Morphological Studies on the Mouth Cavity of Urodeles
IV. The Teeth of the Upper Jaw and the Palate in *Necturus maculosus* (Rafinesque) (Proteidae: Amphibia)

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Summary. Adults of the neotenic (paedomorph) *Necturus maculosus* possess in the upper jaw and the palate rather uniform, conical, monocuspid teeth arranged in a single line ("Zahnzeile"; monostichous pattern) and showing a broad dividing zone, which separates the pedicel and the distal crown. This zone consists of globular and fibrous material obviously mineralized. Both premaxillaries are provided with teeth by one continuous dental lamina, whereas the vomer and palatopterygoid are accompanied by two dental laminae on each side of the palate. The results are compared to the conditions observed in other larval, neotenic, and metamorphosed Urodela.

The arrangement of the dentary bones, dental patterns and the structure of the teeth have been regarded as a useful tool for characterizing Urodela and for considering their evolutionary relationships (see Parsons and Williams, 1962, 1963; Regal, 1966; Wake, 1966).

In a series of papers on the mouth cavity of various larval, adult, and neotenic urodeles we have redescribed some of these elements of the upper jaw and the palate in detail (Clemens and Greven, 1974, 1977, 1979; Greven and Clemens, 1976). Our findings have supported the idea that there are not only the commonly known morphological differences between adult and larval dentition, but also variations in larval tooth structure depending on age. Until recently, only little attention has been paid to the possible significance of the number of dental laminae accompanying the vomers and palatopterygoids and the molding and reorganization of the laminae and the palatal dentary bones during metamorphosis. On the basis of such criteria at least two primary lines can be distinguished in Urodela (see Clemens, 1978a; Clemens and Greven, 1977; 1979).

In larvae, however, the course and number of dental laminae, the shape and structure of teeth, and the dental patterns seem to follow a more uniform type, but some modifications of this basic plan may occur in different groups. The material so far investigated by us does not allow us, however, to draw definitive conclusions.

In the present paper we therefore describe the toothed premaxillaries, vomers
and palatopterygoids as well as the dental laminae in the permanently larval *Necturus maculosus*. Although in principle the morphology of these elements and the structure of its teeth have been described by several investigators (e.g. Stadtmüller, 1936; Parsons and Williams, 1962; Means, 1972; Larsen and Guthrie, 1974) it appears useful to reconsider the upper jaw and palate of this extremely ancient perennibranchiate (Larsen and Guthrie, 1974) under the aspects mentioned above.

**MATERIALS AND METHODS**

One adult male and two females of *N. maculosus* were examined during this investigation.

For light microscopy the heads were fixed in Bouin's solution, decalcified for some days in 5% trichloracetic acid, and then embedded in paraplast. Serial sagittal and transversal sections, 8-10 μm thick, were stained with azan Heidenhain (Romeis, 1968).

For scanning electron microscopy the head of one specimen was macerated in water. The upper jaw, the vomers and the palatopterygoids were cleaned in 5% NaOH using small needles, rinsed by distilled water, dehydrated through a graded series of alcohol and air dried. They were mounted on metal stubs, sputtered with gold (Metalloplan, Fa. Leitz), photographed, and then examined in a scanning electron microscope Leitz AMR 1000 (grant Al 11/13 by the Deutsche Forschungsgemeinschaft).

**OBSERVATIONS**

1. **Gross morphology**

The pattern of the upper jaw and the palate in *N. maculosus* is principally characterized by the toothed premaxillaries, the vomers, and the palatopterygoids; the maxillaries are missing. A deep groove in the oral tissue in front of the premaxillaries separates the labial area from the upper jaw, a further groove separates the upper jaw from the palate (Fig. 1a).

The premaxillaries are not fused medially; each bone consists of a tooth bearing portion (pars dentalis), the pars palatina, and an elongate spine directed posteriorly (Fig. 1b). On the lingual side of the pars dentalis the vomers possess a posteromedial projection (Fig. 1c). The palatopterygoids are large and elongated; only their palatinal portion bears some teeth (Fig. 1d). Between the choana and the posterior edge of the premaxillaries there is a bulge of tissue decreasing in thickness caudally (Fig. 1a).

The teeth of the premaxillaries, which progressively decrease in size from the anterior to the posterior, are arranged in a monostichous pattern. The single lines ("Zahnzeilen") converge anteriorly (Fig. 1a). The palatal dentition consists of single lines of teeth on each side. The line of each vomer and the line of each palatopterygoid are arranged parallel to the curvation of the jaws (Fig. 1a). Between them a small gap is visible, where teeth are absent. The tooth line of the palatopterygoid extends beyond the choana (Fig. 1a).
Fig. 1. a-d. Gross morphology of the upper jaw and the palate. a. Ventral view of the skull with choana (ch) and the tooth line of the palatopterygoid (p), premaxillary (pm) and vomer (v). Groove between the premaxillary and the labial area (two small arrows). Groove between the upper jaw and the palate (small arrow). Gap between the vomerine and palatinal tooth line (big arrow). ×5.5. b. Premaxillary. ×3. c. Vomer. ×3. d. Palatopterygoid. ×3

2. The dental lamina

Dental laminae extend along the entire lingual margin of the premaxillaries, vomers and palatopterygoids and give rise to the enamel organs of the developing tooth buds. The laminae are deeply invaginated in a lingual direction into the connective tissue and are composed of cells from the basal layer of the stratified oral epithelium (Fig. 2a). On the lingual side the dental lamina rests upon a connective tissue layer rich in collagen (tunica propria, corium), whereas on the labial side, where the dental units are formed, such a layer seems to be absent. The free end of the dental lamina, which is arched in a labial direction and does not exhibit tooth germs, is double-layered (inner and outer dental epithelium; KERR, 1960; SMITH and MILES, 1972); distally the laminae appear to be multilayered (Fig. 2a). The same applies to the early enamel organ, which is basally double-layered and distally multilayered (Fig. 2b). The functional tooth attached to the dentary bone is still surrounded by remnants of the enamel organ (Fig. 2c).

The dental lamina of both premaxillaries extends as a continuous unseparated
Fig. 2. a–c. Dental lamina and enamel organ. a. Cross section through the palate showing the oral epithelium (ep), the dental lamina (dl), the tunica propria (tp) and the vomer (v). Note the highly vascularized connective tissue. ×90. b. Nearly horizontal section through the double-layered (arrow) enamel organ (eo) and dental lamina (dl). ×120. c. Cross section through the basal part of a functional tooth fused to the vomer (v). Pedicel (pe), remnants of the enamel organ (eo), pulp cavity (pu). Note the capillaries within the pulp cavity (arrows) and the pulp opening. ×120
Fig. 3. a–e. Dental laminae. a. The dental lamina of the premaxillaries begins caudally with an epithelial thickening (arrow), cross section. ×95. b. Deeper invagination of the dental lamina more rostrally than in Figure a. ×95. c. Gap (arrow) between the vomerine (left) and the palatinal (right) free process of dental laminae (dl). Enamel organ (eo), tunica propria (tp), longitudinal section. ×110. d. The gap between the dental laminae is filled with fibrous connective tissue, cross section. ×120. e. Beginning of the vomerine dental lamina (arrow), cross section. ×120
A sheet along the upper jaw. It begins on its caudal ends with an epithelial thickening, which invaginates progressively deeper into the connective tissue in a rostral direction (Fig. 3a, b). The dental lamina forms dental units only in the immediate neighborhood of the dentary bone.

The dental laminae of the vomer and the palatopterygoid are arranged in one line. The right and left vomerine dental laminae—separated by a small gap in the medial palate—extend from the middle of the premaxillary to the anterior edge of the choana. Their caudal ends have lost the connection with the epithelium representing now short unproductive processes embedded in the connective tissue (Fig. 3c, e).

The palatal dental lamina is separated from the vomerine by a distinct gap measuring 80–100 μm which is filled with connective tissue (Fig. 3c, d). The lamina begins with a short free process (Fig. 3c); more caudally, when the connection with the epidermis is established, the lamina becomes productive. Posteriorly the palatal dental lamina ends rather abruptly and only a very short free process is seen in the subepithelial connective tissue (Fig. 4).

3. **The teeth and dentary bones**

The teeth of the upper jaw and the palate are of rather uniform shape, except that the teeth of the premaxillaries are smaller compared to those of the palate (Fig. 6).

The teeth are slightly curved, elongated, monocuspid cones with a rather...
roundish apex (Fig. 6). In most cases a slight boundary between the dentine shaft and the enamel cap (apex) is visible (Fig. 7a). The crown has a smooth surface up to the edge of a broad, rather deep, well-marked groove, which divides each tooth into a proximal pedicel and a distal crown (−dentine shaft and apex: SMITH and MILES, 1971). In histological preparations after azan staining a clear dividing zone cannot be identified which agrees well with earlier investigations suggesting an undivided tooth in Necturus (HOFFMANN, 1873-1878; see also LARSEN and GUTHRIE, 1974).

At the distal edge of the groove small globules extending to the deepened area can be seen (Fig. 7c, d, e); a prominent characteristic of this zone are fibers running parallel to the longitudinal axis of the tooth and mingling with the material of the pedicel (Fig. 7b, c, d). On the lingual face the dividing zone possesses a more or less extended opening to the pulp cavity (Fig. 6c, 7e). The crown is horizontally (acrodont) attached to the pedicel.

The distal part of the pedicel is coarsely structured but to a lesser degree than the dividing zone (Fig. 7b, c, d). It is ankylosed to the bone in pleural condition which causes a reduction in height on the labial face (Fig. 6b). On its lingual side the pedicel exhibits a triangular opening to the pulp cavity (Fig. 6c, d, 7d, f). Around
Fig. 7. a–f. Structure of teeth. a. Slight boundary between the enamel cap (apex) and the dentine shaft, premaxillary. ×90. b. Transition of dentine shaft to dividing zone respectively dividing zone to the pedicel, labial face. Arrows indicate additional openings to the pulp cavity, palatopterygoid. ×100. c. Dividing zone containing globules and fibres, palatopterygoid. ×200. d. Pedicel with opening to the pulp cavity, lingual face. Note the distinct boundary between the pedicel and the underlying palatopterygoid (arrows). ×100. e. Opening in the dividing zone surrounded by globules and fibers, vomer. ×165. f. Opening to the pulp. The arrow indicates the possible boundary between the pedicel and mineralized tissue perhaps of former dentitions. The stippled lines mark additional openings connecting the pulps of apposed pedicels. ×170
the teeth there are holes of various diameters greater than those of the osteocytes seen within the dentary bone (Fig. 6d, 7b, f); obviously they represent additional openings to the central pulp and may form channels between apposed pedicels (in particular Fig. 7f). The tissue containing these holes is localized between the tooth and the bone exhibiting an irregular arrangement of fibers and some more or less distinct layers as seen in paraplast sections (Fig. 5); perhaps it represents at least partly remnants of earlier dentitions (Hertwig, 1874; Oltmanns, 1952).

The vomerine teeth are also ankylosed in a (weak) pleural condition as the anterior labial margin of the bone is heightened. The same applies to the teeth of the palatopterygoids, whose pedicels often are so flat that they appear to be attached to the bone directly with the dividing zone (Fig. 7b).

**DISCUSSION**

As simple monocuspid teeth in urodèles normally occur before metamorphosis (Kerr, 1960; Gaunt and Miles, 1967) all teeth of *N. maculosus* may be regarded as being larval. It should be noted, by the way, that Larsen and Guthrie (1974) examining the teeth of the same species have observed incipient bicuspid teeth in a few cases. A striking feature, however, is the distinct, broad zone, which separates each tooth in the distal crown and the basal pedicel as a rather deep groove. Such a dividing line often defined as zone of weakness is known in the teeth of almost all species of metamorphosed Amphibia (Kerr, 1960; Parsons and Williams, 1962, 1963; for exceptions see Means, 1972).

In *N. maculosus* the weak zone obviously does not entirely consist of fibrous tissue (Parsons and Williams, 1962; see also Oltmanns, 1952), but is at least partly composed of calcified material. This is indicated by the fibers and globules resistant to maceration and NaOH and by the fact that the dentine shaft remains attached to the pedicel even after these crude treatments (see also Means, 1972). In adult teeth of *Salamandra salamandra* we were able to show by electron microprobe analysis that the weak zone is partly calcified (Clemen et al., in prep.).

There is no doubt that the neotenic adult *N. maculosus* possesses pedicellate teeth (Parsons and Williams, 1962; Means, 1972; Larsen and Guthrie, 1974). Assuming that the Amphibia are monophyletic and pedicellate teeth arose once (Parsons and Williams, 1962, 1963; Hinderstein and Boyce, 1977) and that the non-pedicellate condition perhaps is associated with neotenic (paedomorph) forms (Means, 1972; Larsen and Guthrie, 1974; Estes, 1975) the question arises how to classify the pedicellate tooth in these forms which characteristically retain larval and juvenile features in the adult morphology. Considering the data from literature, apparently there is a mosaic of the non-pedicellate and pedicellate conditions in fossils and also in recent Urodela. Undivided, non-pedicellate teeth have been reported for many fossil forms (for exceptions see among others Bolt, 1969; Estes, 1975), for the larvae of recent Urodela and for the neotenic *Siren lacertina* (Means, 1972; see also Parsons and Williams, 1962).

The identification of the weak zone sometimes is obscure. In very young *Ambystoma mexicanum* we believed we recognized a trace of a division line (Clemen and Greven, 1977) and also scanning micrographs of the teeth of the miocene salamander
Batrachosauroides dissimilans, which are described as being undivided, in our opinion show some indications of such a zone (see in particular Fig. 2c in the paper by Hinderstein and Boyce, 1977).

Meanwhile we know that in larval Urodela so far investigated there is not only a dentition differing from that of the metamorphosed adults, but there are also undivided (in very young larvae) and divided (in old or superannuated larvae) teeth, always monocuspid during postembryonic development up to metamorphosis (Clemen and Greven, 1974, 1977, 1979). Monocuspids occur also in postmetamorphosis (Kerr, 1960; Clemen and Greven, 1974, 1977). Thus, in Urodela a larval dentition is found which is gradually replaced during metamorphosis by bicuspid teeth. Even before metamorphosis intermediate stages of the weak zone occur (Clemen and Greven, 1979). Lawson (1965) pointed out that even during the early stages of tooth development in Hypogeophis rostratus (Gymnophiona) a distinction is made between the crown and the pedicel but nevertheless both portions of the tooth are produced by the same continuous layer of odontoblasts. Kerr (1960) further suggested that the larval and adult teeth of urodeles may represent consecutive stages resulting from a functional change of the dental lamina.

In neotenic Triturus helveticus the occurrence of bicuspid teeth is dependent on the amount of TSH (Gabrion and Chibon, 1973). This perhaps applies also to the formation of the dividing zone, which, however, remains to be investigated.

The monocuspid, pedicellate tooth of N. maculosus as well as the palatal tooth of the neotenic A. mexicanum (Clemen and Greven, 1977) is similar to that of an old urodelan larva. Thus it can be concluded: Not only the non-pedicellate tooth of some neotenic Urodela (e.g. Siren lacertina), of fossil forms and of young larvae represents an early stage ("primitive") in the evolution of a fully divided (bicuspid) tooth—we do not assume here a secondary loss of the division as tentatively stated by Schultze (cit. after Means, 1972)—, but also the incompletely or completely divided monocuspid tooth is a juvenile feature, but obviously of a later developmental stage.

Already Noble (1931) reported that many characters of Necturus are common to larvae and neotenes of all urodele families (see also Larsen and Guthrie, 1974) and that Proteus and Necturus have reached a later stage of urodele ontogeny. We will consider here only those characters concerning the upper jaw and the palate. As Urodela show a successive development of the skull bones (Stadtmüller, 1936) the lack of the maxillaries may be regarded as a feature of very young larvae, (see however Clemen and Greven, 1979), whereas the pedicellate monocuspid tooth, however, would be a character of an old larva. It will be of interest to learn something about the conditions in very young N. maculosus. The marginal dentition of the palate paralleling the curvature of the jaws, also has been observed in larval and neotenic forms (Regal, 1966). The monostichous pattern of the vomers and the palatoptyergoids occurs for instance in the neotenic adult of A. mexicanum, in the fossil proteid Opisthotriton kai (Estes, 1975) or in larval (?) plethodontids (Wake, 1966). The extinct forms are not known to change over from polystichy to monostichy or to change their tooth form, but among the recent urodeles both phenomena occur.

The vomers and palatoptyergoids were provided with teeth by two dental laminae on each side of the palate. In histological sections the gap between the vomerine
and palatinal dental lamina is very distinct. This corresponds exactly to young *A. mexicanum*, but not to young larvae of *Triturus vulgaris* and *S. salamandra*, where the palatinal and vomerine portions are connected at least partially (Clemens, 1978b; Clemens and Greven, 1979). Speculating that the fully divided palatal dental lamina represents a "primitive" stage, it may be presumed that these patterns perhaps occur also in the more advanced Salamandridae but only in very young (embryonal) stages. Studies concerning this matter are in progress.

It seems convenient to summarize our studies hitherto existing with regard to the features mentioned above.

In larval *A. mexicanum, T. vulgaris* and *S. salamandra* the teeth are monocuspid and arranged in a monostichous pattern on the premaxillaries and, if present, maxillaries. In very young larvae, however, the dentition is polystichous. Areas of monocuspid teeth ("Zahnfelder") occur on the vomers and palatopterygoids. There are teeth without (young larvae) and with (old larvae) a dividing line. Both premaxillaries (and maxillaries) are toothed by one, the vomers and palatopterygoids by two separated (*A. mexicanum*) or two partially connected dental laminae (*T. vulgaris, S. salamandra*).

In the neotenic adults of *A. mexicanum* and *N. maculosus* there are either bicuspid, monostichous teeth on the premaxillaries and maxillaries (*A. mexicanum*) or monocuspid, exactly monostichous teeth on the premaxillaries (*N. maculosus*). Monocuspid predominantly (*A. mexicanum*) or exactly monostichous (*N. maculosus*) teeth are found on the vomers and palatopterygoids. The teeth are always pedicellate. The premaxillaries were toothed by one, the vomers and the palatopterygoids by two fully separated dental laminae.

Metamorphosed adults of *A. mexicanum, T. vulgaris, S. salamandra* and *Hydromantes italicus* generally possess bicuspid, pedicellate teeth, which are arranged in a monostichous order on the premaxillaries and maxillaries and either on the vomeropalatinum developing during metamorphosis in *A. mexicanum* (Clemens, 1979) or on the definitive vomer including the vomerine bar in *S. salamandra* (Clemens, 1978a) and *T. vulgaris* (Clemens and Greven, 1979). In the first case the palatal and vomerine dental laminae remain separated and both provide the vomeropalatinum with teeth, in the second case the palatinal portion of the dental lamina disappears and only the vomerine one accompanies the outgrowing vomer. In the adult plethodontid *Hydromantes italicus* there are two separated dental laminae accompanying the vomer and its process growing out along the ventral surface of the parasphenoid. The process exhibits toothed areas ("Zahnfelder") not continuous with the vomerine tooth line (see Wake, 1966). It is unclear, whether these two dental laminae represent the former larval vomerine and palatinal laminae or whether parts of the vomerine dental lamina are amalgamated leaving two fully divided laminae (Greven and Clemens, 1976).
REFERENCES


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