articulates with the quadrates.

The lower jaw (Fig. 1 c, f) is composed of the dentaries, which both form a broadly rounded arch. The prearticular invests the lingual side of the Meckel's cartilage (Fig 2 a, b). A small coronoid is present at the inner margin of each dentary overlying the prearticular.

Dentigerous bones and dentition

General aspect and histology. The ventral view of the upper skull shows a continuous row of small teeth (plus replacement teeth) on the premaxillary arcade. Posteriorly a second row of larger teeth extends from the middle of the mouth roof to posterior optic region on each side. This row includes the vomerine and the palatinal teeth. Vomeres are separated medially of each other; a gap between the vomerine and the palatinal row is hard to recognize (Fig. 2 a). A single row of likewise small teeth is present also on the dentaries and coronoids. Dentaries are clearly separated in the middle and tooth rows are bent slightly inwards (Fig. 2 b). The number of tooth loci counted on the various dentigerous bones is shown in table 1.

Although of modest quality, histological sections reveal dental laminae accompanying the tooth rows at their posterior face. Premaxillae have a single, continuous dental lamina (Fig. 2 g), whereas dentary, coronoid, vomer and palatine have their own dental lamina each (not shown). The transition between the posterior end of the vomer and the anterior tip of the palatine is shown in figures 2 c–f. The gap between the bones contains some bony tissue, but no dental lamina (see below) (Fig. 2 e).

Shape and attachment of teeth: Dentition is homodont and teeth are invariably monocuspid. Teeth of the premaxillae, dentaries, and coronoids are largely similar in size. They are juxtaposed with a narrow space, attached in a slight pleurodont (premaxillae, dentaries) or acrodont condition (coronoids and the posterior teeth of premaxillae) to the bone, and tooth height decreases slightly posteriorly (Fig. 3 a, b, f). Posterior teeth possess relatively enlarged bas-
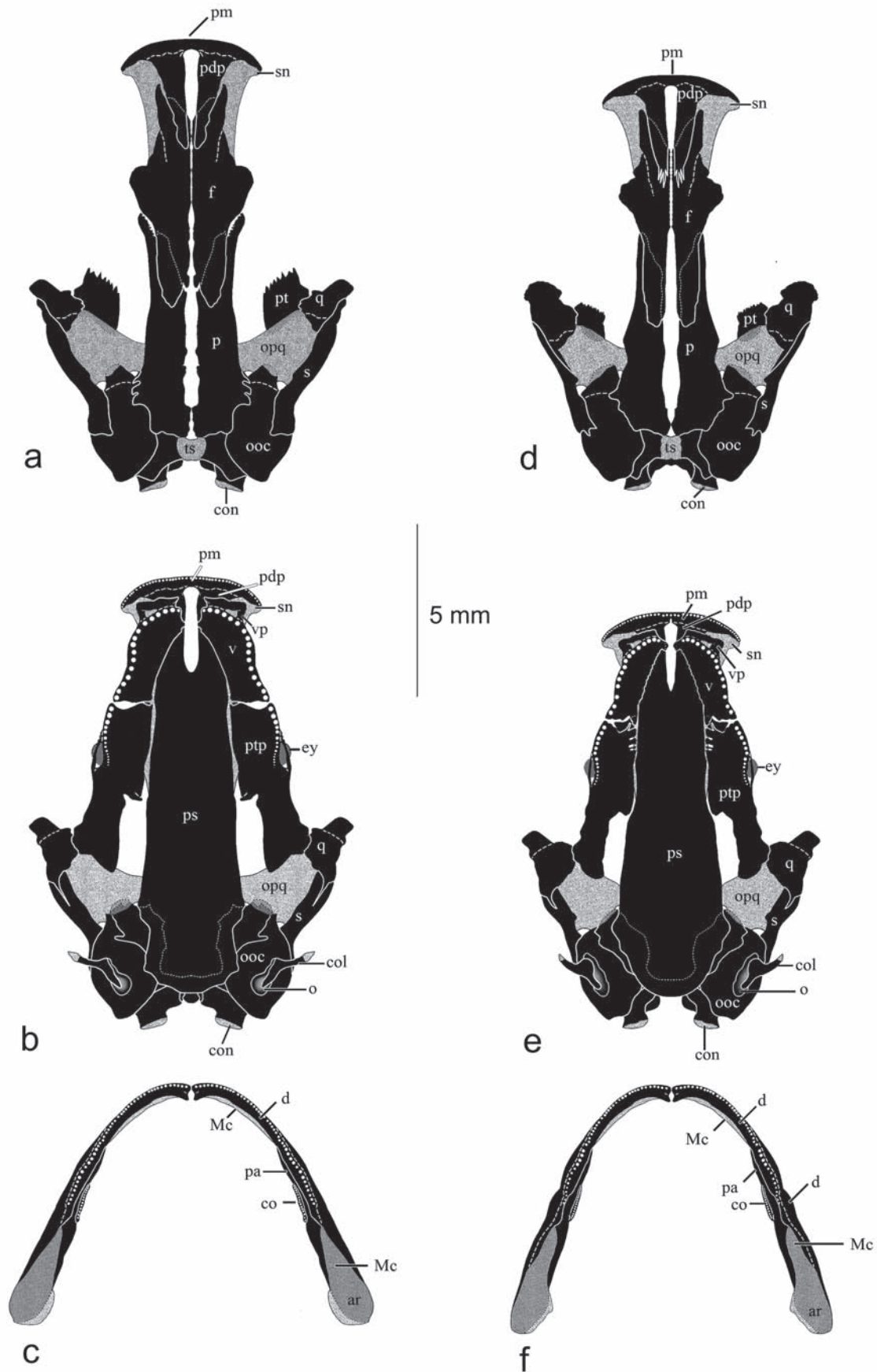
Fig. 1 a–f. The skull and lower jaw of *Eurycea rathbuni*. Male, dorsal (**a**) and ventral (**b**) view of the skull and dorsal view of the upper jaw (**c**). The same of the female (**d**, **e**, **f**). Abbreviations: **ar** articular; **co** coronoid; **col** columella; **con** condylus; **d** dentary; **ey** eye; **f** frontal; **Mc** Meckel's cartilage; **o** operculum; **ooc** occipito-otic complex; **opq** otic process of the palato-quadrate; **p** parietal; **pa** prearticular; **pdp** *processus dorsalis praemaxillaris*; **pm** premaxilla; **ps** parasphenoid; **ptp** palatopterygoid; **pt** pterygoid; **q** quadrate; **s** squamosal; **sn** *solum nasale*; **ts** tectum synoticum; **v** vomer; **vp** vomerine process.
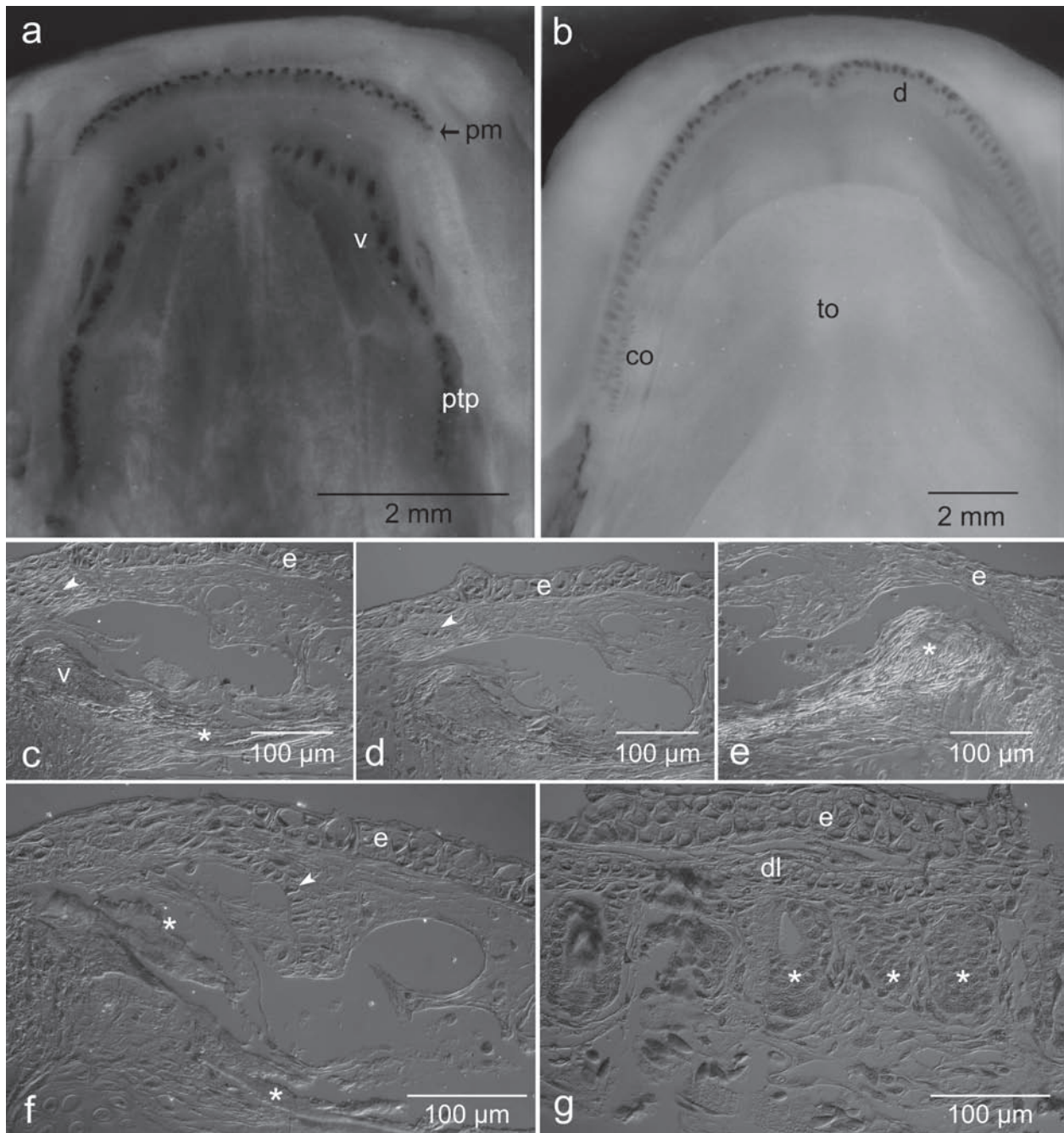
Fig. 2 a–d. Mouth roof (**a**) and floor (**b**) of a female *Eurycea rathbuni*. Abbreviations see fig. 1. Tongue (to). Head stained *in toto* with Alizarin Red. **c–f** sections of a series showing the vomerine-palatinal transition. **c** Posterior end of the vomerine dental lamina (arrowhead); vomer (v) and *pars palatina* of the vomer (asterisk). **d** The vomerine dental lamina (arrowhead) terminates in the connective tissue without contact to the oral epithelium (oe). **e** Gap between vomer and palatine without a dental lamina, but with bony material (asterisk). **f** Dental lamina of the palatine dental lamina (arrowhead); palatine (asterisk). **g** Transversal section showing the midst of premaxillae (arrowhead), tooth buds (asterisks) and a continuous dental lamina (dl). Oral epithelium (e).

es (Fig. 3e). Each tooth is a relatively simple cone with a more or less sharply pointed apex, which is recurved lingually except the most posterior teeth of the dentaries and premaxillaries and most teeth of the coronoid (Fig. 3 c, h). In some preparations remnants of the enamel cap are visible (Fig. 3 h). The basal component (the prospective pedicel) is weakly demarcated from the dentine cone (crown). A demarcation line (dividing zone) is indicated by an irregular surface, e.g., seen as slight external annular incision broader lingually than labially and/or as a more fibrous zone (Figs. 3 c–d, e, g–i). This zone is located approximately at mid-height of the tooth shaft. (Fig. 3 f, h) or deeper (Fig. 4 e). A prominent pulpal opening is located on the lingual face of the basal component of the teeth (Fig. 3 b).

Teeth of the mouth roof are located on the vomeres and palatines. Vomerine teeth are approximately 60 %
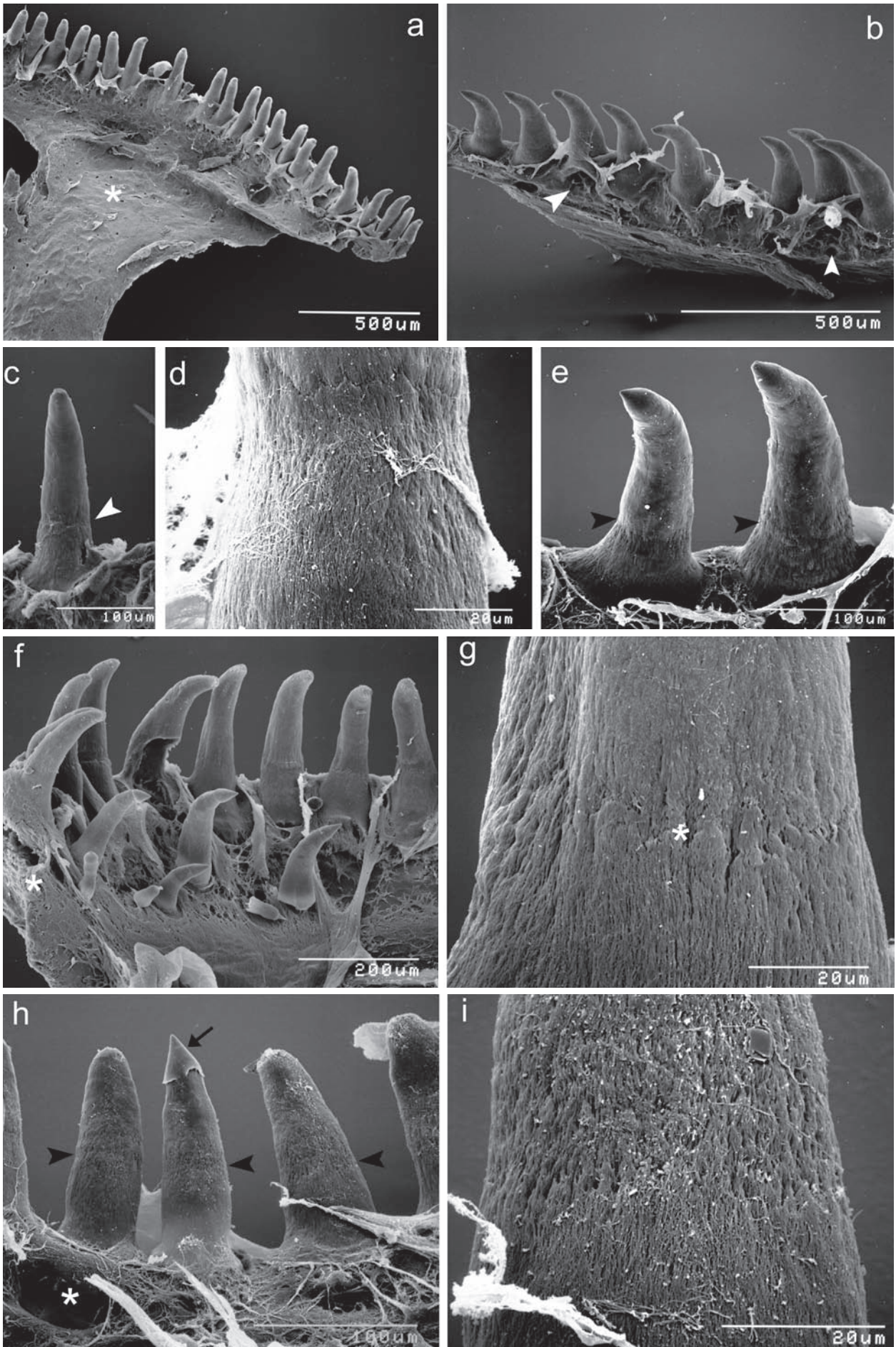
larger than the largest premaxillary, dentary and palatinal teeth (this estimation refers to the lingual face, because premaxillary teeth have reduced pedicel labially). Vomerine teeth decrease slightly and palatinal teeth decrease more markedly in height posteriorly (Figs. 4 a, b, d). The smallest teeth are found on the posterior end of the palatines (Fig. 4 a, b, d, e). The border between the posterior end of the vomer and the anterior region of the palatine appears variable. In both cases examined by SEM the *partes palatinae* appear to be fused together to some extent (Fig. 4 a, b). In the male a (artifactual?) fissure was seen between the two bones (Fig. 4 a) and in the female a gap occurred in the tooth row (Fig. 4 b), bridged by a replacement tooth (Fig. 4 c). In a third preparation the tissue could not be removed completely leaving a strand of fibrous connective tissue along and between the vomerine and palatinal tooth row. This gives strong evidence that the dental laminae of both systems are separated (Fig. 4 d).

The *pars dentalis* of the vomer is located at the outer margin of the bone, is slightly elevated and possesses large openings at its lingual face (Fig. 5 a). Teeth are recurved inwards and show a broad demarcation line between the base (=pedicel) and dentine shaft (Fig. 5 b, c). The latter is two or even three times higher as the pedicel. Teeth are attached horizontally to the bone over a wide contact area (Fig.5 a, c). Openings at the lingual face of the *pars dentalis* grant access to the pulp cavity (Fig. 4 b, d, 5 a).

The anterior teeth of the palatine are recurved and larger than more posterior teeth. Posterior teeth stand almost upright on a moderately elevated *pars dentalis* (Fig. 4 e, 5 f, g). Depending on the position of teeth, a demarcation line between pedicel and dentine shaft is more or less visible (Fig. 5 d, e) or practically absent (Fig. 5 f, g) as in the most posterior teeth (Fig. 5 f, g). Openings, which communicate with the pulp cavity, are at the lingual face of the palatinal *pars dentalis* (Fig. 4 e). In the female, there is some evidence for partial bistichy, i.e. teeth are arranged in two rows (Fig. 5 f).

Discussion

Our illustrations of the cranium of *Eurycea rathbuni* correspond with previous descriptions of this species (EMERSON, 1905; HILTON, 1945; WAKE, 1966) and largely with those known from other paedomorphic and larval *Eurycea* species (e.g., WILDER, 1925; STADTMÜLLER, 1936; WAKE, 1966; CLEMEN & GREVEN, 2000). All these authors emphasize the typical larval condition in *E. rathbuni*.

However, comparison with various *Eurycea* spp. showed that in *E. rathbuni* the anterior portion of the skull is extremely broad and depressed. Proportionally most modified are the anterior cranial elements including elongation of the premaxillae, frontal, vomers and palatopterygoids (for details and deformation grids see MITCHELL & SMITH. 1965; POTTER & SWEET, 1981). This becomes apparent in our drawings, too. In addition, WAKE (1966: 28) observed that in the elongate gill arches, "the ceratobranchial arms swept posteriorly and make considerably smaller angles with each other than in other genera."

Our findings reveal only slight differences in size and proportions between males and females, i.e., a noticeable sexual dimorphism in cranial elements is not obvious in *E. rathbuni* (for some possibly sexually dimorphic skeletal traits in *Eurycea neotenes*, see CLEMEN & GREVEN, 2000).

The number of tooth systems in *E. rathbuni* is unsurprisingly the same as in other larval urodeles. Tooth systems comprise the premaxillary system (premaxillae are fused into a single element) accompanied by a continuous dental lamina, the paired dentaries and coronoids, and the paired vomerine and palatinal systems. Each of the paired bones has its own dental lamina (for review see CLEMEN & GREVEN, 1994). Although vomerine and palatinal portion of the palatopterygoid are very closely adjoined in *E. rathbuni* and seemingly bear a continuous row of teeth as drawn by EMERSON (1905) and HILTON (1945), the preservation of the fibrous connective tissue accompanying the in-

Fig. 3 a–i. Dentition of the premaxillae (a-e), dentary (f, g) and coronoid (h. i). **a** Premaxilla, female (left side), lingual, with a single continuous tooth row; *processus dorsalis praemaxillaris* (asterisk). **b** Premaxilla, male (right side), labial; note pulpal access (arrowhead) and curvature of teeth. **c** Straight premaxillary tooth, male, lingual with dividing zone (arrowhead). **d** Premaxillary tooth, male, lingual; a dividing zone is practically not existent. **e** Posterior premaxillary teeth with broad base, male, lingual. Note the different appearance of the dividing zone (arrowheads). **f** Dentary, female, medio-lingual aspect; the anterior rows are replacement teeth; symphysis (asterisk). **g** Dentary tooth, female, lingual; hinted dividing zone (asterisk). **h** Posterior coronoid teeth, female, lingual, with a slightly developed dividing zone (arrowheads) and enamel cap (arrow); pulpal access (asterisk). **i** Coronoid, female, lingual, detail of the dividing zone.
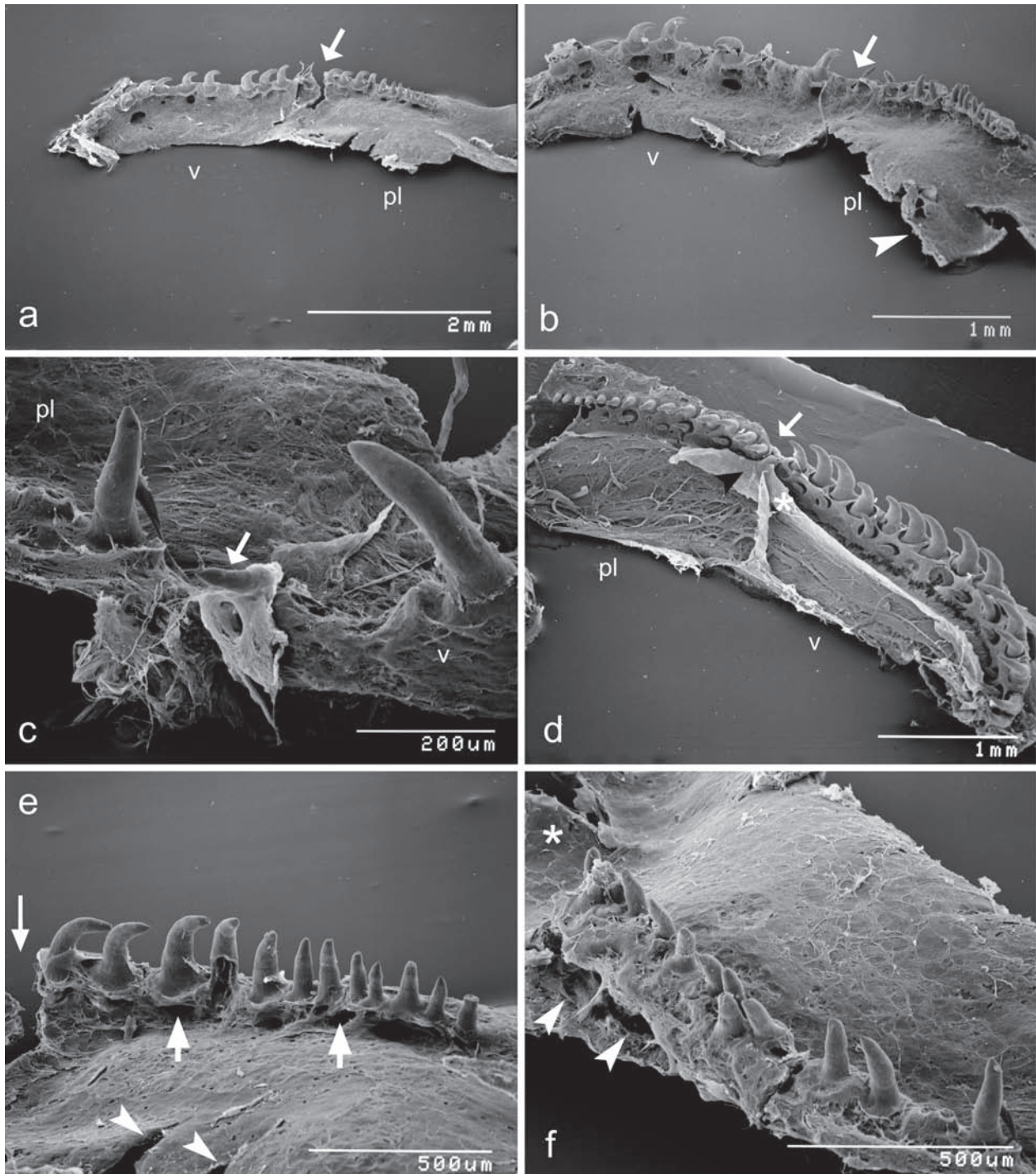
Fig. 4 a–f. Bones and dentition of the palate. **a** Vomer (v) and palatinum (pl), left side, male, lingual; fissure between the single row of teeth (arrow), but not between the *partes palatinae* (in front). **b** Vomer (v) and palatinum (pl) left side, female; gap between the tooth row (arrow); the *partes palatinae* (in front) are fused. **c** Fused vomer (v) and palatinum (pl) left side, labial, female; replacement tooth (arrow) in the area, where both bones appear connate. **d** Vomer (v) and palatinum (pl) right side, male, lingual; the connective tissue attached lingually to the dental lamina is retained during preparation and separates vomerine and palatinal dental lamina (arrowhead). **e** Palatinum, left side, male. The *pars palatina* shows notches (arrowheads) and a fissure towards the vomer (large arrow). Openings to the pulp cavity (small arrows). **f** Palatine right side, female, labial, and transition to the pterygopalatinal bony bridge (asterisk); large accesses to the pulp (arrowheads).

ner faces of and filling the gap between dental laminae proves the presence of two dental laminae. In the SEM preparations only a small fissure indicates the border between the two bones, and further details are partly obscured by remnants of adhering soft tissue.

Also, histological sections reveal some bony tissue between vomer and palatopteygoid indicating partial fusion. We noted a similar fusion in old-aged paedomorphic *Ambystoma mexicanum* (unpublished observations).

To our knowledge, studies on the dentition of *E. rathbuni* are limited to counts of teeth. Our own counts (in brackets behind the numbers given from literature) slightly exceed the values given in literature. Number of teeth varied from 20 to 40 (47–49) on the premaxillae, from 30 to 31(32) on the vomers, 21 (29) on the palatopterygoids, 71 (84–86) on the dentaries, and 26 (27–30) on the coronoids (e.g., EMERSON, 1905; HILTON, 1945) with the highest values (means of six specimens of 50–57 mm standard length) noted by POTTER & SWEETS (1981). The number of at least the premaxillary teeth increases during ontogeny (BRANDON, 1971). The comparably high numbers counted by us strongly suggest that our specimen were adult. Previous authors did not distinguish between sexes, but judging from our (few) data, a sexual dimorphism in the number of teeth does probably not exist. The number of premaxillary and lower jaw teeth exceeds that of other *Eurycea* spp. (MCBRIDE STEWART, 1958; BRANDON, 1971; CLEMEN & GREVEN, 2000). The high numbers as well as the modified anterior cranial elements (see above) of *E. rathbuni* have been interpreted as adaptations to the living space and feeding of these salamanders. Generally, the specialisations described may increase efficiency in catching and holding prey that is sparsely distributed in the environment the animals live (see BAKER, 1957).

Teeth of premaxilllae, dentaries and coronoids are small and similar in size in both the male and the two females of *E. rathbuni*. This contrasts to the paedomorphic *E. neotenes*, where males have longer teeth, mainly on the premaxillae (CLEMEN & GREVEN, 2000). A much more pronounced sexual dimorphism regarding size and number of teeth is known from transformed plethodontids, where the fewer premaxillary and dentary teeth change from bicuspidity to a (secondary) monocuspidity under the influence of androgens (e.g. MCBRIDE STEWART, 1958; for further reading see GREVEN *et al.*, 2004).

All dentigerous bones of *E. rathbuni* bear a single row of teeth. In one specimen the palatine had two teeth closely adjoined at its anterior end, which may indicate previous bi- or polystichy (teeth are arranged in two or several rows). In the larvae of transforming urodeles, fully developed coronoids and palatines are toothed with multiple rows of teeth at first and this polystichy is then reduced to a single row of teeth (monostichy) and finally the remaining teeth and the bones are resorbed (e.g., HERTWIG, 1874; WILDER, 1925). Actually, disintegration of the palatopterygoids, namely its median portion (bony bridge of the pterygoid and palatine), was considered as an early indication of the onset of metamorphosis (e.g., WILDER 1925; REILLY, 1986; REILLY & ALTIG, 1996), but this process very probably has to be proceeded by the disintegration of the respective dental lamina. The same holds for the coronoids.

Palatopterygoids and coronoids of our *E. rathbuni* specimens did not show any signs of degradation, and their dental laminae appear to be intact (not shown), but bear a single tooth row each. Early larval stages of most plethodontids with free-living larval stages possess tooth patches on their palatines and coronoids that later become a single row (e.g., *Typhlotriton nereus* up to 36 mm total length BRANDON, 1966; some *Eurycea* spp.: BRANDON, 1971; MUTZ & CLEMEN, 1992). However, in several troglobites including some *Eurycea* spp. BRANDON (1971) noted a single row of palatinal teeth even in the smallest specimens he examined. Brandon (1971) reported that snout-vent lengths of the smallest specimens were 32 mm (*E. rathbuni*), 25 mm (*E. tridentifera*) , and 26 mm (*E. troglodytes*). Either BRANDON's specimens were already in late stage larvae or two patterns of palatinal (and perhaps coronoid) dentition in plethodontids are realized, i.e., exclusive monostichy or monostichy proceeded by polystichy. The vomer of *E. rathbuni* generally has the larval form with a broad *pars palatina*, and bears a single row of teeth, a condition that is realized very probably from the beginning (WILDER, 1925; MUTZ & CLEMEN, 1992). However, contrary to larvae, in which teeth are located in the middle of the vomer, teeth in *E. rathbuni* are shifted to the anterior margin of the vomer. This trait might be considered as typical for a more advanced larval stage.

During ontogeny urodele teeth change from small, conical and straight, and undivided to most often bicuspid, more or less curved, and divided. Transition to bicuspidity appears abrupt, whereas the zone of division, size and curvature develops gradually. At least the development of elaborated cusps is a thyroxin-dependent process, whereas triggers of the formation of the zone of division are unknown (e.g., for review see GREVEN, 1989; CLEMEN & GREVEN, 1994; DAVIT-BÉAL *et al.*, 2006)

The teeth of *E. rathbuni* largely resemble "early larval" teeth being monocuspid without a dividing zone or only with traces of such a zone. Traits arguing for a development further than "normal larvae" are the size, and curvature and the fact that the palatinum, which in transforming Urodela normally degrades at a developmental stage, in which teeth are conical without a zone of division (CLEMEN & GREVEN, 1994), bears recurved teeth with traces of a dividing zone.

Although not thoroughly studied, the pattern of attachment changes during development. DAVIT-BÉAL *et al.* (2006) have shown that the first generation of dentary teeth have an enlarged base attached to the upper surface in nearly horizontal (acrodont) fashion, whereas the next generations are attached to the developing labial wall of the bone, in a pleurodont
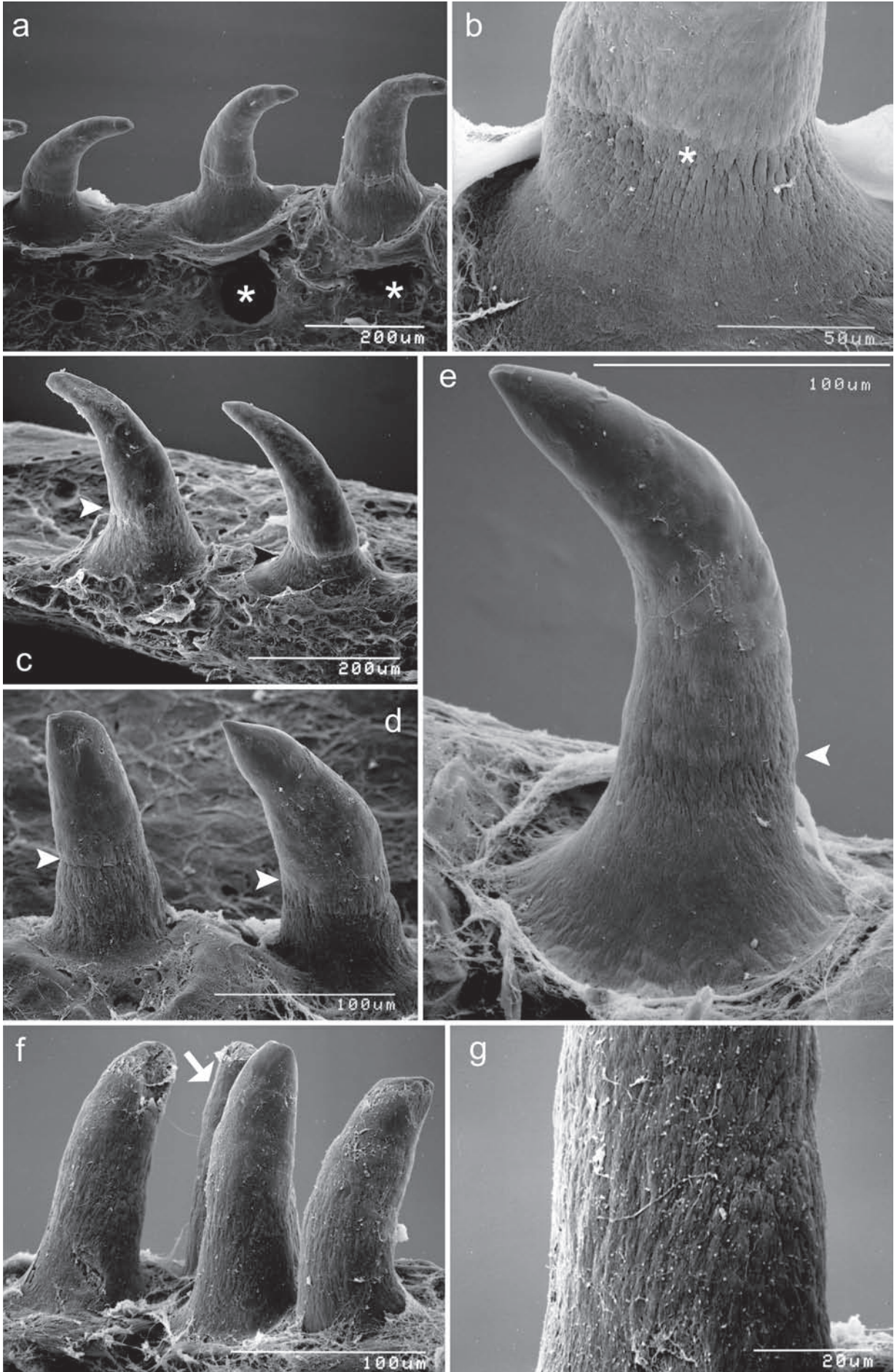
fashion. This holds very probably also for the upper jaw dentition. On the vomeres and palatines repeated dentitions may cause an elevation of the *pars dentalis* and, thus, occasionally a slight pleurodont attachment (see the discussion in Greven et al., 2006).We think that the attachment of teeth over a broad contact zone, i.e., with an enlarged base, as seen in the teeth of *E. rathbuni* can be considered as juvenile trait.

Acknowledgements

References

Alberch, P. (1989): Development and the evolution of amphibian metamorphosis. – In: Splechtna, H. & Hilgers, H. (eds.): Trends in Vertebrate Morphology. – Gustav Fischer Verlag, Stuttgart, pp. 163–173.

Baker, J. K. (1957): *Eurycea troglodytes*: a new blind cave salamander from Texas. – Texas Journal of Science, **9**: 328–336.

Bolte, M. & Clemen, G. (1991): Die Zahnformen des Unterkiefers beim adulten *Ambystoma mexicanum* Shaw (Urodela: Ambystomatidae). – Acta Biologica Benrodis, **3**: 171–177.

Brandon, R. A. (1966): A reevaluation of the status of the salamander, *Typhlotriton nereus* Bishop. – Copeia, **1966**: 555–651.

Brandon, R. A. (1971): North American troglobitic salamanders: some aspects of modification in cave habitats, with special reference to *Gyrinophilus palleucus*. – Bulletin of the National Speleological Society, **33**: 1–21.

Bruce, R.C. (1976): Population structure, life history and evolution of pedogenesis in the salamander *Eurycea neotenes*. – Copeia, **1976**: 129–137.

Clemen, G. (1979a): Beziehungen zwischen Gaumenknochen und ihren Zahnleisten bei *Salmandra salamandra* (L.) während der Metamorphose. – Wilhelm Roux's Archives, **185**: 19–36.

Clemen, G. (1979b): Untersuchungen zur Bildung der Vomerspange bei *Salamandra salamandra* (L.). – Wilhelm Roux's Archives, **185**: 305–321.

Clemen, G. & Greven, H. (1977): Morphologische Untersuchungen an der Mundhöhle von Urodelen. III. Die Munddachbezahnung von *Ambystoma mexicanum* Cope (Ambystomatidae: Amphibia). – Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere, **98**: 95–136.

Clemen, G. & Greven, H. (1980): Morphologische Untersuchungen an der Mundhöhle von Urodelen. VII. Die Munddachbezahnung von *Amphiuma* (Amphiumidae: Amphibia). – Bonner zoologische Beiträge, **31**: 357–362.

Clemen, G. & Greven, H. (1988): Morphological studies on the mouth cavity of Urodela. IX. Teeth of the palate and the splenials in *Siren* and *Pseudobranchus* (Sirenidae: Amphibia). – Zeitschrift für zoologische Systematik und Evolutionsforschung, **26**: 135–143.

Clemen, G. & Greven, H. (1994): The buccal cavity of larval and metamorphosed *Salamandra salamandra*: Structural and developmental aspects. – Mertensiella, **4**: 83–109.

Clemen, G. & Greven, H. (2000): Dentigerous bones and dentition in the paedomorphic plethodontid salamander *Eurycea neotenes*. – Alytes, **18**: 51-61.

Davit-Béal, T., Allizard, F. & Sire, J.-Y. (2006): Morphological variations in a tooth family through ontogeny in *Pleurodeles waltl* (Lissamphibia, Caudata). – Journal of Morphology, **267**: 1048–1065.

Davit-Béal, T., Chisaka, H., Delgado, S. & Sire, J.-Y. (2007): Amphibian teeth: current knowledge, unanswered questions, and some directions for future research. – Biological Reviews, **82**: 49–81.

Duellman, W. E. & Trueb, L. (1986): Biology of Amphibians. – McGraw-Hill, New York, 670 pp.

Dundee, H. A. (1957): Partial metamorphosis induced in *Typhlomolge rathbuni*. – Copeia, **1957**: 52–53.

Emerson, E. T. (1905): General anatomy of *Typhlomolge rathbuni*. – Proceedings of the Boston Society of Natural History, **32**: 43–76.

Gorbman, A. (1957): The thyroid gland of *Typhlomolge rathbuni*. – Copeia, **1957**: 41–43.

Gould, S. J. (1977): Ontogeny and phylogeny. – Cambridge, Mass, Belknap Press, 501 pp.

Greven, H. (1989): Teeth of extant amphibian: morphology and some implications. – Fortschritte der Zoologie, **35**: 451–455.

Greven, H. & Clemen, G. (1979): Morphological studies on the mouth cavity of urodeles. IV. The teeth of the upper jaw and the palate in *Necturus maculosus* (Rafinesque) (Proteidae: Amphibia). – Archivum histologicum Japonicum, **42**: 445–457

Fig. 5 a–g. Dentition of the vomer (a-c) and palatinum (d-g). **a** Vomer, male, lingual, recurved teeth with a broad basis, pulpal accesses (asterisks) in the *pars dentalis*. **b** Detail of a; tooth has a fissured dividing zone (asterisk). **c** Vomerine teeth, male, labial with traces of a dividing zone (white arrowhead) and a distinct dividing zone (blach arrowhead). The *pars dentalis* extends to the labial edge. **d** Palatinal teeth, labial, female. The left tooth shows signs of wear. The dividing zones are differently developed (arrowheads). **e** Recurved anterior palatinal tooth, male, with broad basis and slightly developed dividing zone (arrowhead). **f** Worn palatinal teeth on the anterior palatine, female, labial. Note partial bistichy (arrow). **g** Palatine tooth, labial, female, a dividing zone is not visible.

GREVEN, H. & CLEMEN, G. (1980): Morphological studies on the mouth cavity of urodeles. VI. The teeth of the upper jaw and the palate in *Andrias davidianus* (Blanchard) and *A. japonicus* (Temminck) (Cryotobranchidae: Amphibia). – Amphibia-Reptilia, **1**, 49–59.

GREVEN, H. & CLEMEN, G. (1990): Effects of hypophysectomy on the structure of normal and ectopically transplanted teeth in larval and adult urodeles. – Acta Embryologiae et Morphologiae Experimentalis, ns, **1**: 33–43.

GREVEN, H. & CLEMEN, G. (2009): Early toot transformation in the paedomorphic hellbender *Cryptobranchus alleganiensis* (Amphibia: Urodela) – Vertebrate Zoology, **59**: 71–79.

GREVEN, H., SCHUBERT-JUNG, M. & CLEMEN, G. (2004): The dentition of European *Speleomantes* spp. (Urodela, Plethodontidae) with special regard to sexual dimorphism. – Annals of Anatomy, **186**: 33–43.

GREVEN, H., JÖMANN, N. & CLEMEN, G. (2006): Dentigerous bones, dentition, and dental laminae in the hynobiid salamander *Ranodon sibiricus* Kessler, 1866 (Amphibia, Urodela). – Acta Biologica Benrodis, **13**: 195–217.

HERTWIG, O. (1874): Über das Zahnsystem der Amphibien und seine Bedeutung für die Genese des Skeletts der Mundhöhle. – Archiv für mikroskopische Anatomie und Entwicklungsmechanik **11**: 1–208.

HILLIS, D. M., CHAMBERLAIN, D. A., WILCOX, TH. P. & CHIPPINDALE, P.T. (2001): A new species of subterranean blind salamander (Plethodontidae: Hemidactyliinae: *Eurycea*: *Typhlomolge*) from Austin, Texas, and a systematic revision of central Texas paedomorphic salamanders. – Herpetologica, **57**: 266–280.

HILTON, W. A. (1945): The skeletons of *Typhlomolge* and *Haideotriton*. – Journal of entomological Zoology, **37**: 100–101.

IUCN Read list of threatened species, 2008: www.iucn-redlist.org

KEZER, J. (1952): Thyroxin induced metamorphosis of the neotenic salamanders *Eurycea tynerensis* and *Eurycea neotenes*. – Copeia, **1952**: 234–237.

LARSON, A., WEISROCK, D.W. & KOZAK, K.H. (2003): Phylogenetic systematics of salamanders (Amphibia: Urodela), a review. – In: SEVER, D.M. (ed.): Reproductive Biology and phylogeny of Urodela; Vol 1. – Science Publishers, Inc. Enfield, USA, pp. 31–108.

MCBRIDE STEWART, M. (1958): Seasonal variation in the teeth of the two-lined salamander. – Copeia **1958**: 190–196.

MITCHELL, R.W. & SMITH, R.E. (1965): Some aspects of the osteology and evolution of the neotenic spring and cave salamanders (*Eurycea*, Plethodontidae) of Central Texas. – The Texas Journal of Science, **23**: 343–362.

MUTZ, T. & CLEMEN, G. (1992): Development and dynamics of the tooth systems in *Eurycea* and comparison of the definite dentition of the palate of *Gyrinophilus* (Urodela: Plethodontidae). – Zeitschrift für zoologische Systematik und Evolutionsforschung, **30**: 220–233.

PARK, E. H. & KIM, D. S. (1984): A procedure for staining cartilage and bone of whole vertebrate larvae while rendering all other tissues transparent. – Stain Technology, **58**: 269–272.

POTTER, F. E. & SWEET, S. S. (1981): Generic boundaries in Texas cave salamanders, and a redescription of *Typhlomolge robusta* (Amphibia: Plethodontidae). – Copeia, **1981**: 64–75.

REILLY, S. M. (1986): Ontogeny of cranial ossification in the eastern newt, *Notophthalmus viridescens* (Caudata: Salamandridae), and its relationship to metamorphosis and neoteny. – Journal of Morphology, **188**, 315–326.

REILLY, S. M. & ALTIG, R. (1996): Cranial ontogeny in *Siren intermedia* (Caudata: Sirenidae): paedomorphic, metamorphic, and novel patterns of heterochrony. – Copeia, **1996**: 29–41.

ROMEIS, B., 1989: Mikroskopische Technik (17. Auflage). – Urban und Schwarzenberg, München, Wien, Baltimore. 697 pp.

ROSE, C. S. (2003): The developmental morphology of salamander skulls. – In: H. HEATWOLE, H. & M. DAVIES, M. (eds.): Amphibian Biology, Vol. 5. Osteology. – Surrey Beatty & Sons, Chipping Norton, pp. 1684–1781.

SEVER, D. M. (1985): Sexually dimorphic glands of *Eurycea nana, Eurycea neotenes,* and *Typhlomolge rathbuni* (Amphibia: Plethodontidae). – Herpetologica, **41**: 71–84.

STADTMÜLLER, F. (1936): Kranium und Visceralskelett der Stegocephalen und Amphibien. – In: BOLK, L., GÖPPERT, E., KALLIUS, E. & LUBOSCH, W (eds.): Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd. 4. – Urban und Schwarzenberg, Berlin, Wien, pp. 501–698.

SWEET, S. S. (1977): Natural metamorphosis in *Eurycea neotenes*, and the generic allocation of the Texas *Eurycea* (Amphibia). – Herpetologica, **33**: 364–375.

WAKE, D. B. (1966): Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. – Memoirs of the Southern California Academy of Sciences, **4**: 1–111.

WILDER, I. W. 1925. The morphology of amphibian metamorphosis. – Northhampton, Massachusetts, Smith College Pub., **l**: 1–100.