A SINGLE TOOTH REPLACEMENT PATTERN GENERATES DIVERSITY IN THE DENTITION IN CICHLIDS OF THE TRIBE ERETMODINI, ENDEMIC TO LAKE TANGANYIKA (TELEOSTEI : CICHLIDAE)

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Abstract. Cichlids from the tribe Eretmodini, endemic to Lake Tanganyika, provide a unique example of diet-associated differences in dentition (especially tooth shape) within a group of closely related species. Here, we examine the tooth pattern and sequence of tooth replacement in four representative eretmodine taxa, as a starting point of a new study that will focus on the mechanisms responsible for ontogenetic and phylogenetic divergence of tooth shape. New teeth are formed in adjacent positions labial to but alternating with older ones in waves that sweep from mesial to distal. Only a minor shift (different spacing of newly developing germs) is necessary to produce the different dental arcades observed in eretmodine cichlids. The position and state of development of the replacement teeth, as well as localized growth and resorption of the jaw bone, add histological evidence in support of the replacement pattern described for the four taxa. The tooth replacement pattern proposed here is uncommon among teleosts.

Key words : teeth, dentition, tooth replacement, cichlids, Lake Tanganyika.

INTRODUCTION

Vertebrate teeth provide exciting material to biologists of disciplines as diverse as paleontology, taxonomy, functional morphology and developmental biology. Morphological characteristics, and in particular shape, of vertebrate teeth have been considered to have a high heritability and have therefore been widely used as taxonomic characters defining species in many taxa of toothed vertebrates (*e.g.*, GREENWOOD, 1981 ; THENIUS, 1989). Yet, recent studies have shown that dental characters of vertebrates that replace their teeth throughout life, may be susceptible to environmentally-induced variation (*e.g.*, HUYSSEUNE, 1995). Moreover, phylogenies based on taxonomic characters such as tooth shape have turned out to be in conflict with molecular-based phylogenies as is nicely illustrated by recent studies of cichlids of the tribe Eretmodini, endemic to Lake Tanganyika (East-Africa) (VERHEYEN *et al.*, 1996 ; RÜBER, 1998).

The tribe Eretmodini, as defined by POLL (1986), comprises four nominal species currently assigned to three genera: *Eretmodus cyanostictus* Boulenger, 1898, *Spathodus erythrodon* Boulenger, 1900, *S. marlieri* Poll, 1950, and *Tanganicodus irsacae* Poll, 1950. The shape of the oral teeth is the main defining character to delineate taxa within this tribe (POLL, 1986). The teeth of *Eretmodus* are spatula-shaped with a slender neck region, those of *Spathodus* are cylindrical-shaped with flattened and truncated crown, and those of *Tanganicodus* are slender and pointed. In a recent phylogenetic study of the tribe Eretmodini using mitochondrial DNA (mtDNA) sequences, six genetically distinct lineages were observed (lineages A-F) (RÜBER, 1998). Genera and species are polyphyletic, suggesting the occurrence of cryptic species in this tribe, and the need for a reconsideration of the generic classification based mainly on tooth shape. The results have further indicated that the resemblance in tooth shape between some lineages might be the result of parallel evolution rather than common ancestry. This claim is further substantiated by genetic and morphological differences between *E. cyanostictus* and *E.* cf. *cyanostictus*. The eretmodine cichlids thus provide an excellent model to study what causes the apparent conflict between high heritability and strong adaptive potential of teeth. Before such a study can be undertaken, however, and before any experiment can be conceived, it is necessary to understand how, and in what order, new teeth arise in their dentitions, i.e., to know their replacement pattern (cichlids, like most teleosts, replace their teeth throughout life).

The anatomy of the feeding apparatus, the feeding behaviour and the evolution of the Eretmodini has been studied before by LIEM (1979). YAMAOKA *et al.* (1986) have examined the dentition and ecomorphology of three of the four nominal eretmodine species and have come to the conclusion that differences in dental morphology (as well as the position of the mouth and the morphology of the dental arcade) are related to trophic differences. Dietary differences range from algae scraping in *E.* cf. *cyanostictus* and *S. marlieri* to invertebrate picking in *T. irsacae*, whereas *S. erythrodon* is thought to have a more intermediate feeding behaviour (POLL, 1956; YAMAOKA *et al.*, 1986). In the same paper, YAMAOKA *et al.* (1986) present, in a schematic way, the manner in which teeth are replaced in *E.* cf. *cyanostictus* (the taxon that was investigated in their study) and *S. marlieri*, and state that *T. irsacae* replaces its teeth in a different, yet unexplained, way. A critical examination of the schemes proposed by YAMAOKA *et al.* (1986) reveals, however, that they contain features unlikely to occur during tooth replacement in any cichlid.

We therefore reexamined the tooth replacement pattern and collected additional histological data of the replacement teeth in four eretmodine taxa: *E. cyanostictus*, *E.* cf. *cyanostictus*, *S. erythrodon*, and *T.* cf. *irsacae*. The results of this study will form the starting point for future investigations that will focus on the mechanisms responsible for ontogenetic and phylogenetic divergence of tooth shape within the Eretmodini.

MATERIAL AND METHODS

Natural populations were sampled in 1996 during an expedition along the western Lake Tanganyika shorelines. The specimens were fixed and stored in 80% ethanol. The following, adult, specimens were used:

– *Eretmodus* cf. *cyanostictus* (lineage A): 3 specimens (46.5, 51.5 and 52.5 mm standard length, SL);

– *E. cyanostictus* (lineage C): 3 specimens (51.5, 53.0 and 56.5 mm SL);

– *Spathodus erythrodon* (lineage F): 3 specimens: 50.0, 53.0 and 53.5 mm SL);

– *Tanganicodus* cf. *irsacae* (lineage E): 3 specimens: 41.5, 44.0 and 44.5 mm SL).

The four lineages studied here are derived from a mtDNA-based phylogeny that defined six genetically distinct lineages within eretmodine cichlids (RÜBER, 1998; RÜBER *et al.*, unpublished data).

The oral jaws were examined both before and after dissection. Some jaws were rinsed to eliminate the ethanol and were fixed and decalcified in 1.5 % paraformaldehyde-glutaralde-hyde in 0.1M cacodylate buffer, containing 0.1M EDTA. Subsequently, they were rinsed in the same buffer, dehydrated in a graded series of ethanol, cleared in propylene oxide and embedded in epon. Sections of 2 µm thickness were cut with a glass knife and stained with toluidine blue. The terminology used here is represented schematically in Fig.1.

RESULTS

On the oral jaws, teeth are present on the premaxillary and dentary bones. Since the characteristics of the oral jaw dentition have been described by YAMAOKA *et al.* (1986), only the data relevant for the interpretation of the tooth replacement pattern are presented here.

In all four taxa studied, both the premaxillary and the dentary teeth are implanted in what we have called tooth groups, arranged in adjacent oblique tiers (Figs 1, 2a-f, 3a,b, 4a,b, 5a). The number of tooth groups differs between the taxa, between specimens of a taxon, and even between left and right side of an individual. It ranges from 3 to 5 in *E.* cf. *cyanostictus*, from 5 to 7 in *E. cyanostictus*, and from 3 to 5 in *S. erythrodon*. In *T.* cf. *irsacae*, there are usually 2 or 3 well identifiable groups. YAMAOKA *et al.* (1986) reported the presence of only 2 to 4 groups in *E.* cf. *cyanostictus*.

The angle between the aligned teeth within each tooth group and the occlusal surface of the bone differs among the taxa (Figs 1, 2a-f, 3a,b, 4a,b, 5a). It is steep in *E. cyano-stictus* and *E.* cf. *cyanostictus* (Figs 2a,b, 3a,b) and shallow in *S. erythrodon* (Figs 2c,d, 4a,b) and *T.* cf. *irsacae* (Figs 2e,f, 5a). Because of this difference in angle, the most lin-gual position within a tooth group in *S. erythrodon* and *T.* cf. *irsacae* is more mesial than in *Eretmodus*. The groups consist of maximally three erupted teeth in *Eretmodus* (Fig. 3b) and maximally four erupted teeth in *S. erythrodon* (Fig. 4b) and *T.* cf. *irsacae* (Fig. 5a). These data fit with those of YAMAOKA *et al.* (1986). In addition, tooth germs are visible by transparancy within the medullary cavity of the bone in all three species.

Within each tooth group, the tooth located at the highest level of the bone (the occlusal surface) is found in a lingual position. The teeth in lingual positions show various degrees of wear (as shown by the reduced amount of orange-coloured enameloid) and can be considered to be the functional teeth. The other teeth within a group are of the same size as the functional teeth, except in *T.* cf. *irsacae*, where tooth size within a group diminishes labially. Unlike the functional teeth, they appear to be unworn, and the degree to which they protrude from the bone diminishes in a labial direction (rather distal in *S. erythrodon* and *T.* cf. *irsacae*). These

teeth can be considered to represent erupted replacement teeth. Teeth of more posterior groups are smaller than those of anterior groups; this is more pronounced in *T.* cf. *irsacae*, where tooth size distinctly decreases from the second group onwards. Functional teeth and erupted replacement teeth all show separate perforations of the oral mucosa.
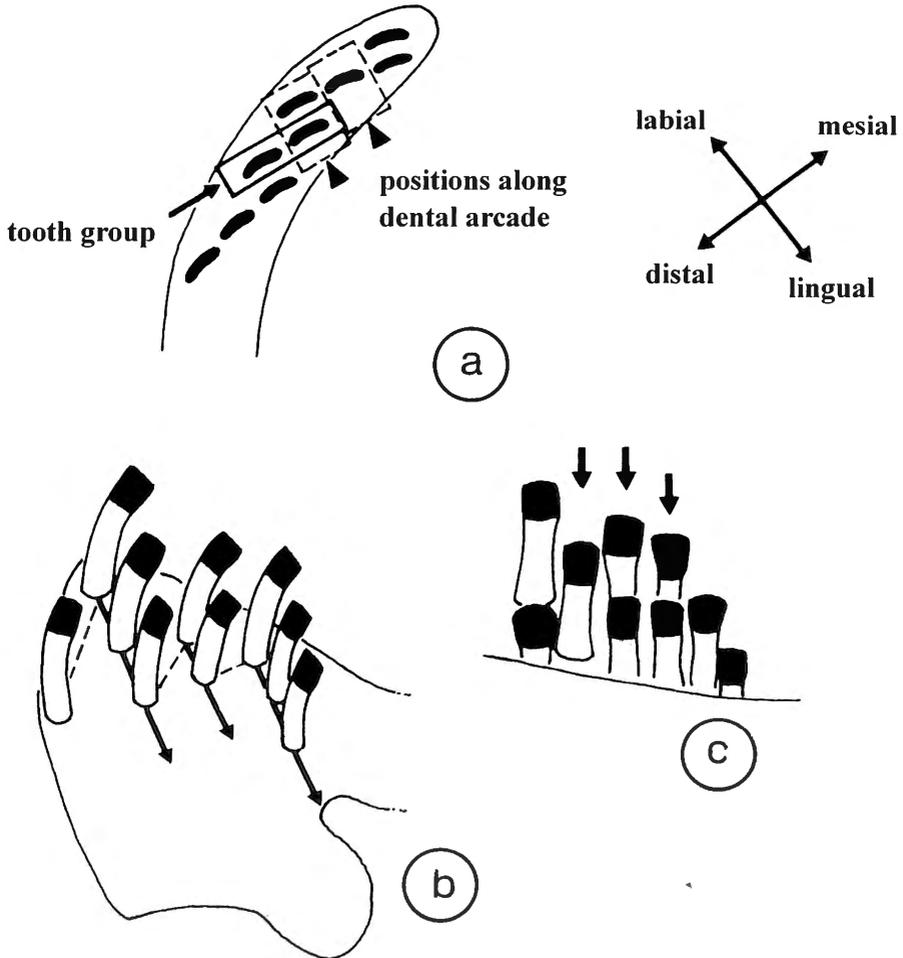

Fig. 1. – Orientation terminology used for the oral dentition of the eretmodines, shown on a schematic representation of an *E.* cf. *cyanostictus* left dentary dentition. (a) occlusal view; (b) labial view; (c) frontal view (*in situ*). In (b) broken lines connect teeth located on the same position along the dental arcade; arrowed lines interconnect teeth of a single tooth group. Arrows in (c) indicate adjacent tooth positions along the dental arcade.

Tooth replacement

For every single specimen of each of the four taxa, and for all four bones in each specimen (two premaxillaries, and two dentaries), the tooth positions, along with the state of

development at a particular position (non-erupted germ visible in transparancy, or erupted tooth) were recorded on a two-dimensional chart. On these charts, tooth groups were set out on lines, and tooth positions were evenly spaced within a group. From these individual charts, we have deduced a general chart for each of the four taxa, which is discussed below (Fig. 6a,b). Ascending numbers on the general charts reflect the mere order of development of the teeth, and are significant only as a ranking device to compare individual teeth; they do not reflect a true number in the dentition (tooth n° 1 is not the first tooth ever-formed in the animal's life, but the oldest possible tooth of a dentition at a given life-stage of an individual). Moreover, individual dentitions never express the full range of this general chart (meaning that not all the tooth numbers ever develop in a dentition). In all cases examined, however, numbers that are lacking occur only at the margins of the dentition, i.e., in mesial, distal and labial positions, in accordance with the extent of the dentition (i.e., the number of tooth groups). When the general chart is used as a template, individual charts are found to match the general chart in different areas. We fitted the individual chart as much as possible into the area with lowest numbers, to make comparisons easier (see Figs 3c, 4c, 5b).

E. cyanostictus and E. cf. cyanostictus

Fig. 6a shows the general chart as deduced from the observation of 24 bones of the two taxa with *Eretmodus*-like spatula-shaped teeth. According to this chart, starting from tooth n° 1, the next teeth to form lie labial to this tooth in an anterior (mesial) and posterior (distal) direction (teeth n° 2 and 3, respectively). New teeth will develop in the same relative positions with respect to teeth n° 2 and n° 3, yielding teeth n°s 4, 5 and 6. This process is repeated and produces the pattern depicted in Fig. 6a. If this chart is used as a template onto which the chart of a particular bone is grafted, tooth numbers on the template can be copied on the individual chart. Such a superimposition of individual and general (template) chart is shown for a left dentary bone of an *E.* cf. *cyanostictus* specimen in Fig. 3c. In nearly all the jaw bones of the specimens examined, the tooth that is, by ranking, the oldest tooth according to the template chart, also shows the heaviest degree of wear. Such teeth are always lingually situated in a tooth group, but do not necessarily belong to the most anterior tooth group. They most likely represent the first teeth to be shed. *E.g.*, in Fig. 3c, the oldest tooth (tooth n° 3) is placed lingually in the third tooth row; upon inspection of the dentition, it appears that this tooth is also the most worn tooth as indicated by the severely reduced amount of orange-coloured enameloid (Fig. 3a).

From the general chart, it appears that new teeth develop in adjacent positions along oblique lines, with teeth on one oblique line alternating in position with those of a more lingual line. If the oblique lines are considered waves of tooth development, labial waves are initiated after more lingual ones. The oldest teeth are found lingually, the youngest teeth along the labial side of the dentition.

The individual charts of both *E. cyanostictus* and *E.* cf. *cyanostictus* can be grafted on the same template chart. A wider area of the template is, however, expressed in *E. cyanostictus*, because these specimens contain more tooth groups. In the same way, although left or right bone, or premaxillary or dentary bone of one side, do not necessarily show the

same pattern, their individual charts can still be grafted on the same general chart. The observed differences relate to losses of lingually placed teeth and/or a delay in appearance of germs on the labial side.

S. erythrodon

The chart drawn after the observation of 12 bones of *S. erythrodon* (*e.g.*, Fig. 4a,b) differs slightly from the chart for *Eretmodus* (compare Fig. 6b with 6a). The major difference resides in a larger (mesio-distal) distance between newly developing germs. Therefore, the oblique lines that connect adjacent teeth are less steep than in *Eretmodus*. For this taxon too, tooth positions on every single bone can be grafted onto the general chart, and the oldest positions in the template correspond to the most heavily worn teeth in the dentition (*e.g.*, Fig. 4c).

T. cf. irsacae

The observations on 12 bones of *T.* cf. *irsacae* (*e.g.*, Fig. 5a) fit with a chart that is identical to the one for *S. erythrodon*. In each of the 12 bones examined, tooth size and degree of eruption diminish in a labial (distal) direction within each tooth group. This matches the order of appearance as suggested on the general chart (Fig. 5b, 6b). As for the other three taxa, the teeth on the « oldest » positions on the general chart are the most heavily worn teeth.

Histological observations of the jaws

Light microscopical observations on serial sections through the premaxillary and dentary bones of the four taxa studied revealed the presence of replacement teeth in various phases of development within the medullary cavity of the bone. In the two taxa with the *Eretmodus*-like tooth shape, numerous germs are present (Fig. 7a). In *Tanganicodus*, only a few replacement teeth are observed in the medullary cavity. The position of the germs, and their state of development, fits with what can be expected from the general chart (compare Figs 6a and 7a). The tips of the germs are located labially in the medullary cavity; however, their proximal ends lie more lingually.

Collars of attachment bone (ovals in the section shown) are found at different levels in the medullary cavity (Fig. 7a). They consist of a compact bone ring firmly anchored to a mass of cancellous bone that fills this part of the medullary cavity (Fig. 7a). Collars still in the process of deposition lie deepest with respect to the oral epithelium. They support fully-grown teeth, the tips of which erupt more labially (and less apically) along the jaw bone than do those supported by attachment bone that lies nearer to the surface. So far, we have not been able to trace the origin of the replacing teeth, whether it is from a dental lamina associated with the predecessor, or whether it is totally separate from the oral epithelium.

Depending on the place along the jaw bone, specialized cell types line the bone tissue. Numerous osteoclasts engulf the free bone margins below the oral mucosa (Fig. 7b). At the opposite side of the jaw bone, numerous intensively basophilic osteoblasts surround the end of the free bone spicules or are arranged in a pseudo-epithelial manner along the bone surface (Fig. 7c).
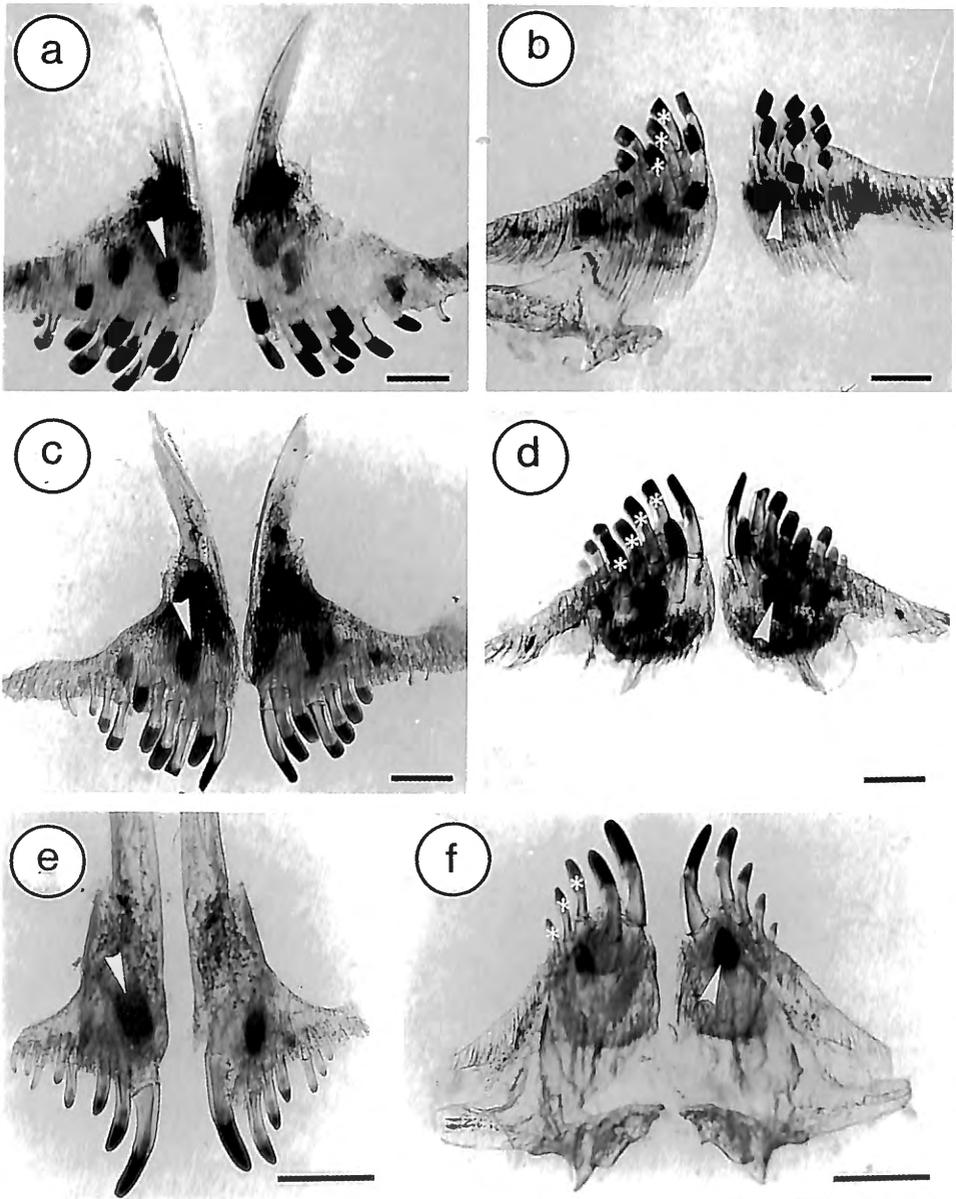
Fig. 2. – Labial view of dissected premaxillaries (a,c,e) and dentaries (b,d,f) of *E.* cf. *cyanostictus* (a,b), *S. erythrodon* (c,d), and *T.* cf. *irsacae* (e,f). The dark tips of the teeth are the (orange-coloured) enameloid caps. Note the presence of tooth germs in the medullary cavity, visible in transparancy (arrowheads). In (b), (d) and (f), asterisks indicate teeth belonging to a single tooth group. Scale bars in (a) to (f) = 1mm.
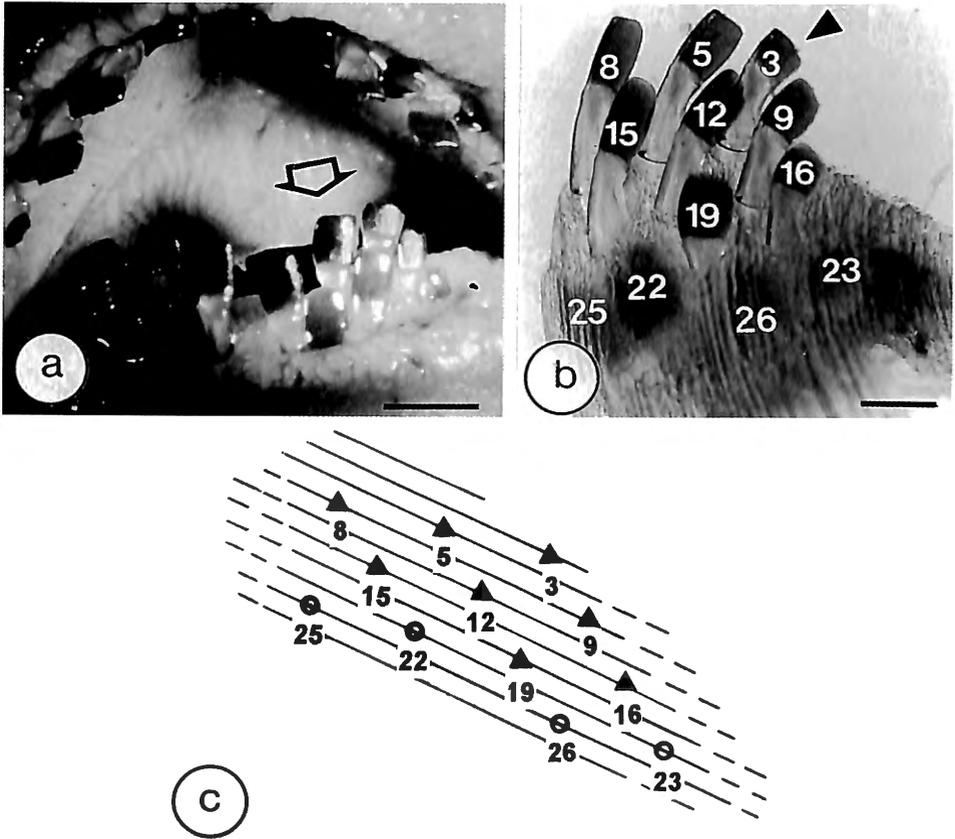
Fig. 3. – Left dentary of an *E*. cf. *cyanostictus* (51.5 mm SL), shown *in situ* (a, arrow; frontal view) and after dissection (b, labial view). In (c) the dentition of this left dentary is depicted schematically to show how the scheme of the replacement pattern relates to actual morphology. Erupted teeth are indicated by triangles, tooth germs within the medullary cavity (at least those visible in transparancy) by circles. The teeth are set out according to the general chart as presented in Fig. 6a. Tooth numbers are then added and reflect the order of development of the teeth. Lines interconnect successively developing teeth. In (b) an arrowhead points to the most heavily worn tooth on the lingual side of the dentition. Scale bar in (a) = 1 mm, in (b) = 0.5 mm.
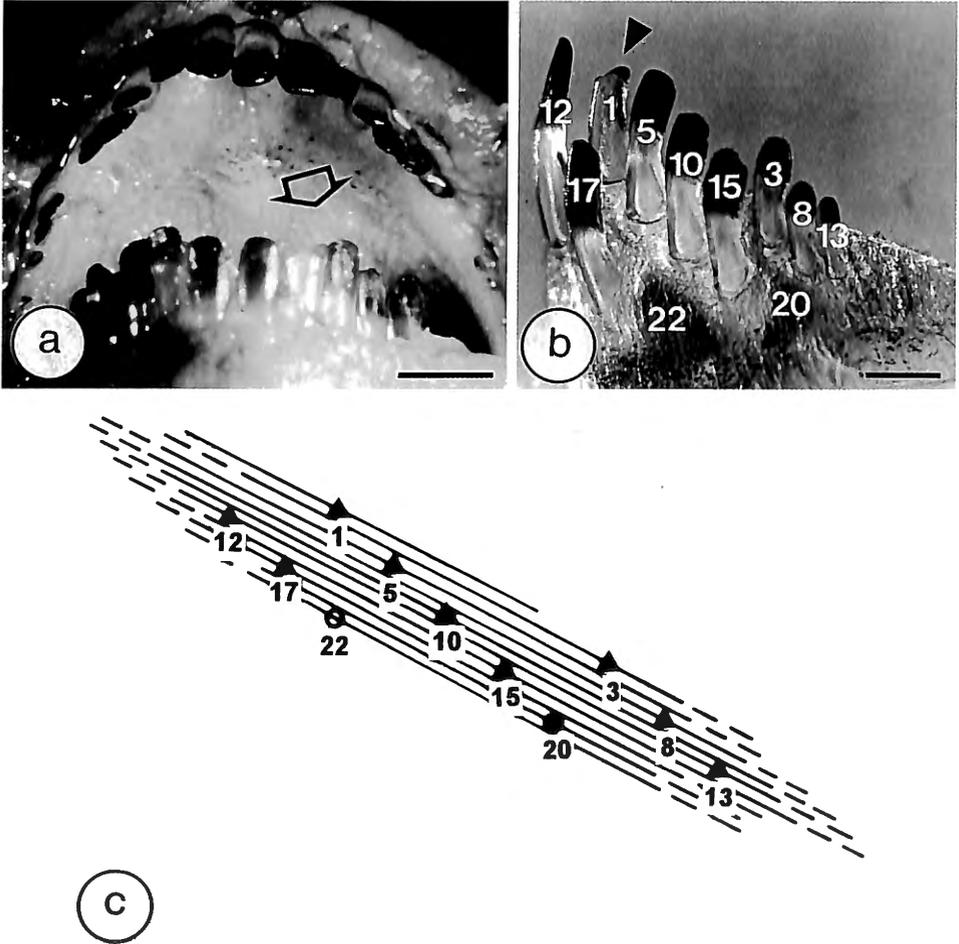
Fig. 4. – Left dentary of a *S. erythrodon* (53 mm SL), shown *in situ* (a, arrow) and after dissection (b). In (c) the dentition is shown schematically and grafted onto the general chart shown in Fig. 6b in the same way as was done for Fig. 4c. In (b) an arrowhead points to the most heavily worn tooth (note the reduced amount of enameloid). Scale bar in (a) = 1 mm, in (b) = 0.5 mm.
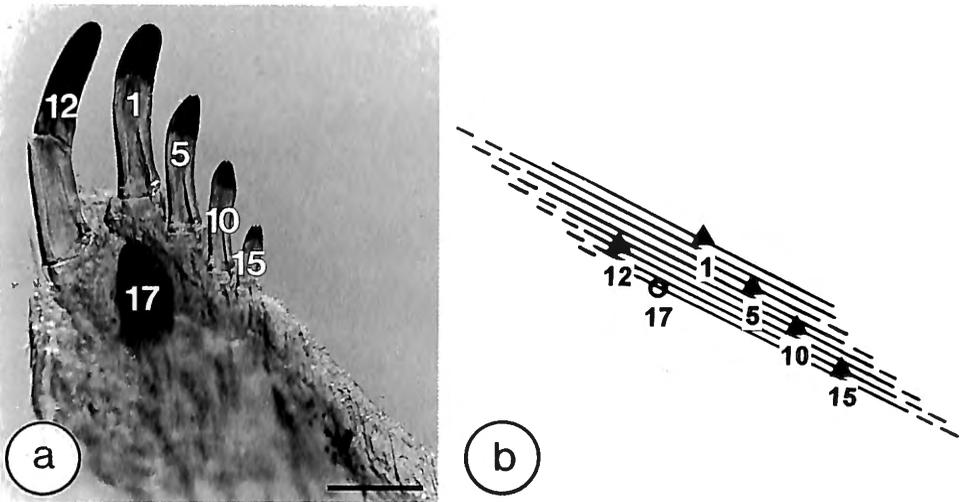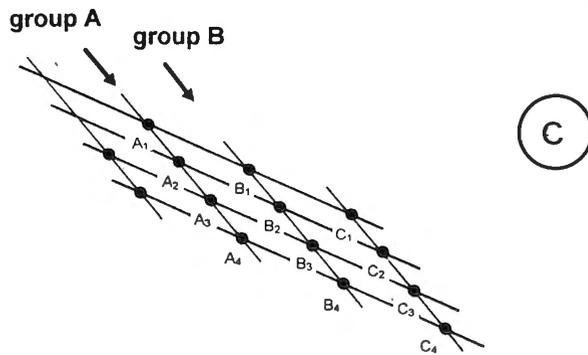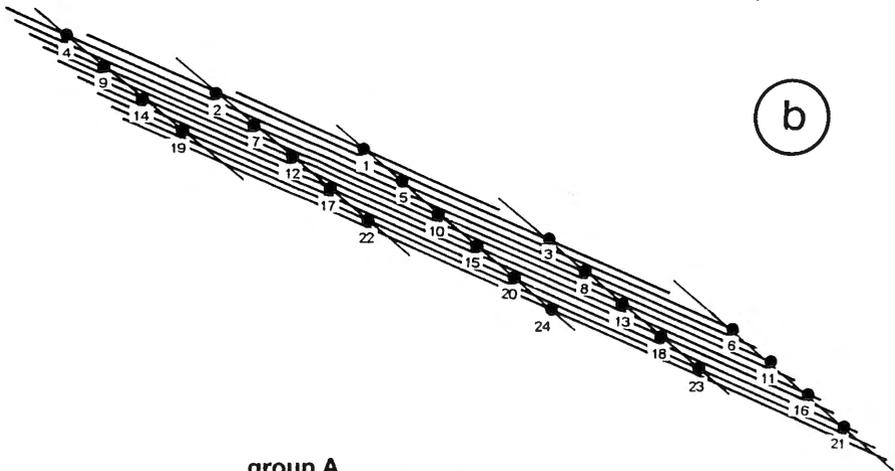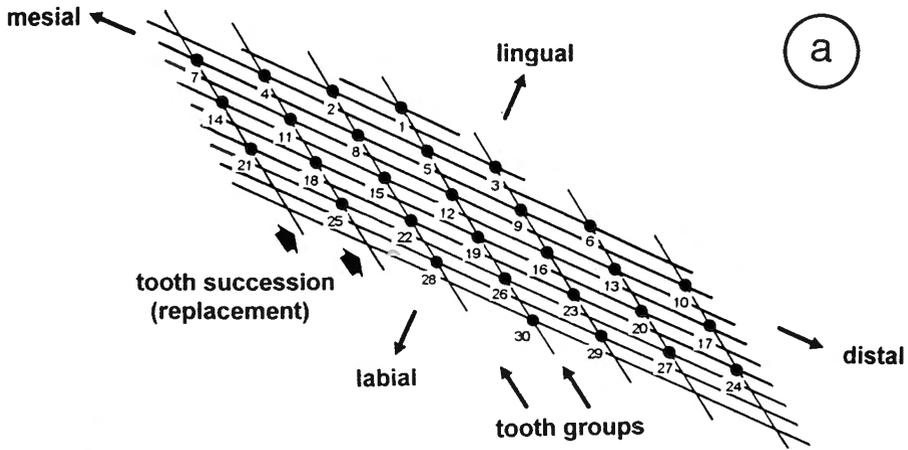
Fig. 5. – (a) Left, dissected, dentary of a *T.* cf. *irsacae* (44 mm SL). The most anterior tooth was broken during preparation. The same dentary, and its contralateral counterpart, are also shown on Fig. 2f. In (b) the dentition is shown schematically and grafted onto the general chart shown in Fig. 6b in the same way as was done for Fig. 4c. Scale bar in (a) = 0.5 mm.

Legend to the figure (see opposite page)

Fig. 6. – General charts of the adult dentition in *Eretmodus* (a), and in *S. erythrodon* and *T.* cf. *irsacae* (b). The figures are applicable to left premaxillary and dentary, and the mirror images to right premaxillary and dentary. Teeth (unerupted and erupted) are indicated by circles. Oblique lines connect successively developing teeth. The number of tooth groups on charts (a) and (b) corresponds to the maximal number of tooth groups observed in the respective taxa (7 in *E. cyano-stictus*, 5 in *S. erythrodon*). In (c), the replacement pattern in *E.* cf. *cyanostictus*, as erected by YAMAOKA *et al.* (1986), is redrawn to match the graphical representation used here. According to this scheme, A_1 succeeds to A_2 which itself succeeds to A_1.
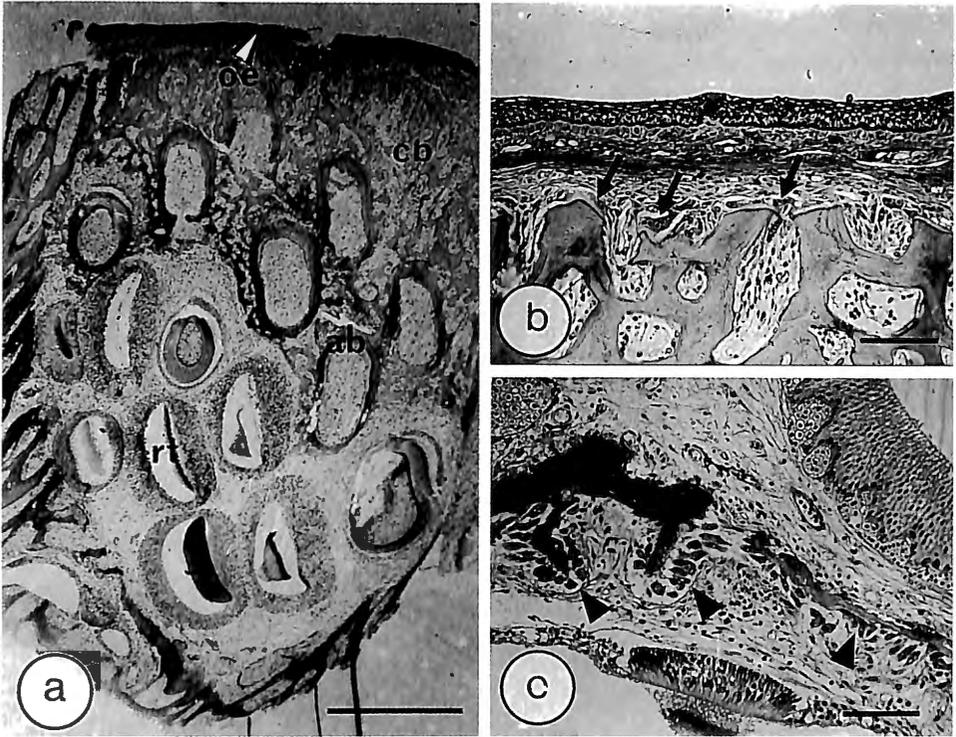
Fig. 7. – Microphotograph of a vertical section parallel to the mesio-distal axis through the right dentary of an *E.* cf. *cyanostictus* (a) and details of the occlusal (b) and opposite, basal (c) side of the jaw bone. Mesial is to the left. Note the presence of numerous osteoclasts (arrows) resorbing the free margins of the bone surface (arrows) and abundant, intensively basophilic osteoblasts on the opposite side of the jaw (arrowheads). ab : young attachment bone of labial, erupted tooth ; cb : cancellous bone ; oe : oral epithelium ; rt : replacement tooth. Scale bar in (a) = 0.5 mm ; in (b) and (c) = 50 μm.

DISCUSSION

Tooth replacement pattern in eretmodine cichlids

Based on 48 individual charts of tooth positions, we have been able to deduce general charts that fit for all specimens of each taxon, irrespective of the bone considered (Figs 6a,b). These charts indicate the order in which teeth have developed at a given stage and in which they will replace older teeth. Below we will discuss the evidence that supports the proposed patterns of tooth replacement.

Firstly, it appears that new teeth develop labial from older ones. The youngest tooth germs are found along the labial side of the dentition, the oldest, functional, teeth along the lingual side of the dentition. These observations agree with our histological findings, indicating that tooth germs develop and erupt labial to older teeth. The labial formation of new germs is uncommon among teleosts ; usually teeth develop lingually from functional

teeth (*e.g.* in *Amia*: MILLER & RADNOR, 1973; in *Salmo gairdneri*: BERKOVITZ, 1977; in *Serrasalmus*: BERKOVITZ & SHELLIS, 1978; see also FINK, 1981). In cichlids the most common situation is that teeth, at least those of the outer row, are replaced within the same row and that replacement teeth develop from below (SNOEKS, personal communication). In rare cases, such as in *Prionurus,* replacement teeth develop both lingual and labial to the functional teeth (WAKITA *et al.*, 1977).

Secondly, if one assumes that the speed of development of germs is constant along the mesio-distal axis of the dental arcade, the order in which teeth become functional should be a reflection of the order of tooth development. Since it is likely that functional teeth are more or less equally submitted to wear, teeth showing the heaviest wear should therefore represent the oldest teeth. Our observations show that this is the case: the teeth showing the heaviest wear always coincide with the oldest teeth. These may well be in the posterior region of the dentition, *e.g.* in a situation when teeth n°s 1 to 5 are shed, and tooth n° 6 is the oldest persisting tooth in the dentition, as observed on several occasions.

The oblique lines that connect the positions of successively forming teeth represent successive waves of tooth development. New germs alternate along these waves with respect to teeth along a previous (older) wave. If the space between teeth of a single tooth group is considered to be constant, as in Fig. 6a,b, the place along the dental arcade where new germs will form along the oblique lines depends on the slope of these lines. In the *Eretmodus*-like dentitions, germs form successively at every third position along the dental arcade. In *S. erythrodon* and *T.* cf. *irsacae*, where the slope is very shallow, new germs arise at only every seventh position along the dental arcade. Inevitably, this raises the question of whether and how teeth in a particular position are replaced. Interestingly, the sections reveal that erupted teeth, even those that emerge low along the labial side of the jaw bone (*e.g.* the third or fourth tooth of a tooth group), are firmly anchored to attachment bone deep within cancellous bone of the medullary cavity, and that they have separate perforations through the oral mucosa. It is highly unlikely that teeth will become detached from this attachment bone and move upward to take a more apical position on the bone, *i.e.*, more towards the occlusal surface. In such a process, the tooth would repeatedly become loose and again attached. It is unlikely that tooth replacement would proceed in such an inefficient way. We suggest that the most likely explanation for our observations is that the tooth does not move once its attachment bone has been deposited. Rather, the jaw bone is remodeled to expose the most apical tooth in a tooth group once an even more lingually placed tooth of that tooth group has been shed. The presence of numerous osteoclasts indicating severe resorption along the apical (occlusal) side of the bone, and intense osteoblastic activity indicative of new bone formation along the opposite side, support this hypothesis. We therefore propose that, as waves are lost lingually through shedding of the teeth, the next wave will deliver the next functional teeth, without these having to move but with bone remodeling instead to expose them. That teeth become functional in such a passive way by exposure resulting from bone resorption progressing apically and lingually, and deposition basally and labially, appears to be a novel mechanism, to our knowledge not previously reported in any bony fish. It requires that the rate of bone remodeling be tuned to the rate of tooth formation. This can be tested by injecting bone markers in living fish.

After three waves have been shed in the *Eretmodus*-like dentitions (seven in *Spathodus* and *Tanganicodus*), a tooth eventually ends up in the position along the dental arcade previously taken by a tooth of a more posterior group; *e.g.* in Fig. 6a, tooth n° 15 will eventually succeed n° 5 on that position along the dental arcade. A tooth in a certain position is thus « replaced » by a tooth of an anterior tooth group (*i.e.*, between-group replacement). Within-group replacement (*e.g.*, in the same example, tooth n° 15 succeeding n° 8) is unlikely because teeth would have to move continuously into more mesial positions. Should this occur, replacement teeth should often be found in intermediate positions along the dental arcade; this is not the case (*e.g.* on Fig. 6a, teeth n°s 5 and 15, or 3 and 12, are aligned in one position along the dental arcade, compare with the *in situ* view on Fig. 3a). In addition, within-group replacement cannot explain other features such as the presence of incomplete tooth groups (not possessing the full number of erupted teeth). Evidence for between-group replacement can also be drawn from left-right comparisons. If between-group replacement is operating, the large tooth (tooth n° 1) on the dentition shown in Fig. 5a, will be replaced by tooth n° 17. This is exactly what is found on the contralateral side (cf. Fig. 2e). This observation also suggests that a phase difference may exist between both sides. The tooth germs which succeed each other at a given position along the dental arcade constitute tooth families *sensu* REIF (1982, 1984) (*i.e.*, a functional tooth and its successors). So far, we have not been able to trace any epithelial links between these tooth germs, unlike what could be expected from teeth of a single tooth family (the germs are separated by three, or even seven, waves).

In most bony fish, the successor expands beneath or around the base of the tooth in function, resulting in its resorption. The mechanism of shedding in the eretmodine oral jaws is clearly different. Although we have observed wearing of functional teeth down to below the level of the enameloid cap, it is unlikely that this is the only way for the tooth to be shed. Probably resorption along the lingual side of the premaxillary or dentary bone affects the attachment bone as well. Further histological studies are needed to clarify this point.

While successive waves are lost, tooth groups migrate in a posterior direction. Tooth groups are temporary assemblages, the composition of which changes as successive waves deliver the functional teeth. Depending on the number of waves that have been shed, tooth groups that lie anteriorly along the dental arcade, will eventually end up in the middle of, or even beyond the middle of the dental arcade. The mechanism of between-group replacement explains (i) why left and right halves of the dentition often contain different numbers of tooth groups: this simply depends on which wave has been lost, and this does not need to be synchronous left and right; (ii) why the dental arcade may show only half a group at its anterior or posterior end, and (iii) why, upon first inspection of the dentition, some tooth groups overlap each other with one, others with two teeth.

The general charts represent the state of the dentition in adults. At present, it is unknown to what extent the pattern of replacement relates to the order of tooth appearance in the larva, in other words whether the pattern of succession is established upon the first appearance of the teeth in the larva. Such a correspondance was found earlier in piranhas by BERKOVITZ & SHELLIS (1978), but is not always the case. In cyprinids, for example, distinct differences between larval and adult dentitions reflect differences in tooth replacement patterns (NAKAJIMA, 1984).

Different models have been proposed to explain tooth replacement patterns in lower vertebrates (OSBORN, 1984). The most important models are the field model of Zahnreihen (EDMUND, 1960, 1969), and the clade model of local inhibition (first defined by OSBORN, 1971, 1978, but later refined by WEISHAMPEL, 1991). Our observations seem to be at variance with both models. At first sight, the tooth groups as defined in this study could correspond to Zahnreihen. However, the Zahnreihe model postulates the emission of signals at the rostral tip of the jaw, eliciting tooth formation at regular intervals from the front to the back of the jaw. The observation that teeth like formed anterior to existing teeth is incompatible with Zahnreihen, an argument already raised by WEISHAMPEL (1991). On the other hand, although local inhibition may well account for the pattern seen here, it does not explain the gradual size decrease of the teeth towards the distal side of the dentition. A decrease in the number of cells with odontogenic potential from mesial to distal along the dental arcade is compatible with Zahnreihen. Clearly, the pattern described for the eretmodines must be seen as the empirical outcome of a tooth generating mechanism which is still not fully understood.

As described above, the proposed tooth replacement pattern allows the frequently observed differences between left or right bone, or between premaxillary or dentary bone, to be understood in terms of a phase difference in tooth development between the jaw quadrants. It is interesting to note that LIEM (1979) found that the morphologically symmetrical muscular apparatus can act with pronounced asymmetrical firings of multiple muscles. This asymmetric firing could provoke differences in wear between left and right jaw bones and result in a phase difference in the replacement of the dentition. Nevertheless, tooth replacement has repeatedly been shown to be independent, to a marked extent, in the different jaw quadrants (BERKOVITZ & MOORE, 1974, 1975; REIF, 1976; BERKOVITZ & SHELLIS, 1978).

To compare the tooth replacement patterns proposed here with those from YAMAOKA et al. (1986), we have redrawn their scheme for *Eretmodus* in a way that matches our type of presentation (Fig. 6c). First, they suggested that the most lingually placed tooth of each tooth group has the same age. Our observations on the overall organisation of the dentition, and the state of wear of these particular teeth, suggest that this is not the case. Secondly, YAMAOKA et al. (1986) suggested that a tooth group consists of a functional tooth and its successors. Inevitably, they failed to explain how a tooth would « move up » (their expression) along the bone as is required according to their tooth replacement scheme. According to the tooth replacement pattern described here, teeth do not « move up » since the replacement teeth are already positioned where they will replace the current functional tooth.

Inter(generic) taxon comparisons

The chart onto which the dentitions of *S. erythrodon* and *T.* cf. *irsacae* are easily grafted, is essentially identical to the chart for *E. cyanostictus* and *E.* cf. *cyanostictus*. The only difference is the larger distance between successively initiated germs in *S. erythrodon* and *T.* cf. *irsacae* compared to the *Eretmodus*-like dentitions. This results in a pattern where tooth groups are shifted more with respect to each other, because of the smaller

angle of tooth groups with respect to the occlusal surface. As a result, it seems that, although there is superficial resemblance between the *Spathodus* dentition and that of *Eretmodus* (at least with respect to tooth size and shape), the *Spathodus* dentition is actually more similar to the *Tanganicodus* dentition.

It appears that a single pattern explains the different dentitions observed among the eretmodines. Differences between taxa can be related to differences in extent of the theoretically possible dentition being expressed: *e.g.* when the two *Eretmodus* type dentitions are superimposed on the general chart, *E. cyanostictus* appears to express a far more extensive part of the scheme compared to *E.* cf. *cyanostictus*. The same reasoning can be applied to the intraspecific differences that are sometimes found: these always concern positions at the mesial or distal margin of the dentition, and can be explained in terms of smaller parts of the theoretical pattern being expressed.

In conclusion, the different dental arcades in these closely related species, which allow them to utilize different food resources, are the outcome of a single, regular pattern of tooth formation and replacement. The difference in angle of the tooth groups with respect to the occlusal surface, the different number of tooth groups, and number of teeth within a tooth group, can all be related to a small shift in spacing of the newly developing germs. The challenge for future studies will be to understand how different tooth shapes are generated and genetically controlled within this group of closely related species.

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