Early tooth transformation in the paedomorphic Hellbender *Cryptobranchus alleganiensis* (Daudin, 1803) (Amphibia: Urodela) *

* Dedicated to Prof. Dr. H. Hartwig, Cologne (Germany), on the occasion of his 99th birthday

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> Abstract

Dentition of the upper and lower jaws and the palate of three larvae of different sizes (29 mm, 47 mm, 53 mm long) and one adult specimen of the paedomorphic *Cryptobranchus alleganiensis* is described. The 29 mm larvae had ossified, but not fully developed premaxillae and vomeres, partly ossified incomplete palatines, dentaries and still developing coronoids. Teeth were present only on the premaxillae, dentaries and vomeres, but were still not ankylosed to the bones; they were monocuspid and non-pedicellate. However, in the 47 mm larva teeth on all dentigerous bones were bicuspid and pedicellate as typical for urodele teeth after metamorphosis. Thus, paedomorphosis influences dentition already in a relatively early time in ontogeny in *C. alleganiensis*. Such heterochronous effects on dentition obviously occur in different degrees within paedomorphic Urodela and deserve closer attention. Presently, however, knowledge of them is still fragmentary. With the exception of the palatines and the coronoids, which were toothless, praemaxillae, vomeres and dentaries bore a single row of established teeth. Course and number of dental laminae was consistent with the conditions found in other Urodela (a continuous dental lamina in the upper jaw arcade; a discontinuous in the lower jaw arcade and two vomerine dental laminae). However, in contrast to other Urodela we found no signs of dental laminae accompanying the coronoids and the palatines, which explains the total absence of teeth on these bones.

> Kurzfassung

Wir beschreiben die Bezahnung auf Ober- und Unterkiefer sowie Palatinum von drei Larven unterschiedlicher Länge (29 mm, 47 mm, 53 mm) des paedomorphen *Cryptobranchus alleganiensis* und eines erwachsenen Exemplars. Die 29 mm lange Larve hatte ossifizierte, aber noch nicht vollständig entwickelte Praemaxillaria und Vomeres, teilweise ossifizierte, unvollständige Palatina und Dentalia sowie sich noch entwickelnde Coronoide. Zähne waren nur auf den Praemaxillaria, Dentalia und Vomeres vorhanden, jedoch noch nicht auf den Knochen verankert; sie waren monocuspid und hatten in diesem Stadium noch keine Ringnaht. Bei der 47 mm langen Larve waren auf allen zahntragenden Knochen die Zähne bicuspid und wiesen eine deutliche Ringnaht auf, wie es für Urodelenzähne nach der Metamorphose typisch ist. Die Paedomorphose beeinflusst die Bezahnung von *C. alleganiensis* bereits relativ früh in der Ontogenese. Solche Heterochronien in den Zahnsystemen kommen innerhalb der paedomorphen Urodelen offenbar in verschiedenen Abstufungen vor und verdienen nähere Aufmerksamkeit. Die Kenntnis hierüber ist zurzeit noch sehr lückenhaft. Mit Ausnahme der Palatina und Coronoide, die zahnlos waren, trugen die Praemaxillaria, Vomeres und Dentalia eine einzige Zeile etablierter Zähne. Verlauf und Anzal der Zahnleisten stimmen mit den Verhältnissen bei anderen Urodelen überein, d.h. eine zusammenhängende Zahnleiste im Oberkieferbogen, eine in der Mitte getrennte Zahnleiste im Unterkieferbogen und je eine Zahnleiste für jeden Vomer. Im Gegensatz zu anderen Urodelen fanden wir keine Zahnleiste entlang der Coronoide und der Palatina. Dies erklärt auch, dass auf diesen Knochen keine Zähne stehen.

> Key words

Paedomorphosis, dentition, bicuspidity, heterochrony, *Cryptobranchus alleganiensis*.

Introduction

In Urodela first larval tooth generations are typically non-pedicellate and monocuspid ("early larval teeth"). They are replaced by monocuspids with an incipient annular suture between the pedicel and the crown ("late larval teeth") and, in turn, by distinct pedicellate bicuspids ("transformed teeth") at metamorphosis (summarized in Greven, 1989; Clemen & Greven, 1994; Davit-Béal *et al*., 2006, 2007). There is indirect evidence that bicuspidity develops under the influence of the metamorphosing hormone and that monocuspidity suddenly changes to bicuspidity (Gabrion & Chibon, 1973; Clemen, 1988; Greven & Clemen, 1990; Davit-Béal *et al*., 2006).

In several Urodela metamorphosis is incomplete leading to a number of paedomorphic characteristics in terminal forms, which do, however, not reflect phylogenetic relationships among paedomorphic taxa (Wiens *et al*., 2005). There are non-transforming paedomorphic taxa (Amphiumidae, Cryptobranchidae, Proteidae, Sirenidae), taxa containing paedomorphic and transforming species (Ambystomatidae, Dicamptodontidae, Plethodontidae), and taxa with some facultatively paedomorphic species (Ambystomatidae, Hynobiidae, Salamandridae) (Duellman & Trueb, 1986; Wiens *et al*., 2005). Adults of the naturally non-transforming paedomorphic species may have either a fully larval dentition in the upper jaw and palate, i.e. early and/or late larval monocuspid teeth (e.g.. Proteidae: Means, 1972; Greven & Clemen, 1979; Sirenidae: Clemen & Greven 1988; Reilly & Altig, 1996; Plethodontidae: Clemen & Greven, 2000), or transformed teeth in the upper jaw and monocuspids in the vomer and palatine (e.g. Ambystomatidae: Kerr, 1960; Clemen & Greven, 1977; Beneski & Larsen, 1989). In other paedomorphic ambystomatids, in which mainly teeth of the upper and lower jaw were investigated either exclusively larval teeth were present or monocuspids interspersed with incipient bicuspid teeth (Beneski & Larsen, 1989). The lower jaw, largely neglected in this respect, includes in *Ambystoma mexicanum* Shaw, 1789 the dentaries with a mosaic of monocuspid and more or less bicuspid teeth and the coronoid, which bears exclusively monocuspid teeth (Bolte & Clemen, 1991).

In the Amphiumidae teeth in the upper jaw and vomer – a palatine is missing in adults – are exclusively bicuspid (see Clemen & Greven, 1980; Erdmann & Cundall, 1984 and citations therein). Similar conditions are found in the Cryptobranchidae and teeth in adults are from the transformed type (*Andrias* spp.: Schmidt, 1958; Greven & Clemen, 1985; *Cryptobranchus alleganiensis* (Daudin, 1803): Kerr, 1960; Elwood & Cundall, 1994). To our knowledge dentition in larvae has not been studied yet.

In the present article we report on a strikingly early presence of fully transformed teeth in the upper and lower jaw and the palate of larval stages of the hellbender *C. alleganiensis* and discuss our findings in the context of current knowledge on tooth transformation in Urodela.

Material and methods

Four larvae and one shrivelled, dried adult *Cryptobranchus alleganiensis* (Daudin, 1803) (Cryptobranchidae; subspecies-state of the specimens was unknown) were available, two larvae from museum collections, two larvae from a commercial dealer and the adult from the collection of the Zoological Institute of the University Vienna Zoological (see below). The age of the specimens was estimated according the table in Nickerson & Mays (1973)

The head of one (AMNH 37294) of 29 mm TL fixed in formalin with external gills, front limbs with three buds of digits and hind limbs seen as small protuberances, obviously a few days after hatching (see Nickerson & Mays, 1973), was embedded in paraplast, serially sectioned at 5 μm and sections were stained with Heidenhain-Azan (Romeis, 1968)

A second larva of 47 mm TL (approx. 4-6 months old) from a commercial dealer was fixed in Bouin's solution and sectioned and stained as described.

A third larva of 53 mm TL (7 - 8 months old, full number of limbs and digits) also from a commercial dealer and a fourth larva of 61 mm (AMNH 103 160) were cleared and stained with Alizarin Red (Dingerkus & Uhler, 1977). After examination of the cleared and stained specimen, the dentigerous bones were carefully excised and adhering tissue was removed using pancreatin and a fine brush. Isolated bones were dehydrated in a graded ethanol series and critical-point-dried (CPC 020, Balzer). Samples were glued to aluminium plates using Tempfix, coated with gold, and examined with a SEM (Hitachi S-530).

The dried adult specimen was hydrated for several days and then macerated in 3-4% KOH to remove tissue from tooth-bearing bones. These bones were rinsed in water, dehydrated, air-dried and treated for SEM as described.

In addition, we could roughly inspect the mouth roof and the lower jaw of a 71 mm long larva (AMNH 194590)

Results

Dentigerous bones

Fig. 1

Description mainly focuses on the dentigerous bones and dentition of the cleared and stained 53 mm larva, supplemented by the analysis of the serial sections of the 29 and 47 mm larvae. The 61 mm larva and the 71 mm larva did not differ noticeably. Adult skull morphology has been treated in REESE (1906), DUELLMAN & TRUEB (1986) and ELWOOD & CUNDALL (1994).

Premaxillae and maxillae of the upper jaw articulate with one another and possess a single row of teeth on their antero-ventral border (Fig. 1 a, a', b, b'). The maxilla of the 53 mm larva is nearly as long as the premaxilla (Fig. 1 b, b', c, c'), whereas the maxilla of the largest specimen is three times longer than the premaxilla. The *pars palatina* of each premaxilla is spread posteriorly, that of each maxilla is developed only at the anterior end of this bone where it articulates with the maxillary process of the vomer (Fig. 1 a, a'). Dorsally, the alary process (= *processus dorsalis praemaxillaris*) of the premaxilla runs caudally to a tapered point and inserts dorsally on the nasal. A dorsal projection of the maxilla (= *processus facialis maxillaris*) extends in a posterior direction between the frontal and prefrontal (Fig. 1 b, b').

In the palate only the large vomeres are dentate. The antero-ventral single row of teeth is approximately as long as the premaxillary-maxillary row (Fig. 1 a, a', b, b'). Mediorostrally each vomer possesses a compact premaxillary process that supports the alary process of the premaxilla (Fig. 1 a, a'). A maxillary process situated in the middle of the labial border of each vomer extends to the *pars palatina* of the maxilla and bends dorsally touching the inner surface of the facial process of the maxilla (Fig.. 1 a, a', b, b'; 2). In the oldest specimen examined this curvature is missing, but both vomerine processes are oriented dorsad (Fig. 3).

The palatopterygoids are separated from the posterolateral borders of the vomeres. The anterior palatine portion seems to be absent and the mid-part of the palatopterygoid appears partially split or perforated (Fig. 1 a, a', b, b').

Main elements of the lower jaw are the dentaries, which bear a single row of marginal teeth each, parallel to the maxillae and premaxillae, and the edentate coronoids. Dentaries are syndesmotically fused anteriorly (Fig. 1 c, c'). The coronoids accompany the dentaries more than two-thirds mediocaudally. Anteriorly, the coronoid and dentary are apposed to each other, but clearly separate over the caudal third of the lower jaw (Fig. 1 c, c').

The 29 mm larvae possesses ossified, but not fully developed premaxillae; maxillae are still absent. Also the vomer is ossified; the partly ossified palatine grows in posterior direction arising near the posterior border of the *processus antorbitalis*. The pterygoidal portion is still missing. In the lower jaw dentaries are ossified; the coronoid develops at the inner side of Meckel's cartilage. All bones, which in older stages bear teeth, are still edentate. Teeth are present, but have not ankylosed yet

In the 47 mm larva premaxillae, maxillae, vomeres, and palatines, as well as dentaries and coronoids are present. With the exception of the palatine and the coronoid all bones bear a single row of established teeth.

Teeth and dental laminae

Fig. 2 and 3

In the 53 mm larva teeth are pleurally (premaxilla, maxilla, dentary) or horizontally (vomer) attached to the bone labio-marginad (Fig. 1 a, a', 2 a, d). All teeth are bicuspid, pedicellate and slightly curved lingually (Fig. 2 a–f). Both cusps are of similar size and possess sharp blades (Fig. 2 b-f) extending laterally to the lower half of the crown (Figs 2 d, e). The labial blade ends further basally; the lingual blade is more strongly curved (Fig. 2 c-f). Blade ends are oriented linguad (Figs. 2 d, f). Due to differing basal levels, the lingual cusp towers above the labial cusp (Fig. 2 b, c, f). The annular zone is lingually broad and labillay small and deeply incised (Fig. 2 c, f). There is a slight latero-labial bulge on each side of the crown base (Fig. 2 c) and the labial side of the crown base sits flat on the equally flat upper edge of the pedicel (Fig. 2 b, d). Collagen fibres, which bind the pedicel and crown, appear to be absent in this region. Laterally and lingually the ring suture becomes closed off (Fig. 2 d, f). The surfaces of the crown base and pedicel are furrowed longitudinally (Fig. 2 b, c). The pedicel, barely protruding above the pars dentalis labially (Fig. 2 d), is perforated by a large lingual pulp opening (Fig. 2 f). The pedicels of adjacent teeth are clearly separated (Figs. 2 a, d), whereas in the 47 mm larva their bases are often fused (Fig. 3 f).

There are only slight differences between the larval and adult bicuspid teeth. In the latter, both cusps are lancet-shaped (Fig. 2 g, h). Their laterobasal ends, especially those of the deeper set labial cusps, are clearly pointed (Fig. 2 h). The bicuspid apex covers nearly two thirds of the crown (Fig. 2 g, h). The crown base possesses longitudinal furrows that run parallel to the
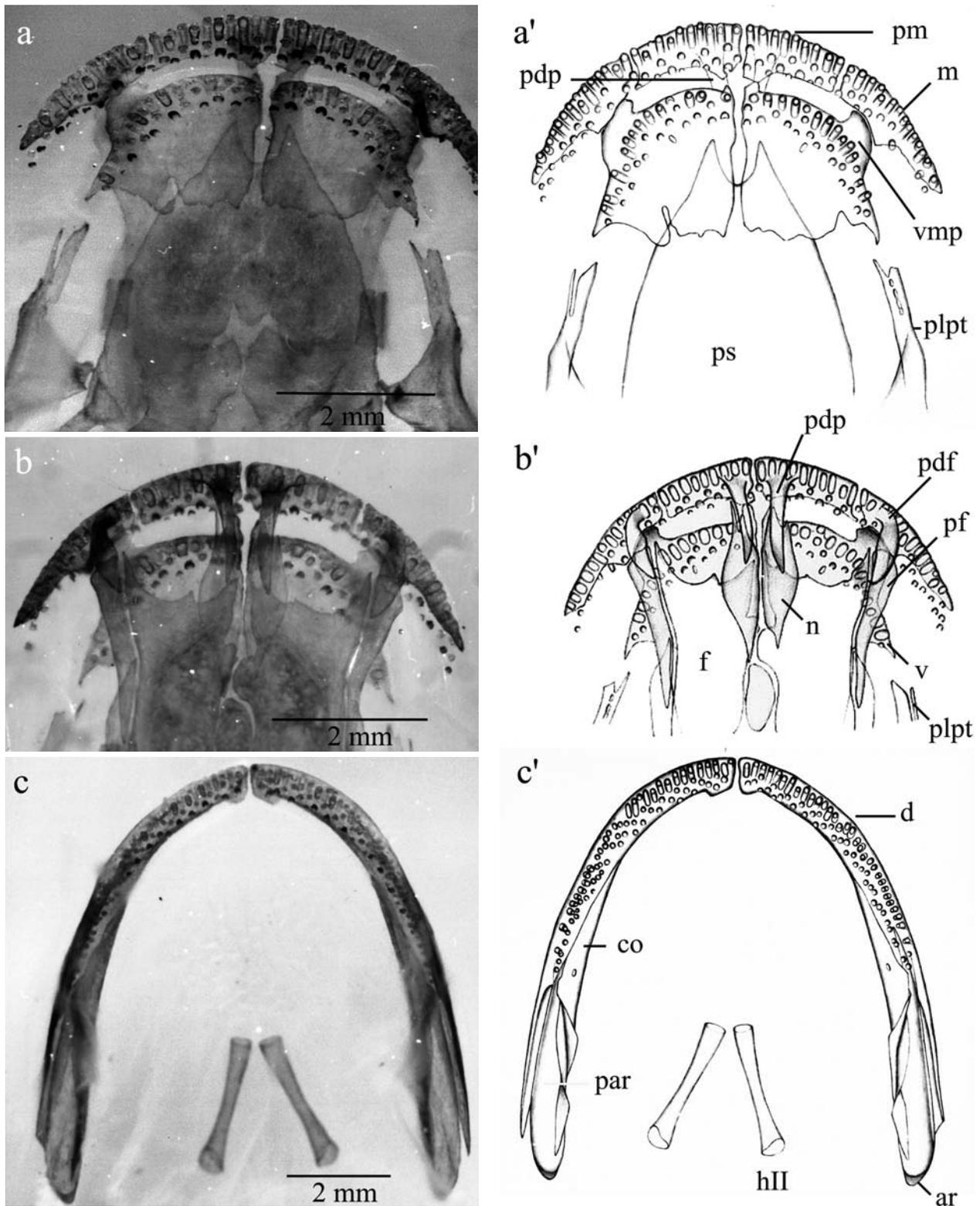
Fig 1 a–c. Bones of the skull (upper jaw) and lower jaw with functional teeth (single row on the outer edges of the dentigerous bones) and replacement teeth (in front of the functional teeth) of the 53 mm larva. **a, b, c** Cleared and stained specimen. **a', b', c'** Drawings; **a, a'** Ventral view of the skull. **b, b'** Dorsal view of the skull. **c, c'** Dorsal view of the lower jaw; note gleaming of various structures due to the transparency of the bones, e.g the dorsally situated anterior processes of the vomer (in a, a') and dentition (in b, b'); ar = articular, co = coronoid, d = dentary, f = frontal, hII = second hyobranchial, m = maxilla, n = nasal, pdp = *processus dorsalis praemaxillaris*, pf = prefrontal, pfm = *processus facialis maxillaris*, plpt = bony bridge of the palatine and pterygoid, pm = premaxilla, ps = parasphenoid, pt = pterygoid, v = vomer, vmp = vomerine maxillary process
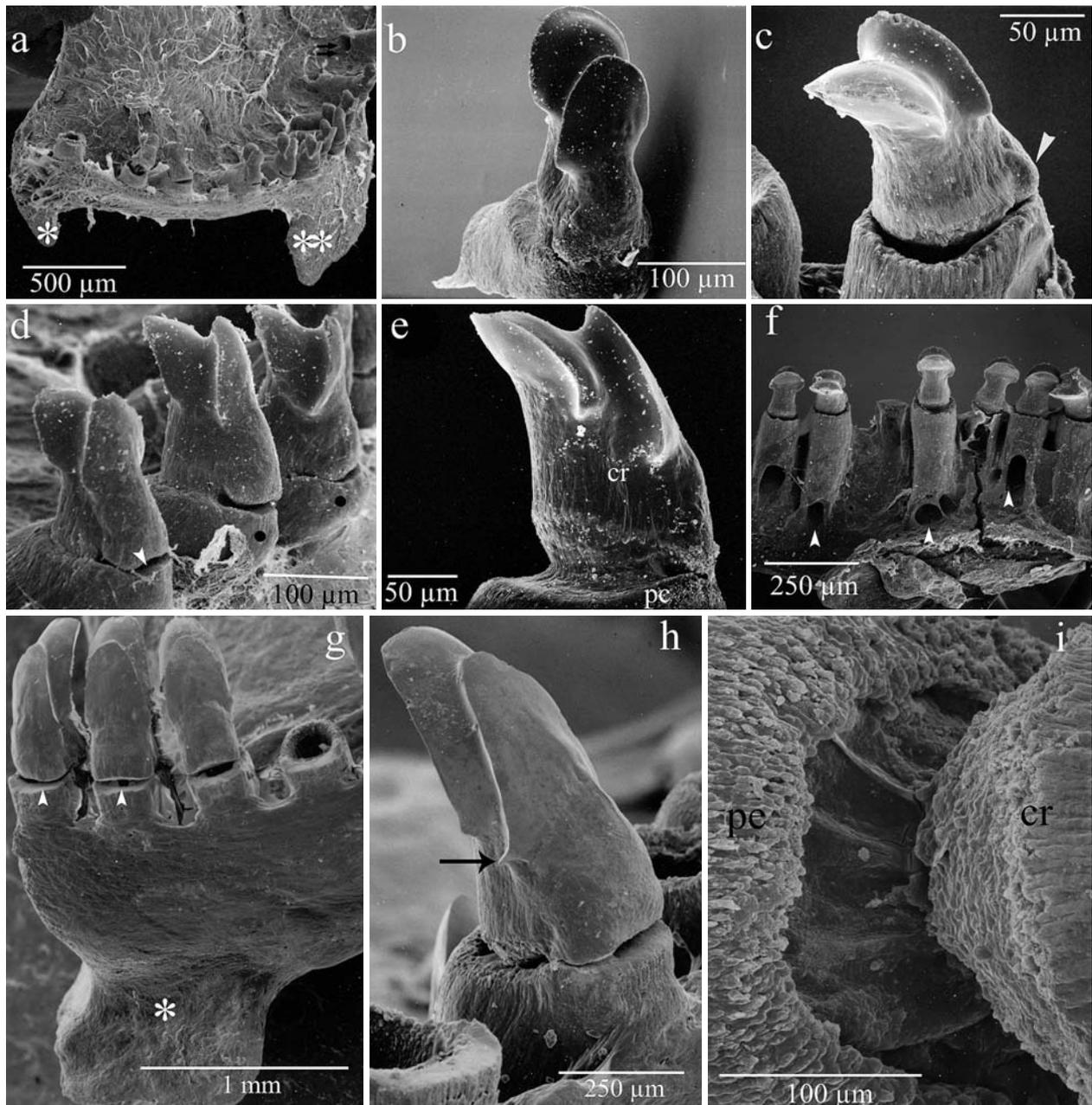
Fig 2 a–i. Dentition of the 53 mm larva (a–f) and the adult specimen (d–h), SEM. **a** Right vomer with maxillary (asterisks), and premaxillary process (asterisk) and single row of teeth. **b** Older replacement tooth with rounded sharp cusps. **c** Maxillary tooth; pedicel and crown are striped lengthwise, the latero-labial portion of the crown base (arrowhead) is clearly enlarged. **d** Vomerine teeth with labially short pedicels (black circles); note the deep suture labially (arrowhead). **e** Premaxillary tooth with labially flat, broad contact areas between pedicel (pe) and crown (cr). **f** Right maxilla, lingual; pleurally ankylosed bicuspid teeth with large pulpal accesses (arrowheads). **g** Labio-medial section from the left vomer with maxillary process (asterisk) and monostichously arranged teeth; labial ring suture area (arrowheads). **h** Lancet-shaped blades of the cusps; pointed sharp tips (arrow) of a vomerine tooth. **i** The lingual area of the pedicel (pe) appears globular; dentine crown (cr).

long axis of the tooth (Fig. 2 i). The reduced upper surface of the lingual pedicel is partially built up of loosely arranged globules that extend into the upper portions of the inner pedicel wall (Fig. 2 i). Vomerine teeth are now pleurally attached to the bone.

In the 29 mm larva dental laminae, tooth buds and teeth ready for ankylosis, but attachment bones are still not fully developed (Fig. 3 a) run posteriorly to the future row of established teeth. Teeth are not anky-losed as yet; all are monocuspid and non-pedicellate (Fig. 3 d). In the upper jaw (premaxillae only) the dental lamina is continuous extending laterocaudally beyond the ends of the bones. Also here tooth buds are present (Fig. 3 a). Vomeres have their own dental lamina each and teeth and tooth buds are found along the anterior border of this bone. The palatines neither are broadened anteriorly, nor are they accompanied by dental lamina (Fig. 3 b). The dental lamina of the
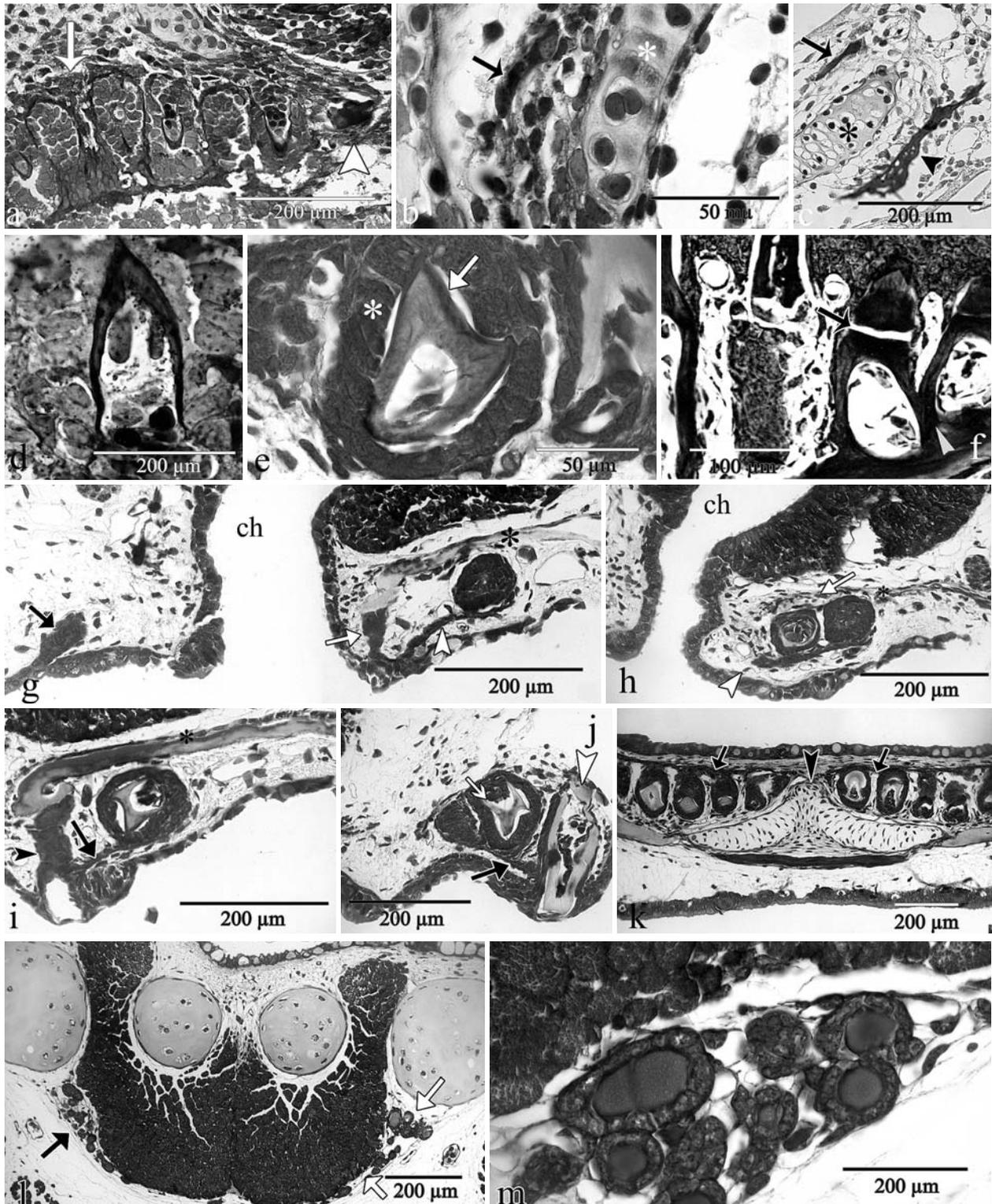
Fig 3 a–m. Dentition, dental laminae and thyroid follicles of the larvae: 29 mm (a–d), 47 mm (e–m). **a** dental lamina of the upper jaw with tooth buds medially (arrow); teeth are not established; premaxilla (arrowhead). **b** Edentate palatinal portion of the palat-opterygoid (arrow) at the level of the antorbital process (asterisk). **c** Edentate coronoid (arrow) and dentary (arrowhead); Meckel's cartilage (asterisk). **d** Early tooth generations are monocuspid and undivided. **e** Bicuspid tooth germ with enamel cap (arrow), dentine tubules and two-layered enamel organ (asterisk). **f** Divided premaxillary teeth (arrow) with fused pedicel bases (arrowhead); **g** Left side: end of the upper jaw dental lamina (black arrow); right side: vomer (asterisk) with active dental lamina (arrowhead) a single tooth bud and a established tooth (white arrow). **h** Active dental lamina with tooth buds near the posterior edge of the vomer (asterisk) without contact with the oral epithelium (arrowhead), choana (ch). **i** Vomer (asterisk), more anteriorly with established tooth (arrowhead; only the enamel organ is cut) and dental lamina (arrow) with a bicuspid tooth germ. **j** Upper jaw dental lamina (arrow) anterior to the choana with a bud containing a bicuspid and a tooth established on the premaxilla (arrowhead). **k** Anterior portion of the dental lamina (arrows) and Meckel's cartilage (arrowhead) of the lower jaw; note the gap in the middle. **l** Position of the thyroid gland (arrows). **m** Detail showing the colloid-filled follicles

lower jaw arcade (dentaries) is not continuous showing a gap in the zone (better seen in the 47 mm larva: Fig. 3 k), where these bones are fused syndesmotically (not shown). Along the coronoid the dental lamina is missing (Fig. 3 c). Number, course, structure and extension of dental laminae are mainly illustrated for the 47 mm larva here (see Figs. 3 e–m), because of the better preservation of this specimen compared to the 29 mm larva and the fact that number and course of dental laminae remain unchanged in the further development. However, in this larva tooth germs (so far the crown is already developed), replacement teeth and established teeth are distinctly pedicellate (Fig. 3 e, f, i, j) and bicuspid. The end of the dental lamina of the upper jaw, still inactive, extends beyond the bone (Fig. 3 g, left). In addition, examination of the series show the growing posterior edge of the vomer with an active dental lamina still not connected with the oral epithelium (Fig. 3 h), whereas more anteriorly the bone is developed possessing established teeth and a dental lamina connected with the oral epithelium (Fig. 3 i). The thyroid follicles of the 47 mm larva are of varying size; the larger ones are tightly packed with homogenous or variably tinted colloid (Fig. 3 l, m).

Discussion

The adult cranial morphology of Cryptobranchidae is similar to that of transforming salamanders (REESE, 1906; DUELLMAN & TRUEB, 1986; ELWOOD & CUNDALL, 1994; ROSE, 1999). Regarding the dentition and dentigerous bones, adults of *Andrias davidianus* (Blanchard, 1871) and *A. japonicus* (Temminck, 1836) possess a single row of bicuspid and pedicellate teeth on the upper jaw (premaxilla, maxilla) and the vomer. In contrast to all transforming Urodela, where the teeth are ankylosed near or at the posterior border of the vomer, vomerine teeth of cryptobranchids are established at the anterior border of the bone (e.g. CLEMEN & GREVEN, 1994). A few teeth of the upper jaw in *A. japonicus* appeared to be monocuspid, which, however, can be assigned to the transformed type due to its sharp blades and traces of a secondary cusp. The palatine portion of the palatopterygoid and its teeth are absent (GREVEN & CLEMEN, 1980). The same holds for adults of *C. alleganiensis* (see REESE, 1906; DUELLMAN & TRUEB, 1986; ELWOOD & CUNDALL, 1994).

Ontogeny of dentition in Cryptobranchidae, however, has not been studied in detail yet. As derived from our sections of the 29 mm larva, the first tooth generation(s) in *Cryptobranchus alleganiensis* is conical-monocuspid and undivided. This type of teeth has been found in early larvae of all urodeles so far studied (e.g. GREVEN, 1989; DAVIT-BÉAL *et al.*, 2006, 2007) and appears typical for gnathostomes in general (SIRE *et al.*, 2002). However, already in the 47 mm and 53 mm *C. alleganiensis* larvae, teeth of all bones bearing teeth in these developmental stages are pedicellate and bicuspid. Because of the undoubted larval character, we would have expected these specimens to possess early or late larval teeth.

Hellbenders loose their gills at about 125 mm total length at an age of approximately a year and a half or two years after hatching and attain sexual maturity at about 256 to 300 mm at an age of 4–5 years (males) or at 330 to 380 mm at an age of 7 years (females) (for review see NICKERSON & MAYS, 1973). Judging from the normal table of *C. alleganiensis*, transformation of teeth may take place at a point in time when the hind legs are forming (see NICKERSON & MAYS, 1973; PETERSON *et al.*, 1983). This is in contrast to all other Urodela hitherto examined in this respect. Thus, development of most bony tooth support, degeneration of the palatine (see below) and its teeth (if present), dentition of the coronoid (if present) and anchorage of teeth on the developing dentigerous bones and their replacements by bicuspid teeth (see DAVIT-BÉAL *et al.*, 2006), still not present in the 29 mm larva, must have taken place within the period the larvae have grown up from 2.9 to 4.7 cm.

Transformation of teeth in urodeles has been suggested to depend on pituitary hormones and thyroxine (TSH), respectively. The latter either acts permanently to establish and maintain bicuspid teeth or only once to trigger permanent presence of bicuspid teeth (e.g. GABRION & CHIBON, 1973; CLEMEN, 1988; GREVEN & CLEMEN, 1990; for a more general discussion of TH-mediated changes during metamorphosis in larval reproducers such as cryptobranchids see ROSE, 1999). Further, the different tooth systems appear to react variably, as upper jaw teeth always appear to replace larval teeth first, suggesting that their dental laminae respond to lower levels of thyroid hormone (GABRION & CHIBON, 1973; CLEMEN, 1988; GREVEN & CLEMEN, 1990). The histological appearance of the thyroid gland in the 47 mm larva indicates a certain activity and storing of hormone, at best, which has been demonstrated in other non-transforming or partially transforming species (LARSEN, 1968). Plasma levels of thyroid hormone, however, are unknown in developing *C. alleganiensis*. GRENELL (1939) has shown that the anterior pituitary, which controls the secretory and synthetic activity of the thyroid, appeared reasonably developed in Hellbender-larvae at the time of hatching (23-26 mm in length), and was markedly larger in larvae of 35 to 60 mm. This possibly takes place in larvae also at the time the hind legs are developing. Thus, cryptobranchid lineages may have in part not only lost tissue TH-sensitivity (see ROSE, 1999),

but may also have changed TH activity and/or tissue sensitivity (LARSEN, 1968; see also MARTIN & GORDON, 1995). These conditions clearly influence paedomorphosis and leads to heterochronous effects, which can be seen to occur in different degree in tooth systems of paedomorphic taxa, but this has not been sufficiently studied in paedomorphic taxa other than Ambystomatidae (KERR, 1960; CLEMEN & GREVEN, 1977; BENESKI & LARSEN, 1989; BOLTE & CLEMEN, 1991),

Not only dentition, but also some other skull characters appear already "transformed" in the larvae of *C. alleganiensis* available to us. Worth mentioning are the absence of an anteriorly broadened palatine, the absence of a palatinal dental lamina, the absence of a dental lamina of the coronoid and the absence a vomerine tooth patch already in the 47 mm-larva.

In the cryptobranchid *A. japonicus* first signs of a palatine with teeth were described for a 55 mm larva and absence of this bone was noted in a 76 mm juvenile specimen (AOYAMA, 1930). Our findings give some evidence that in *C. alleganiensis* a toothed palatine may not develop. The anterior edge of the palatopterygoids in the 47 mm and 53 mm larvae show degradation. Generally, this process is considered as a strong indication for the onset of metamorphosis in Urodela, which is followed by total disintegration of the palatine normally dentate with monocuspid larval teeth (REILLY, 1986, 1987; REILLY & ALTIG, 1996). If so, disintegration of these structures takes place remarkably early in ontogeny of *C. alleganiensis* or, relative to tooth development, remarkably late. Also noticeable is the absence of the dental lamina of the coronoid, which also may not develop in *C. alleganensis*.

Vomeres of all stages of *C. alleganiensis* examined bore a single row of established teeth. Vomerine tooth patches with several rows seem to be entirely absent in the ontogeny of this species and very likely in other Cryptobranchidae, e.g. *A. davidianus* (unpublished). In the Hynobiidae which are closely related to the Cryptobranchidae (e.g. LARSON *et al.*, 2003; WIENS *et al.*, 2003), with which they form the suborder Cryptobranchoidea, larvae so far studied exhibit vomerine tooth patches (see GREVEN & CLEMEN, 1985; LEBEDKINA, 1979, 2005; VASSILIEVA & SMIRNOV, 2001; GREVEN *et al.*, 2007). An interesting exception is *Onychodactylus fischeri*; here larvae have also a single row of vomerine teeth (SMIRNOV & VASSILIEVA, 2002). We think it is premature to discuss the possible phylogenetic significance of this feature, because knowledge of the organisation of the mouth roof in early ontogenetic stages of Urodela, namely in paedomorphic species, is still fragmentary.

Acknowledgements

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