Comparison of Teeth and Dermal Denticles (Odontodes) in the Teleost *Denticeps clupeoides* (Clupeomorpha)

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ABSTRACT The present work is a contribution to an extensive comparative structural and developmental study we have undertaken to understand the evolution of the dermal skeleton in osteichthyans. We have investigated the structure of developing and functional tooth-like dermal denticles located on the head of *Denticeps clupeoides*, a clupeomorph, and compared their features to those of oral teeth. Morphological (scanning electron microscopy) and structural (light microscopy and transmission electron microscopy) observations clearly demonstrate that these small, sharp, conical and slightly backward-oriented denticles are true odontodes, i.e., homologous to oral teeth. They are composed of a dentine cone surrounding a pulp cavity, the top being covered by a hypermineralized cap. These odontodes are attached to a circular pedicel of attachment bone by a ligament that mineralizes, and the attachment bone matrix merges with that of the bony support. The pedicel of attachment bone surrounds a vascular cavity that is connected to the pulp cavity which is devoid of blood vessels and of nerve endings. Once the odontode is functional, the deposition of collagen matrix (called circumpulpar dentine) continues against the dentine, ligament, and attachment bone surfaces, thereby provoking a narrowing of the pulp cavity. Odontodes are shed by resorption occurring at the base, but their pedicels of attachment bone persist at the bone surface and become embedded in the bone matrix, within which they are clearly visible. The oral teeth are similar in shape, size, and structure to the odontodes, and they show only small differences probably related to the different function of these elements: They are more firmly anchored to the attachment bone, and the amount of dentine is relatively smaller than in odontodes. Despite their different functions, this close structural agreement between teeth and odontodes in *Denticeps* suggests that 1) competent cells from the same (ecto)mesenchymal population might be involved and 2) the genetic control of the developmental processes could be identical. It is suggested that the odontode expression in extra-oral positions is a relatively late novelty in this lineage. J. Morphol. 237:237-255, 1998. © 1998 Wiley-Liss, Inc.

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On September 13, 1958, during field work in southwestern Nigeria, an unknown, herring-like, small teleost species was captured in the River Yimoji by H.S. Clausen. The examination of several juvenile and adult specimens revealed features it shared with the teleost families Elopidae, Albulidae, Clupeidae, and Osteoglossidae, and some unusual and unique characters that led Clausen ('59) to erect not only a new genus but also a new family. The most striking character is "... the possession of an extensive

extra-oral (i.e., dermal) dentition covering most of the dermal bones of the head" With the generic name *Denticeps*, the author referred to this dermal dentition, and he placed it in the new family, Denticipitidae, with a single species, *D. clupeoides*. In modern actinopterygian cladograms (Lecointre,

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'94; Nelson, '94), Denticipitidae appear as the sister group of the suborder Clupeoidei (which include, e.g., the Clupeidae), and together form the order Clupeiformes.

The pictures presented by Clausen ('59) from an alizarin red-stained specimen demonstrate tooth-like elements, i.e., they could be odontodes as defined by Ørvig ('67). This particular character has been well accepted by taxonomists (e.g., Greenwood, '60, '68; Grande, '85) and cited in numerous text books and review articles (e.g., Whitear, '86; Smith and Hall, '90; Nelson, '94). However, the absence of clear data demonstrating the "dental" structure of these elements has led some authors to question them as true odontodes (e.g., Reif, '82).

For over a decade we have undertaken extensive comparative studies of the structure and development of the dermal skeleton (i.e., teeth and tooth-derived elements, scales, finrays, and some dermal bones in the head and pectoral girdle) in vertebrates, in an evolutionary perspective (see review in Huysseune and Sire, '98). Understanding the structural identity of the "extra-oral denticles" on the head of *Denticeps* is thus of some importance for us, to get the best possible view of the tissue diversity within the dermal skeleton in osteichthyans.

Odontodes are probably among the oldest skeletal elements, covering the early jawless vertebrates, some 500 millions years ago (Janvier, '96). During evolution odontodes were either conserved, slightly or strongly modified, or lost. Among the living vertebrate lineages, the odontodes have given rise to a number of superficial "tooth-derived" structures (see reviews in Ørvig, '77; Reif, '82; Smith and Hall, '90, '93; Huysseune and Sire, '98) including odontocomplexes (Ørvig, '67, '77). Among extant taxa, the presence and structure of isolated odontodes (extra-oral elements having the structure and organization of teeth) is well known in chondrichthyans (sharks, rays, and skates) in which they are called placoid scales or dermal denticles (Reif, '80) and where they have developed various shapes (e.g., Compagno, '88; Deynat and Séret, '96). In the sarcopterygians, odontodes are present on the scale surface of Latimeria chalumnae (Smith et al., '72; Castanet et al., '75). In the actinopterygians, isolated odontodes exist in polypterids (Sewertzoff, '32) and in garpikes (lepisosteids) (Nickerson, 1893); among teleosts, odontodes are known in the armored catfish (e.g., Callichthyidae, Loricariidae; Siluroidei) in which they are attached to al-most all the dermal skeletal elements (Bhatti, '38; Sire, '93; Sire and Meunier, '93). Two recent descriptions of the structure and development of odontodes and first-generation teeth in some armored catfish have shown that both elements share many characters (Sire and Huysseune, '96; Huysseune and Sire, '97a). The structure of dermal denticles has been also described on the rostra of xiphiids and istiophorids (Xiphioids, Perciformes) by Carter ('19). These are highly specialized teleosts, and the histological sections presented by Carter clearly illustrate that these denticles are odontodes similar in shape and structure to oral teeth. To the best of our knowledge there is no histological study available which definitively demonstrates that the denticles on the head of Denticeps are odontodes. The aim of the present study was to elucidate the nature of these dermal denticles and eventually to compare their structure and attachment with those of teeth in the same species and with the odontodes of armored catfish described previously (Sire and Huysseune, '96). To this end, we took advantage of a number of specimens of Denticeps clupeoides available in Museum collections in Paris (France) and Tervuren (Belgium) to undertake a morphological and histological study using light, and scanning, and transmission electron microscopy.

MATERIALS AND METHODS Material

Denticeps clupeoides (Clausen, '59) (Denticipitidae, Clupeiformes, Clupeomorpha) is a small teleost (60 mm maximum length), living in coastal rivers of Nigeria and Cameroon, Africa. Specimens are frequently encountered in these rivers where they swim extremely fast in fast-running streams. The diet of *D*. clupeoides was not reported by Clausen ('59). Nevertheless, while some long and slender gill-rakers on the lower segment of the first branchial arch form a filter mechanism, the presence of numerous oral and pharyngeal pointed and conical teeth suggests active feeding on small prey. Since 1959, several field studies have been undertaken in West Africa by ichthyologists from different countries (e.g., France, Belgium). They were allowed to bring several specimens to the Muséum National d'Histoire Naturelle (MNHN), Paris (France) and the Musée Royal de l'Afrique Centrale (MRAC), Tervuren (Belgium)). The specimens used in this study are from these two collections. Scanning electron microscopic observations (SEM) were performed on three alcoholfixed adult specimens (36, 37, and 39 mm standard length, SL), MRAC 90-20-P-121-180, 1990. Light and transmission electron microscopic (TEM) observations were carried out on one formalin-fixed and alcoholconserved adult specimen (34 mm SL), MNHN 1960-391.

SEM

The anterior part of the specimens was cut off, rehydrated in distilled water, and placed into a solution of 3% sodium hypochlorite to remove the soft tissues from the bone surface with the help of a fine paint-brush. The samples were then dehydrated in a graded series of ethanol, dried, glued on a brass support, and covered with a 20-nmthick layer of gold/palladium in a Balzer apparatus. They were observed in a JEOL JSM-840A.

Histology/TEM

The head was cut off, rehydrated in distilled water, and decalcified for 5 days in a mixture containing 1.5% glutaraldehyde and 1.5% paraformaldehyde in cacodylate buffer (0.1 M, pH 7.4) to which 0.1 M EDTA (ethylenediaminetetraacetic acid) was added. After a quick rinse in the same buffer, the sample was post-fixed for 2 h in osmium tetroxide, then dehydrated in a graded series of ethanol, and embedded in Epon 812. One-micron-thick sections were obtained using a diamond knife and stained with toluidine blue. Ultra-thin sections were contrasted with uranyl acetate and lead citrate and observed in a Philips 201 EM operated at 80 kV.

RESULTS

In *Denticeps* dermal denticles are attached to nearly all the bones of the head, and also laterally on the most anterior scale of the median row (Fig. 1). Most of the denticles are located on the maxilla, premaxilla, and dentary, which also bear teeth on their oral edges. There are also rows of denticles on the ventral edge of the infra-orbitals, interoperculum, and preoperculum.

Morphology

Scanning electron microscopic (SEM) observations have extended Clausen's description ('59), and enabled us to compare the external denticles with the teeth located on the edges of the buccal cavity (Fig. 2).

Denticles

Except in some areas such as the flat surfaces of some bones where they are irregu-



Fig. 1. Lateral view of the anterior part of the body in *Denticeps clupeoides* showing the distribution of the dermal denticles and the bones cited in this study. D, dentary; M, maxilla; IOP, interoperculum; OP, opercu-

lum; P, parietal; PM, premaxilla; POP, preoperculum; S, scale. Slightly modified after Clausen ('59). Scale bar = 0.3 mm.



Figure 2

larly distributed, most of the dermal denticles are densely disposed in rows. On the ventral side of the head these rows constitute denticulate ridges from the anterior extremity of the mandible to the posterior extremity of the head (Figs. 1, 2a). Three to four rows of denticles are present on the dentary, premaxilla, and maxilla, whereas denticles are distributed less densely on the surface of the parietal, preoperculum, and operculum.

The epidermis covers part of the denticle, but the fixation quality was far too poor to identify the precise extension of the epidermis on the denticle surface (Fig. 2d,g). SEM observations indicate that the tip of the denticle pierces the epidermis, but this is clearer in histological sections (Fig. 3). However, the combination of SEM and light microscopic observations defines the slight narrowing at the upper part of the denticle cone as being the level of the upper limit of the epidermal covering (Fig. 2d,f).

The denticles are elongated, spine-shaped elements firmly fixed on the bony support. Removal of the soft tissues by sodium hypochlorite treatment reveals the entire morphology of the denticles (Fig. 2c,f,j,k). Although they are usually conical with a sharp tip, some denticles can be twisted or curved, as, e.g., on the edge of the maxillary bone (Fig. 2g), and some tips may be either rounded or broken.

The denticles located on the anterior region of the head and those of the ventral rows are 160 to 180 μ m long (Fig. 2c,d) with bases 20 to 30 μ m in diameter (Fig. 2h). When they are arranged in rows the denticles are regularly spaced at 50-µm intervals in the same row but the odontodes from two adjacent rows can lie closer (Fig. 2c). The length of the denticles that are located on the flat surface of bones averages 100 µm (Fig. 2f), with some denticles at the posterior edge of the opercular bones being 200 µm. The denticles are generally oriented slightly backward (Fig. 2d) except at the most anterior region of the head where they are perpendicular to the antero-posterior axis of the bones and ventrally oriented (Figs. 1, 2a). The backward orientation is more pronounced for the denticles located on the flat surfaces of bones (Fig. 2c,j,k) than for those in the ventral rows and on the anterior part of the head (Fig. 2a,b).

SEM pictures show that the tip and the upper dentine cone surface of the functional or developing denticles is smooth (Fig. 2cf,j), and this contrasts with the rough surface of the base of functional denticles (Fig. 2c,e,f). This irregular aspect is due to the remains of the attachment of numerous small anchoring bundles. The functional denticles appear to be attached directly to the bony support without intervening ligaments. However, small collagen bundles anchor on the surface of the denticle base (Fig. 2e), and larger ligaments are seen in the prolongation of the base of developing denticles (Fig. 2j). This suggests that these ligaments are later embedded in the denticle matrix (dentine or attachment bone) when the denticle becomes functional. Moreover the different parts of the denticles react differently to the sodium hypochlorite treatment: Some tips can be lost, and the denticles can be shed,

such an anchoring bundle. **f:** Isolated, small denticle which has probably been recently attached as shown by the small depression at the opercular surface below. **g:** This denticle on the maxilla shows an irregular shape and a rounded tip. h: Edge of the premaxilla. Three denticles were lost (arrows), but their circular pedicels persist, surrounding large cavities. The arrowheads point to the openings of smaller vascular cavities. i: Teeth on the buccal side of the dentary. The denticles on the outer side (arrowheads) have not resisted the sodium hypochlorite treatment and were lost. The arrow points to a resorption of a tooth base. Both the attachment bone and the dentine cone are attacked. j: Newly forming denticle parallel to the opercular surface. Two ligaments (arrows) already link its base to the bottom of a circular depression on the bone surface. k: Posterior region of the first anterior scale shown in Figure 1. This was the only scale bearing a denticle in this specimen. Scale bars = 2mm in a; 100 μ m in b,c,k; 50 μ m in d,h,i; 25 μ m in e–g and j.

Fig. 2. SEM micrographs of dermal denticles and teeth attached to the dermal bones of the head (a-j) and to a scale (k) in Denticeps clupeoides. The samples have been photographed untreated (a,d,g) or after slight (b,c,e,f) or strong (h,i,k) cleaning in sodium hypochlorite solution. Anterior is to the left. **a**: Anterior part of the head showing the distribution of the denticles on the dentary (D), the premaxilla (PM), and the maxilla (M). T, buccal teeth. **b**: Anterior edge of the dentary. A fron-tier line can be traced (dotted line) between the teeth (above) and the denticles (below), but except for their orientation, the morphology is similar for both elements. The loss of numerous denticle tips (arrowheads) is due to sodium hypochlorite treatment. Note that most of the tooth tips have resisted the treatment. c: Denticles on the ventral side of the preoperculum are clearly oriented backward. d: Two denticles from the same region showing their spine-like shape and the extent of the epidermal covering. e: Base of two denticles (asterisks) from the same region. The rough aspect of their base is due to the remains of collagen bundles. The arrow points to

depending on the duration of the treatment. When a denticle is shed, its basal region, which we have called the pedicel, remains attached to the bone surface. The pedicels are typically circular crests surrounding large, deep cavities, which are different from the openings of vascular canals at the bone surface (Fig. 2h,i). The rough surface of these pedicels corresponds to sectioned collagen bundles belonging to a large ring-shaped, mineralized ligament which is seen in sections and links the upper part of the pedicel to the dentine base (see Figs. 3, 4). Denticles on the anterior or on the ventral region of the head are generally fixed by means of such pedicels which protrude at the bone surface (Fig. 2h,i). On the flat surfaces of some bones the denticle bases are localized within circular depressions that are progressively filled by attachment bone matrix (Fig. 2f,j,k).

Teeth

Teeth on the oral side of the dentary, premaxilla, and maxilla show the same features as described for the denticles on the outer side of these bones. They are elongated, conical, spine-shaped elements, 150 to 180 μ m long and 30–40 μ m wide; they are spaced by 50 μ m in a single row and are attached to the bone surface through pedicels of attachment bone (Fig. 2b,i). They differ from the denticles only by 1) their orientation, slightly toward the center of the mouth cavity, and 2) their greater resistance to shedding, their tips remaining unattacked after strong sodium hypochlorite treatment (Fig. 2b,i). As for the denticles, teeth are shed when their bases (dentine and part of the attachment bone) have been resorbed following osteoclastic activity (Fig. 2i), and their pedicel persists at the bone surface. Tooth resorption generally occurs in the vicinity of a newly forming tooth.

Structure

The specimen was relatively well fixed in formalin and conserved in sufficiently good condition to enable us to make a detailed description not only of the structure of the dermal denticles and teeth (Fig. 3) but also of some features of their development during replacement (Fig. 4) and the fine structure of their matrices (Figs. 5–7).

Light microscopy

Dermal denticles. The structure of welldeveloped ("old"), functional denticles is always the same whatever their location on the head surface (Fig. 3a,e–k): a dentine cone covered by a hypermineralized cap (probably enameloid as known in teleost teeth, but not confirmed in this study) and surrounding a pulp cavity. At the base of the denticle, the pulp cavity is continuous with a vascular cavity surrounded by attachment bone. The dentine cone is linked to the attachment bone via a well-mineralized ligament, and the attachment bone matrix merges with that of the bony support in such

Fig. 3. One-micron-thick transverse sections of the anterior region of the head showing teeth and denticles attached to various dermal bones in Denticeps clupeoides. Tooth structure is illustrated in a-d, and the dermal denticles are shown in e-k. a: Anterior part of the mandible showing two teeth (arrowheads) and four denticles (arrows) fixed on the same bone, the dentary, which contains large cavities (asterisks). b: Teeth from the median region of the dermo-palatine. The tooth on the left is attached to the bone surface on the left and to the attachment bone of the other tooth on the right. The tips of the teeth were partially resorbed during decalcifi-cation by EDTA. The limit between the primary dentine and attachment bone is clear (arrows). **c**: Tooth on the posterior region of the dermo-palatine bone. The arrowhead points to the limit between dentine and attach-ment bone. **d:** Old functional teeth attached to the dentary. The dentine cone is composed of two, clearly delimited, well-mineralized layers, the primary and circumpulpar dentines (arrowheads). e: Three denticles on the dentary as in a. A denticle (asterisk) has been deposited above the remaining embedded pedicel (arrow) of a shed denticle. The dentine cone is clearly composed of two layers. Note that the circumpulpar dentine layer is also deposited against the attachment bone surface (ar-

rowheads). f: Denticle on the posterior region of the maxilla. Note the typical shape of the pedicel, the two layers of dentine, and the clear limit between the primary dentine and attachment bone (arrows). In contrast, the limit between the attachment bone and the bone support is not clear. **g:** Denticle on the dentary as in a. Its tip pierces the epidermis. The cap was partially decalcified by EDTA treatment but is still visible (arrowhead). It Same region as in (e) but slightly posteriorly on the dentary. On the left, two generations of denticles were superimposed as seen by the remaining pedicels (arrow). After shedding, the central cavities of the pedi-cels were not totally filled, and they are in connection with the adjacent dermis (arrowhead). i: The cavity of the pedicel of this denticle is in connection with the dermis (arrowhead). **j**: Same region as in i. The vascular cavity of the pedicel contains a capillary blood vessel (arrowhead). It is in connection with the pulp cavity of the denticle at another level (not shown). k: Same region as in a but in the most anterior region of the dentary. The attachment bone is fused to the dentary bone, and the pulp cavity of the denticle is connected to a large cavity in the bone (asterisk). Scale bars = $200 \ \mu m$ in a; 50 μ m in e and h; 25 μ m in b–d,f,g,i–k.



Figure 3



Fig. 4. Denticeps clupeoides. One-micron-thick transverse sections through the dentary as in Figure 3a illustrating three developmental stages of replacement teeth a-c and replacement denticles d-f. **a**: The dentine cone of this young tooth (arrow) is well formed. Its base is not mineralized and lies close to the dentary surface (asterisk). The attachment bone is not formed. **b**: The attachment bone of this young tooth (arrow) is not totally deposited. This tooth will attach to the dentigerous bone on the right and to the attachment bone of the adjacent functional tooth on the left. The dentine is well mineralized, and the cap is visible (arrowhead). **c**: Young functional tooth is characterized by a single mineralized. On the left the attachment bone is not totally mineralized.

ized. The limit between the attachment bone and the mineralized dentine is clear (arrowhead). Note the large network of cavities in the bone of this region. **d**: Young denticle developing its dentine cone. The cap matrix has been demineralized (arrow). **e**: Base of the dentine cone of a young denticle (arrow). The denticle has elongated but it is not yet attached to the dentary surface. The latter as well as the attachment bone of the neighbor tooth (arrowheads) are subjected to resorption. **f**: Erected young denticle (arrow) not completely attached to the bone support. Its pulp cavity is in connection with that of an adjacent functional denticle, the base of which was subjected to resorption along with the bone surface (arrowheads). Scale bars = 50 µm in a–c, e, and f; 25 µm in d.

a manner that it is difficult to see the limit between them (see also Fig. 6e,f).

The denticle tips pierce the epidermis (Fig. 3a,g–j), but in most of them the matrix of the denticle cap was either partially or completely dissolved following EDTA decalcification (Fig. 3g,i). However, when some elements of this matrix remain, it is stained less by toluidine blue than the adjacent collagen matrix of the dentine (Fig. 3g). This denticle cap is approximately 5 µm high, but its limit with the adjacent dentine is hardly

distinguishable because both matrices are progressively intermingled.

The dentine cone is clearly composed of two layers, called here primary and circumpulpar dentine, both lacking dentinal tubules (Fig. 3e,f,j). The primary dentine represents the matrix that is first deposited when the denticle is forming, and its base is prolonged by a ligament that penetrates the attachment bone matrix; the entire structure constitutes a young functional denticle (see Fig. 4f). The circumpulpar dentine layer



Fig. 5. Denticeps clupeoides. Transmission electron micrographs. Upper part of a functional denticle on the dentary. **a:** Upper part of the dentine cone showing the organization of the collagen fibrils in the primary dentine layers. Regions numbered 1, 2, 3 are detailed in b–d, respectively. **b:** Region still covered by the epidermis, close to the tip of the denticle. The matrix is composed of large collagen fibrils with many interfibrillar spaces.

The dentine–basal layer epidermal cell junction consists of a thin layer of fine, electron-dense granular substance (arrow). **c:** The dentine is composed of an outer layer of large fibrils (star), of an intermediate layer of woven fibrils (asterisk), and an inner layer of fine fibrils as detailed in d. **d:** The fibrils of the inner layer (star) are parallel to the long axis of the tooth. Scale bars = 5 μ m in a; 1 μ m in b–d.



consists of a collagen matrix that is deposited against the primary dentine, the ligament, and the attachment bone surfaces. This layer is deposited once the denticle is attached and erected, i.e., functional. The frontier between both dentine matrices is distinguishable as a dark line, and this limit is also visible between the primary attachment bone matrix and this secondary deposition (Fig. 3e,f,h,j). This limit is not visible at the level of the ligament that is, however, thicker than elsewhere. This circumpulpar dentine seems to be deposited throughout the life span of the denticles. In the "old" ones, this secondary deposition is as thick as the primary deposit or sometimes thicker, as for instance at the interface between the dentine base and the attachment bone matrix. Even when well mineralized, the matrix of the ligament is often clearly distinguishable from the dentine and the attachment bone matrix (Fig. 3f,h,j).

The pulp cavity of the denticles is small, does not contain capillary blood vessels and nerve endings, and is progressively filled by a centripetal deposition of circumpulpar dentine (Fig. 3e–k). However, blood vessels are visible in the adjacent vascular cavity occupying the center of the pedicels.

The pedicels of attachment bone can show different shapes depending on the amount of resorption and on the mode of fixation of the denticles (Fig. 3a,e,f,h,j). Where the denticles are irregularly distributed on the bone support, the pedicels appear typically pearshaped in transverse sections, being broad at the base and narrowing where the vascular cavity is in connection with the pulp cavity of the denticle (Fig. 3f). The vascular cavity of the pedicel can be in connection either with the adjacent dermis, or with vascular cavities of adjacent denticles, or with cavities of the bone support (Fig. 3h,i,k). The attachment bone matrix of these denticles is generally intermingled with that of the bony support. In regions rich in denticles, adjacent pedicels of denticles belonging to different rows can be attached one to another (Fig. 3e). When the denticles are shed, their pedicels can persist at the bone surface, and then become embedded within the bone matrix below the pedicels of functional denticles, while remaining visible. The embedding of pedicels in the bone matrix depends on the amount of remodeling of the bone support (Fig. 3e,h), which is more important in the bone regions supporting teeth than in those supporting denticles (compare, respectively, Figs. 3b,d to e,h).

Teeth. The teeth (Fig. 3a–d) show a similar organization and structure as described above for the denticles. There are, however, some slight differences. The circumpulpar dentine layer is less developed (Fig. 3d), and in numerous teeth only the layer of primary dentine is present (Fig. 3b,c). Also the region of the ligament is shorter and less visible than for the denticles. In some teeth the dentine matrix seems to merge directly with that of the attachment bone (Fig. 3b-d). The transition between the attachment bone and the bone support matrix is clearer than for the denticles, but this is undoubtedly related to amount of remodeling and to the well-developed network of vascularization of the bone support (Fig. 3d). The pedicels of attachment bone are attached either to the bone support (Fig. 3c) or to the bone support on one side and to the pedicel of an adjacent tooth on the other side (Fig. 3b). The remodeling on the surface of the dentary bone is so intensive that, in the end, this region is constituted mainly of the remains of partially resorbed pedicels (Fig. 3d). As in the denticles, the pulp cavity of the teeth can be reduced to some extent by the deposition of circumpulpar dentine on its walls, and in "old" functional teeth the base of the pulp cavity can be filled with patches of wovenfibered collagen matrix (Fig. 3d).

Development. In the adult specimen studied some denticles and teeth had been shed, and some of them were in the course of replacement (Fig. 4). Features of replace-

Fig. 6. Denticeps clupeoides. TEM. Basal region of functional denticles on the dentary. a: Upper part of the pulp cavity showing the primary (asterisk) and circumpulpar (star) dentine layers. b: Basal region of a denticle showing the limit (arrow) between the primary dentine and the attachment bone. A ligament is visible on the external surface of the base of the dentine cone (arrow-head). Regions numbered 1 and 2 are detailed in c and d, respectively. c: The layer of circumpulpar dentine is not mineralized throughout. d: Detail of the junction between the attachment bone and the two dentine layers. e: Detail of the interface between the attachment bone and the dentary. The limit between the matrices is badly defined and appears as a zone with densely packed collagen fibrils (asterisk). f: In this example, the limit between the attachment bone and the dentary is also difficult to define except for the presence of a zone rich in interfibrillar spaces (asterisk). A large anchoring bundle emerges from the surface of the attachment bone (arrow). AB, attachment bone; D, dentary; PD, primary dentine; SD, circumpulpar dentine. Scale bars = $1 \mu m$ in a and c; 5 µm in b and f; 2 µm in d and e.



Figure 7

ment are seen particularly frequently in regions where the denticles and teeth are numerous (e.g., the dentary), and are often located close to a functional element which is subjected to resorption. The process observed for teeth (Fig. 4a-c) and denticles (Fig. 4d-f), developing on the dentary surface, was the same. On the dentary, the replacement tooth or denticle always forms parallel to the adjacent tooth or denticle, i.e., more or less perpendicular to the bone surface; this is in contrast to replacement denticles forming on the opercular surface (Fig. 2j), a region less rich in denticles. The cap and predentine matrix are deposited (Fig. 4a,e), then rapidly mineralize to constitute the (enameloid) cap and the upper part of the dentine cone, while the base of these elements is not completely formed (Fig. 4b,d). The attachment bone matrix forms at the dentine base and will attach the element directly to the bony support or to an adjacent pedicel (Fig. 4c,f). In all cases resorption areas are clearly visible in the vicinity of a forming elemenť.

Transmission electron microscopy

Denticles. Unfortunately, because of the small size of the denticle tip, the sections examined do not allow the description of the hypermineralized cap matrix-dentine interface, but we have obtained such a section through the extremity of a tooth (see below and Fig. 7a,b). In "old" functional denticles the primary dentine is composed of three distinct layers of collagen fibrils that are well delimited in the upper region of the dentine cone (Fig. 5a–d). From outside inward, the first deposited dentine matrix consists of a layer of 100-nm-diameter collagen fibrils disposed parallel to the long axis of the denticle. This matrix contains many, conspicuous interfibrillar spaces with small, electron-dense granules (Fig. 5a,b). The second layer is formed of a loose, woven-fibered matrix composed of 30-nm-diameter collagen fibrils and ample interfibrillar space (Fig. 5a,c). The third layer, constituting the internal wall of the primary dentine, consists of 30-nm-diameter collagen fibrils parallel to the long axis of the denticle. These fibrils are densely arranged with hardly any interfibrillar spaces in between (Fig. 5a,d). These three layers are also found along the shaft of the dentine cone, but there the first layer is less developed than in the upper region of the denticle. The external surface of this layer appears to be covered by a thin, woven fibered layer composed of 30-nm-diameter collagen fibrils (Fig. 6c). In the upper region of the dentine cone, the junction between the external layer of dentine and the basal epidermal cells is not delimited by a basement membrane, but this interface consists of a thin layer of fine, electron-dense, granular substance (Fig. 5b). The deposition of circumpulpar dentine is well visible along the shafts of the dentine cone of "old" functional denticles. This matrix consists of several layers, of variable thickness, containing 30-nmdiameter collagen fibrils mainly parallel to the long axis of the tooth and with no interfibrillar spaces in between (Fig. 6a). In recently attached denticles, this circumpulpar dentine is not yet well formed and cannot be distinguished from the predentine matrix or from the secondary deposition of osteoid matrix lining the attachment bone (Fig. 6b-d). Nevertheless an uninterrupted layer of matrix is present along the dentine, ligament, and attachment bone surface, with any limit between these three different regions (Fig. 6b). Moreover, there is no structural difference between the matrices of the internal layer of the primary dentine and the newly deposited circumpulpar dentine, or with the attachment bone matrix (Figs. 5d, 6b-d). The region of the ligament is only recognizable as a zone of unmineralized matrix belonging either to the dentine cone or to the attachment bone (Fig. 6b,d). In "young" and "old" denticles (Fig. 6e,f, respectively), the frontier between the attachment bone and the bone support matrix is difficult to define

Fig. 7. Denticeps clupeoides. TEM. Developing and functional teeth on the dentary. a: Young tooth not completely attached to the dentary. The base of the dentine cone is not mineralized (arrow). The asterisk indicates a functional tooth. b: Detail of the tooth in a showing the organization of the collagen fibrils in the upper region of the primary dentine. The matrix of the "enameloid" cap has disappeared after EDTA treatment. The enameloid-dentine junction remains, but the collagen fibrils have been partially destroyed. c: Right side of the base of the dentine cone of the tooth in (a). The predentine (asterisk) is composed of collagen fibrils parallel to the long axis of the tooth. Part of the adjacent functional tooth is seen on the right. **d:** Base of a functional tooth. The primary dentine matrix merges with that of the attachment bone. **e**: Old functional tooth showing a pulp cavity that is filled with patches of collagen fibrils (asterisks). f: In a functional tooth, the limit between the attachment bone and the dentary bone matrix contains crystal ghosts. AB, attachment bone; PD, primary dentine. Scale bars = $5 \mu m$ in a and d; $1 \mu m$ in b, c, and f; $3 \mu m$ in e.

as a clear line or limit. In some areas this interface can be distinguished as a zone in which the collagen fibrils are densely disposed with hardly any spaces in between (Fig. 6e). In other regions this frontier is characterized by a zone which contains more interfibrillar spaces (Fig. 6f). The attachment bone and the ligament increase in thickness by internal and external deposition of collagen matrix. Indeed new osteoid matrix is deposited against the surface bordered by the dermis (Fig. 6b,f). Some small bundles of anchoring fibrils emerge from the attachment bone surface and penetrate into the adjacent dermis where they anchor, close to the epidermal surface (Fig. 6f).

Teeth. The primary dentine matrix of the teeth is similar to that described above for the denticles, in that there is an external layer composed of 100-nm-diameter collagen fibrils parallel to the long axis of the tooth and an internal layer of 30-nm collagen fibrils (Fig. 7a,b). The interface between the upper region of the dentine and the "enameloid" cap, which is entirely demineralized by the EDTA treatment, is well visible in these micrographs. Here the "enameloid" matrix was intermingled with the collagen fibrils of the upper dentine layer which appear partially dissolved on these decalcified samples (Fig. 7b). The comparison of a developing replacement tooth with a functional tooth as in Figure 7c shows that the typical dentine matrix of the external layer in the young tooth is deposited along the dentine shaft without any space left between this matrix and the dental epithelium covering it. However, a thin layer of woven-fibered matrix covers this external layer of dentine in the "old" tooth. This suggests that this layer could be deposited secondarily at the dentine surface, but the poor fixation of the cells does not permit clear distinction as to whether the cell population lining this layer is dermal or epithelial. In well-formed teeth, TEM confirms the observations at the light microscopic level: that 1) the circumpulpar dentine is less developed in teeth than in denticles, and 2) a ligament region is poorly developed between the dentine base and the attachment bone (Fig. 7d, and see Fig. 3b,c). Indeed, except for a less-mineralized region close to the pulp cavity, it seems that the dentine and the attachment bone matrices fuse. In "old" teeth, irregularly shaped patches of woven-fibered 30-nm-diameter collagen fibrils are secondarily deposited in the basal region of the pulp cavity, above the attachment bone (Fig. 7e). The attachment bone matrix is again fused with that of the bone support, but the limit can be defined by an irregular zone which is characterized by a greater electron density due to an electron-dense substance which fills numerous interfibrillar spaces (Fig. 7f).

DISCUSSION

Combining the observations on the external morphology (SEM) and structural (light microscopy and TEM) of denticles and teeth in the clupeomorph *Denticeps clupeoides*, the present study clearly demonstrates that 1) the dermal denticles are odontodes, and 2) the shape, structure, and organization of these odontodes is similar to that of teeth in the buccal cavity. These findings lead us to some developmental and evolutionary considerations.

Odontodes in living vertebrates

Our findings that the dermal denticles in Denticeps clupeoides are odontodes confirm the previous description, based on alizarin red staining, on the presence of "extra-oral teeth" in this species (Clausen, '59). Thus, along with the armored catfish (\approx 700 species distributed in loricariids, doradids, callichthyids of the order Siluriformes) (Bhatti, '38; Sire and Meunier, '93; Sire and Huysseune, '96) and the Xiphioids (a dozen species distributed among the xiphiids and istiophorids, Perciformes) (Carter, '19; Rauther, 40), the denticipitids (Denticipitoidei, Clupeiformes) are a third group of teleosts possessing isolated odontodes. In living gnathostomes, odontodes are widely present in nearly all extant groups of chondrichthyans (\approx 800 species) where they are called either dermal denticles, placoid scales, tubercles, or thorns (e.g., Reif, '85; Compagno, '88; Deynat and Séret, '96). Isolated odontodes are also present in the coelacanth, Latimeria *chalumnae,* in the polypterids (12 species), and in the lepisosteids (seven species).

Isolated odontodes are not the only "toothrelated" elements covering the body of the living osteichthyans. In the coelacanth (a sarcopterygian), the polypterids, and the lepisosteids (actinopterygians), superimposition of several generations of odontode units has given rise to the formation of odontocomplexes (sensu Ørvig, '67, '77) which constitute the superficial region of numerous elements of the dermal skeleton. The term "odontocomplex" includes both superimposed odontode units and flat structures formed by fusion of several odontode units, and composed of a layer of dentine covered by ganoine, an enamel (Sire et al., '87). In the coelacanth. isolated odontodes and/or odontocomplexes have been described on the superficial region of scales, fin rays, and cranial bones (Roux, '42; Smith et al., '72; Castanet et al., '75; Smith, '79; Meunier, '80a). In the polypterids, superimposed odontode families are found in the dorsal spiny rays (pinnulae), and flat odontocomplexes cover cranial bones, scales, and fin rays (Williamson, 1849; Goodrich, '07; Sewertzoff, '32; Meunier, '80b; Sire et al., '87; Géraudie, '88). In the lepisosteids, scales are covered by a layer of ganoine that is derived from an odontocomplex (Reissner, 1859; Nickerson, 1893; Sire, '94). It is clear from these data that several conditions can occur in a single specimen, as for instance in polypterids: 1) isolated odontodes fixed on the gular bone and on the "horseshoe" plates of the pectoral fin, 2) superimposed odontode families on the dorsal spiny rays (pinnulae), and 3) odontocomplexes, derived from superimposed generations of odontode units, on scales and fin rays (Meunier, '80b). The shape, structure, and organization of these odontocomplexes is nevertheless completely different from that of isolated odontodes and of teeth.

In Denticeps, the odontodes have similar shape and structure to teeth

It is well known that odontodes and oral teeth share the same basic structure. i.e., a pulp cavity surrounded by a dentine cone covered by a hypermineralized cap of enamel or enameloid. Nevertheless odontodes (like teeth) show large variations in shape, size, and ornamentation both within a single specimen and among species, and their distribution on the body can vary. These variations are especially pronounced in chondrichthyans, in which they can be a useful character for systematic purposes (e.g., Deynat and Séret, '96), and in armored catfish (Bhatti, '38; Sire and Meunier, '93). Whereas the structure of the teeth is usually constant in a given species, it is known to show large variations between species, especially as to the type of dentine and the mode of attachment (see recent review in Huysseune and Sire, '98). By contrast, the structure of odontodes appears to be rather conserved between the teleost species studied, but this finding cannot be generalized to all odontodes because only few descriptions are available in the literature (Carter, '19; Bhatti, '38; Sire and Huysseune, '96).

In the present study we show that both teeth and odontodes in Denticeps clupeoides have the same shape and structure, except for minor differences probably related to the different functions of these elements. For instance, odontodes have been found to be more sensitive to the sodium hypochlorite treatment than teeth. In particular, there are two fragile regions in the denticles: the interfaces between the enameloid cap and the dentine, and between the dentine and the attachment bone (the latter leading to loss of the odontode). Since sodium hypochlorite is known to dissolve the soft tissues, this reaction of the odontodes suggests that these regions are less mineralized than the adjacent ones, and than the corresponding regions in the teeth. A similar loss of odontodes occurs in armored catfish in which these elements are fixed to the bone support by means of unmineralized ligaments (Sire and Meunier, '93; Sire and Huysseune, '96). The histological and ultrastructural study confirms that the ligament region of the odontodes in *D. clupeoides* is less mineralized than the adjacent dentine or the attachment bone, whereas this region is less developed but well mineralized in teeth. A similar difference in mineral content at the enameloiddentine interface can explain the loss of the odontode tips in contrast to the maintenance of the tooth tips. However, it was not possible to confirm this hypothesis from our decalcified material.

Another slight difference concerns the secondary deposited collagenous material, which we called circumpulpar dentine, which is more developed in odontodes than in teeth. This matrix continues to be deposited against the walls of the pulp cavity and along the surface of the attachment bone and the ligament, even after the tooth or the odontode has become functional (i.e., fixed to the bone support and erupted). It is known that dentine deposition can continue after a tooth has erupted, both in mammals (Linde and Goldberg, '93; Smith et al., '95) and in the cyprinid fish Danio rerio (Huysseune et al., in press). In the present case, the collagenous matrix is deposited on all the surfaces surrounding the pulp cavity. This raises the question of the identity of the cells producing this matrix (odontoblasts, fibroblasts, osteoblasts?) and, as a consequence, of the matrices themselves (of dentine, ligament, attachment bone?). The same question has been addressed already in previous studies dealing with the development of odontodes (Sire and Huysseune, '96) and of first-generation teeth (Huysseune and Sire, '97a,b; Huysseune et al., in press).

It is now generally accepted that the mesenchymal cells responsible for the development of an odontode unit (i.e., dentine cone, ligament plus attachment bone) derive from the same (ecto)mesenchymal population (Reif, '82; Smith and Hall, '90, '93). These cells are able to modulate their activity to build the different components of an odontode provided they receive the appropriate morphogenetic signals (Schaeffer, '77). The cells lining the walls of the pulp cavity could have conserved this ability, and all of them could respond to a same signal resulting in the deposition of a similar matrix against all the surfaces. The difference observed between teeth and odontodes in the amount of circumpulpar dentine deposited seems to be more related to the "age" of these elements than to specific characteristics. Indeed, from the numerous serial sections we have examined, it is clear that teeth are replaced more frequently than odontodes, probably due to their functional constraints, i.e., during catching small prey. Their "life" being shorter, the amount of circumpulpar dentine is smaller compared to that of the odontodes.

The teeth and odontodes in *Denticeps clu*peoides share some structural characteristics with those of the odontodes in armored catfish (Sire and Huysseune, '96) and with the first-generation teeth of armored catfish (Huysseune and Sire, '97a), cichlids (Huysseune and Sire, '97b), and the cyprinid Danio rerio (Huysseune et al., in press). The structure of the dentine is simple: It lacks dentinal tubules, and the pulp cavity houses neither capillary blood vessels nor nerve endings. These features are interpreted as the result of a reduction process, the odontodes and the first-generation teeth being small elements that do not exceed 200 µm in length and 40 µm in diameter. The replacement of the odontodes in armored catfish is also similar to that in Denticeps: i.e., resorption of the basal region of the functional odontodes, slight erosion of the bone surface, and the remaining pedicels capable of being embedded in the bone matrix (see discussion in Sire and Huysseune, '96). In Denticeps, the replacement odontodes can develop either parallel to the bone surface, in regions where they are scarce (e.g., on the operculum surface), or perpendicular to the bone surface (i.e., parallel to functional odontodes) where they are densely arranged, as observed for teeth. In armored catfish the odontodes develop parallel to the bone surface but also are not densely distributed (Sire and Huysseune, '96). In both types of replacement, the developing odontodes are protected from abrasion, either by the neighboring functional odontodes or/and by lying deep below the epidermal basement membrane and parallel to the bone surface.

The slight structural differences we have found between teeth and odontodes are all suspected to be related to the different function and rate of replacement of these elements. It is clear that the role of the odontodes (probably hydrodynamic rather than defensive due to their small size) is completely different from that of the teeth which are subjected to more important constraints (food uptake). Such a hydrodynamic function has been experimentally demonstrated by Burdak ('79) for the small odontodes (named placoid scales) covering the skin of sharks, and it was also proposed for the odontodes covering the scutes in the armored catfish (Sire, '93; Sire and Meunier, '93).

Developmental and evolutionary considerations

Schaeffer's hypothesis ('77) "that the calcified dermal skeleton (including dentition and fin rays) in living fishes develops from a single modifiable morphogenetic system that is established by the interaction of the epithelium and the adjacent mesenchyme" has now been accepted by most authors (Reif, '82; Smith and Hall, '90, '93). As a consequence, the diversity of shape, size, ornamentation, and arrangement of teeth, odontodes, and odontode-derived elements is explained in terms of local modifications in the tissue organization; they would result (under specific epigenetic context) from modifications in the genetic control of the regulation of epidermal-dermal interactions, which have been selected for these organs during evolution (Huysseune and Sire, '98). It is not the aim of the present study to discuss the developmental processes that could be involved in these modifications. Nevertheless we can postulate that, if these modifications occurred early in the evolution of the vertebrates, the dermal skeletal elements, although derived from a common ancestor, have followed different pathways, and are now widely divergent in structure, shape, size, and organization. Indeed during hundreds of millions of years of evolution, several mutations affecting the tissue organization and/or the genetic control of developmental processes have probably been selected. Accordingly, large structural differences between elements that are nevertheless phylogenetically homologous are probably related to the long time since divergence from a common ancestor. Conversely, the later these modifications may have occurred, the closer resemblance of structure, shape, and organization may be expected between these elements; this would imply conservation of a same tissue organization and of a same genetic control of tissue interactions.

Now, if we consider the similarity of shape, size, and structure of teeth and odontodes in Denticeps with the above assumptions in mind, it appears clear that the presence of odontodes in this species is the result of the expression of teeth in extra-oral locations and that this modification may have occurred fairly recently in this lineage, contrary to Clausen's view ('59) that in Denticeps the dermal denticles "represent a truly primitive condition." Denticipitids are the only family possessing odontodes within the clupeomorphs, which probably originated during the Cretaceous (Grande, '85). One fossil denticipitid species, Palaeodenticeps tanganikae, possessing denticulate cranial bones (i.e., odontodes in extra-oral positions) and remarkably close to D. clupeoides, has been described by Greenwood ('60, '68, '84) from the Late Oligocene–Early Miocene of Tanganyika. These denticles cannot be remnants of the odontodes that covered most of the body of many ancient jawless vertebrates. Among higher teleost species such as the xiphioids, most authors have also considered the presence of denticles not as a primitive condition but as a secondary specialization, odontodes (meaning competent cells) possibly having spread secondarily over the rostrum surface from the oral region (e.g., Goodrich, '07; Bertin, '58). The similarity between oral teeth and extra-oral denticles on parts of the rostrum in the xiphioids is not as close as that observed for *Denticeps clupeoides.* In xiphioids the denticles appear as small, round structures, whereas the teeth are sharp. The expression of odontodes in extra-oral positions has probably occurred

less recently in xiphioids than in Denticeps. The literature data on fossil xiphioids are largely based on records of isolated rostra described as bearing denticles. Swordfish (xiphiid-like) and sailfish (istiophorid-like) are known from the Eocene (Fierstine, '74; Fierstine and Applegate, '74). The expression of isolated odontodes in the armored catfish is probably older than in the previously cited teleost species because the shape, size, and organization of the odontodes are quite different among the numerous species. Unfortunately comparisons between odontodes and teeth cannot be done in adult armored catfish because these species lose their teeth at an early juvenile stage (Huysseune and Sire, '97a).

On a larger evolutionary scale, there is little doubt that the dermal skeleton and dentition in sharks and in all other living gnathostomes are ultimately derived from the dermal skeleton of some agnathous stage in the early evolution of vertebrates (see review in Huysseune and Sire, '98), but this hypothesis is currently questioned for teeth in view of the recent discoveries that conodonts are probably remains of the earliest known jawless craniates (Sansom et al., '92, '94; Aldridge et al., '93). In chondrichthyans the odontodes have the same structure as oral teeth, but they show a large range of shape, size, and ornamentation. These elements have probably derived from odontode units forming part of the dermal skeleton in the ancestors of this lineage. These ancestors probably arose some 450 millions years ago among the early, jawless vertebrates (review in Janvier, '96). In all osteichthyan lineages, the fossil record reveals a clear tendency toward reduction and/or modification of the dermal skeletal elements, particularly of the odontode covering (Ørvig, '57, '67, '77), and the dermal skeleton of living polypterids is thought to be the best extant representative of the "ancestral" (plesiomorphic) condition among the living osteichthyans (e.g., Schultze, '66, '77; Meunier, '80b).

Comparative studies of the dermal skeleton in fossil and living osteichthyans have shown that oral teeth and numerous elements of the dermal skeleton (odontodes, various types of scales, fin rays, scutes, dermal plates), even though homologous, have evolved independently from one another. This is illustrated by the large range of shapes and structures of the dermal skeleton among extant forms (review in Huysseune and Sire, '98). We suggest that the extra-oral expression of isolated odontodes may be a derived condition that can occur in diverse unrelated groups of osteichthyans. This could also explain why isolated odontodes can be deposited on the surface of scales, which are themselves considered as derived by reduction from odontocomplexes.

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