Formation of dermal skeletal and dental tissues in fish: a comparative and evolutionary approach

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ABSTRACT

Osteichthyan and chondrichthyan fish present an astonishing diversity of skeletal and dental tissues that are often difficult to classify into the standard textbook categories of bone, cartilage, dentine and enamel. To address the question of how the tissues of the dermal skeleton evolved from the ancestral situation and gave rise to the diversity actually encountered, we review previous data on the development of a number of dermal skeletal elements (odontodes, teeth and dermal denticles, cranial dermal bones, postcranial dermal plates and scutes, elasmoid and ganoid scales, and fin rays). A comparison of developmental stages at the tissue level usually allows us to identify skeletogenic cell populations as either odontogenic or osteogenic on the basis of the place of formation of their dermal papillae and of the way of deposition of their tissues. Our studies support the evolutionary affinities (1) between odontodes, teeth and denticles, (2) between the ganoid scales of polypterids and the elasmoid scales of teleosts, and (3) to a lesser degree between the different bony elements. There is now ample evidence to ascertain that the tissues of the elasmoid scale are derived from dental and not from bony tissues. This review demonstrates the advantage that can be taken from developmental studies, at the tissue level, to infer evolutionary relationships within the dermal skeleton in chondrichthyans and osteichthyans.

Key words: chondrichthyan fish, osteichthyan fish, dermal skeleton, teeth, bone, scales, fin rays, development, evolution.

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I. INTRODUCTION

The dermal skeleton of present-day ‘fishes’, defined herein as non-tetrapod aquatic vertebrates (chondrichthyans, actinopterygians and basal sarcopterygians — coelacanths and lungfishes), is particularly diverse. It encompasses odontodes, teeth and dermal denticles, cranial dermal bones, postcranial dermal plates and scutes, spines and fin rays, elasmoid and ganoid scales, and the elements that include lateral line nerves or neuromasts. [Readers who are not familiar with terms related to the dermal skeleton are referred to definitions given in Francillon-Vieillot et al. (1990), Zylberberg et al. (1992) and Huysseune & Sire (1998).] Moreover, this diversity can be encountered even in a single species. For instance, six different types of dermal elements — teeth, dermal denticles, cranial dermal bones, scutes, spines and fin rays — are found in the teleost Cordylurus arcatus Elwin, 1939, an armoured catfish (Sire, 1993; Sire & Huysseune, 1996; Huysseune & Sire, 1998). Their dermal skeleton was composed either of ‘dental’ units, called odontodes (Orvig, 1977), bony plates, or both. Most authors agree that odontodes and bony plates initially were probably separated (Janvier, 1996). It is only secondarily, probably in the common ancestor of osteichthyans, that the two became connected, i.e. deep bony elements supporting superficial odontode units. The discovery of the conodont animals, their recent assignment to vertebrates (Sansom et al., 1992; Briggs, 1992), and the interpretation of their hard tissues as possibly homologous to the vertebrate hard tissues (Sansom et al., 1992; Sansom, Smith & Smith, 1994) has led a number of
authors to consider that the earliest condition for the mineralised vertebrate skeleton was in the form of an oro/pharyngeal raptorial feeding array composed of odontodes [regarded by Smith & Coates (1998, 2000) as possible prepatterns for a gnathostome dentition]. The bony plates appeared later with the development of the dermal skeleton (but see the recent reviews by Donoghue, Forey & Aldridge, 2000 and Donoghue & Aldridge, 2001).

During the 500 million years of evolution within the various vertebrate lineages, the initial elements of the dermal skeleton were lost, reduced or modified in such a profound way that comparative studies based on the external morphology alone have not always allowed us to reveal homologies between the elements currently existing, and to distinguish true homology from homoplasy (defined as similarity not resulting from common ancestry, cf. Sanderson & Hufford, 1996). Although current tendencies attempt to narrow down the distinction between homology and homoplasy (e.g. Meyer, 1999; B. K. Hall, in preparation), we follow here the phylogenetic (or historical) homology concept in the sense of Rieppel (1992): characters can only be considered homologous if they have a similar structure and position and if they are congruent with a phylogeny of the taxa derived from other characters.

Some very similar-shaped elements have indeed turned out to be obvious examples of homoplasy when examined from a structural viewpoint. For instance, the denticles of the small-spotted catshark, Scyliorhinus canicula (Linnaeus, 1758), and the scutes of the teleost Notopogon xenosoma Regan, 1914, belonging to lineages that separated approximately 450 mya, have similar external morphology (Fig. 1A, B). Yet, the former is an odontode, whilst the latter is a derivative from a postcranial dermal plate (Fig. 1C, D). Similarly, the ctenial spines on the posterior margin of ctenoid scales in cichlids (Fig. 2A, B) resemble the dental denticles on the head of Denticps clupeoides Clausen, 1959, a clupeomorph (Fig. 2C, D) or the dental denticles on the body of an armoured catfish, the callichthyid Corydoras aeneus (Gill, 1858) (Fig. 2E, F). However, the former are
Fig. 2. Examples of homoplasy in the dermal skeleton: similarity in shape but difference in structure. (A–F) Scanning electron micrographs (general view and detail) of (A, B) ctenial spines in the posterior region of a scale in the cichlid Cichlasoma nigrofasciatum, (C, D) denticles on the head of the clupeomorph Denticeps clupeoides, and (E, F) denticles on a scute of the callichthyid Corydoras aeneus. (G, H) 1-μm-thick section (G) and transmission electron micrograph (H) showing the bone-like
derived from the external layer of the elasmoid scale (Fig. 2G, H) while the latter are extra-oral teeth (Fig. 2I, J). It is likely that similar functional constraints at the body surface favoured the selection of similar shapes, whatever the origin (bone or dental) of the skeletal element involved.

The above examples highlight the absolute need for structural data (preferably at the tissue level) to reveal the exact nature of similar-shaped dermal skeletal elements and so to try to infer their evolutionary origin. However, convergence of shape is not the only expression of homoplasy in the dermal skeleton. Homoplasy can also occur at the structural level and in particular that of the tissues involved. For example, a similar lamellar organisation of the collagenous matrix can be found in elasmobranch of the elasmoid scale and in lamellar bone (Fig. 3A, B), and a similar woven-fibered organisation of collagen can be observed in dentine and in bone (Fig. 3C, D). On the other hand, it is difficult to categorise some tissues into one of the standard textbook categories (bone, dentine and enamel). For example, from which tissue does the hypermineralised tissue hyaloidine, which covers the scutes of the armoured catfish, derive (Fig. 4)? Where do the three different tissues (elasmodine, external layer and limiting layer), composing the elasmoid scale in teleosts (Fig. 5) come from? Clearly, the huge diversity of these tissues and the difficulty of categorising them severely hamper the interpretation of evolutionary relationships between some of the elements of the dermal skeleton.

To recognise homologies in the real world, and to distinguish them from homoplasies, three operational criteria are usually to be met: similarity of structure, position (anatomical relationship) and phylogenetic continuity (also called the structural, positional and transitional criterion; Riedl, 1978; Raff, 1996; Meyer, 1999). A fourth criterion is sometimes invoked, called ‘sameness of the underlying developmental basis of two similar structures’ (Meyer, 1999). Although the formation of structures recognised as historical homologies may not follow the same developmental pathway (Hall, 1995; Raff, 1996; Futuyama, 1998), we expect that similar developmental bases certainly can endorse the homology of the character because the structure would have evolved by modification of the developmental programme of a common ancestor. So, having ascertained that a comparative morphological and structural study of extant dermal skeletal elements in fish does not allow the inference of homologies, let us now examine whether a comparative developmental study can teach us more regarding the evolutionary relationships between the elements and/or tissues concerned.

In this review we provide a few examples of such developmental studies. We start with an overview of the features characterising selected steps of development in the different types of dermal skeletal elements in fish. To this end, the elements that have been considered have been grouped into 10 categories (see Section II, and Table 1). The selected steps are: (i) stage prior to initiation (with emphasis on the tissue environment in which the organs will develop), (ii) initiation and early morphogenesis, and (iii) late morphogenesis and differentiation. Next, we focus on resemblances and differences in cell and tissue organisation at similar steps of development in order to find evidence for a similar tissue origin. Eventually, these considerations should help us to uncover the evolutionary relationships between the different components of the vertebrate dermal skeleton.

The data concerning the development of the dermal skeletal elements reviewed in this study mostly derive from the studies compiled in Table 1, as well as from some complementary, unpublished observations (J.-Y. Sire & A. Huysseune, unpublished data).

II. THE TEN CATEGORIES OF DERMAL SKELETAL ELEMENTS IN FISH

(1) Odontodes

This term was proposed by Ørvig (1977) for all isolated hard superficial structures of the skin consisting of a core of dentine, or dentine-like tissue, which may be covered by a hypermineralised cap of enamel or enameland, with a base consisting of bone that functions as an attachment tissue. Initially created for the ‘tooth-like’ dermal denticles covering the head and body of jawless and jawed extinct vertebrates, the term odontode was extended to all dermal denticles having a ‘tooth-like’ structure. Recently, the evidence that such denticles exist in living teleosts, the ancestors of which did not possess them, led Sire (2001) to propose restricting the term odontode to all dermal denticles in lineages sharing a common ancestor, i.e. chondrichthyan (the so-called placoid scales) and in basal living osteichthyans, the coelacanth, polypterids and lepisosteids. The

structure of a ctenial spine in *C. nigrofasciatum*; (I, J) 1-μm-thick sections showing the dental structure of (I) three denticles fixed on the dentary bone in *D. clupeoides*, and of (J) a denticle on the scute surface in *C. ameno*. bm, bone matrix; d, dermis; de, dentine; ep, epidermis; s, scale. Scale bars: A, C, E = 50 μm; B, D, F, G, I, J = 25 μm; H = 5 μm.
Fig. 3. Homoplasious tissues: similarity in structure. (A) The elasmodine of the scale in a young polypterid *Polypterus senegalus* and (B) the lamellar bone in the scute of the callichthyid *Corydoras arcuatus*. (C) The woven-fibred dentine of a young tooth in the
other elements in living teleosts should then be called dermal denticles (see below). We have chosen throughout the following text to illustrate the development of such odontodes in a shark and a ray.

(2) Teeth

Teeth are, with only a few exceptions, located in the oral and/or pharyngeal cavity of most lineages. Indeed, in some species the adults are edentulous but teeth develop in larvae and juveniles, e.g. in the siluriform callichthyids. We have chosen to illustrate the development of the first-generation and replacement teeth in three teleost species.

(3) (Dermal) denticles

As stated above, these elements have to be distinguished from odontodes because they are not directly linked in phylogeny. They represent extra-oral teeth and are known, until now, to develop secondarily on the head surface in four teleost lineages. Three of these are illustrated below.

(4) Cranial dermal bones

Cranial dermal bones are present in all vertebrate species and show different modes of formation (e.g. either developing in the proximity of a cartilage or not). The two examples chosen are the dentary and the frontal bones in a cichlid.

(5) Scutes

This term is used for the postcranial dermal plates of the armoured catfish (Callichthyidae, Loricariidae, Doradidae, etc.) only. Scutes are distinguished from other postcranial dermal plates in that a layer of a hypermineralised, enigmatic tissue, hyaloin, covers them. The development of this element will be illustrated for a callichthyid species.

(6) Postcranial dermal plates

These include the plates and spines, of bony nature, that cover the body of a number of derived teleosts such as gasterosteiiforms (e.g. Gasterosteidae, Syngnathidae, Macroramphosidae), tetraodontiforms

callichthyid Hoplosternum littorale (the dashed line indicates the probable limit between dentine and attachment bone) and (D) the woven-fibred bone in the premaxillary of H. littorale. ab, attachment bone; bm, bone matrix; de, dentine; el, elasmodine. Scale bars: A = 3 μm; B = 2 μm; C, D = 1 μm.
Fig. 5. An enigmatic element of the dermal skeleton: the elasmoid scale. (A) 1-μm-thick section of an elasmoid scale in the cichlid *Hemichromis bimaculatus* indicating the location of the three tissues: elasmodine, external layer and limiting layer. (B–D) Transmission electron micrographs showing the structure of the tissues after ethylenediaminetetraacetic acid decalcification: (B) the woven-fibred external layer (delimited by the accolade), (C) the plywood-like structure of the elasmodine, and (D) the limiting layer nearly devoid of collagen matrix except at the level of the anchoring Sharpey’s fibres. d, dermis; el, elasmodine; ep, epidermis; ex, external layer; ll, limiting layer; Sf, Sharpey’s fibre. Scale bars: A = 50 μm; B–D = 1 μm.
Table 1. The ten categories of dermal skeletal elements studied, species names and literature references

<table>
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<tr>
<th>Dermal skeletal elements</th>
<th>Name of the taxa</th>
<th>References</th>
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<td>Rajiformes Rajidae</td>
<td>Leucoraja erinacea (Mitchill, 1825)</td>
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<td>Siluriformes Callichthyidae</td>
<td>Corydoras arcuatus (Elvin, 1959)</td>
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<td>Cypriniformes Cyprinidae</td>
<td>Danio rerio (Hamilton, 1822)</td>
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<td>Sire (2001); Sire &amp; Allizard (in press)</td>
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<td>Van der heyden et al. (2000)</td>
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<td>Denticles</td>
<td>Siluriformes Callichthyidae</td>
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<td>Clupeomorpha Denticipidae</td>
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<td>Cypriniformes Cyprinidae</td>
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<td>Fin rays</td>
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<td>Oncorhynchus mykiss (Walbaum, 1792)</td>
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<td>J.-Y. Sire (unpublished results)</td>
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(e.g. Diodontidae, Ostraciidae), etc. They are composed of bone tissue only. Two examples are taken from gasterosteiforms.

(7) **Ganoid scales of polypterids**
These have conserved most of the characters of the ancestral rhombic scale, i.e. a bony basal plate covered by an odontocomplex composed of a layer of dentine on top of which a layer of ganoine, i.e. enamel, is deposited. As such, these scales represent a crucial element in the phylogeny of dermal skeletal tissues. Developmental observations were made in two species.

(8) **Ganoid scales of lepisosteids**
These are composed of a bony basal plate covered by a layer of ganoine. Dentine is not present. The basal plate is characterised by the presence of typical structures, the canals of Williamson. Some developmental data are presented from a single species.

(9) **Elasmoid scales**
Elasmoid scales are widespread and characterised by the presence of highly derived tissues among which is the characteristic elasmodine, a plywood-like arrangement of collagen layers. This element is found in the coelacanth, the lungfish, *Amia calva* Linnaeus, 1766, and a large number of the 26 000 teleost species. Two teleosts have been chosen to illustrate the development of this type of scales.

(10) **Fin rays**
Also called lepidotrichia, they are present in all non-tetrapod osteichthyans. They probably derive from modified scales in early vertebrates. Two examples to illustrate their development are taken from teleosts.

**III. MAIN DEVELOPMENTAL FEATURES OF THE DERMAL SKELETAL ELEMENTS**

(1) **Tissue environment prior to initiation**
All dermal skeletal elements form in the mesenchyme (or its differentiated derivative, the dermis), without a cartilaginous precursor and below a multilayered epithelium (or an epidermis) [We here use ‘mesenchyme’ to refer to any connective tissue below the epithelium (whether it is differentiated, as in the dermis, or not). Similarly, the term ‘epithelium’ will refer to the superficial tissue covering the mesenchyme (whether it is external, i.e. the epidermis, or internal, as in the oral or pharyngeal mucosa)]. Prior to initiation, the organisation of the mesenchyme differs strongly depending on the dermal skeletal element considered. Nevertheless, two clear strategies emerge: elements that will form in a well-structured mesenchyme, and those that do not need such an organisation.

(a) **A well-structured mesenchyme**
An advanced state of differentiation of mesenchyme is a prerequisite for the development of odontodes in sharks, rays and skates (Fig. 6A), and scales (Fig. 6B, C), scutes (Fig. 6D, E) and dermal plates of the postcranial dermal skeleton in osteichthyans. As will become clear below, these elements need to be tightly anchored, and the mesenchyme (or rather a differentiated version, the dermis) functions as a firm framework. The need for a well-structured mesenchyme explains why these dermal elements appear late in ontogeny (e.g. 30 days post-fertilization for the elasmoid scales in the *Danio rerio*).

In sharks and skates, the mesenchyme is divided into a superficial thick stratum spongiosum and a deep thinner stratum compactum with mostly rostro-caudally orientated collagen fibrils (Fig. 6A). Both layers are sparsely populated with mesenchymal cells. In teleosts, the mesenchyme consists of a well-defined, acellular stratum compactum, with collagen fibrils organised into an orthogonal plywood-like structure (Fig. 6B–E). There is no superficial stratum spongiosum. Elongated fibroblast-like cells penetrate the mid region of the stratum compactum prior to scale, scute and dermal plate initiation. The epithelial basal layer cells are organised into an uninterrupted layer, which is distinct from the epithelial layers above in that their cytoplasmic content indicates active involvement in protein synthesis. Such a differentiation of the epithelial cells prior to elasmoid scale initiation has been interpreted as a possible indication of the synthesis of signalling molecules involved in epithelial–mesenchymal interactions (Quilhac & Sire, 1998).

Through lack of larval material, we have no information available on the tissue environment prior to the development of the ganoid scales in polypterids and lepisosteids. However, observations of the skin in later stages of scale differentiation in a polypterid allow us to infer that the mesenchyme prior to scale initiation is probably well structured (as a stratum compactum) and sparsely populated with fibroblasts. A loose vascularised region (the stratum spongiosum) may exist between the stratum compactum and the epithelium prior to ganoid scale initiation in polypterids but this needs confirmation.
An unstructured mesenchyme

Teeth and denticles, cranial dermal bones, and fin rays develop in the absence of an organised matrix, in a mesenchyme that can be variably populated by cells (Fig. 7).

The timing of tooth and denticle initiation often depends on the developmental stage of their bony support (but this can vary depending on the ontogenetic stage). Therefore, the tissue environment is also that in which the bony supports will develop, i.e. jaw bones for many teeth, and various cranial dermal bones and postcranial dermal plates for denticles, respectively (Fig. 7A, B).

Some of the cranial dermal bones form early in ontogeny. The dentary bone in teleosts is usually one of the first bones to form [e.g. at 3–5 days post-fertilization (PF) in some teleosts]. Prior to its formation, the mandibular region is occupied by densely packed mesenchymal cells with the extracellular matrix barely visible (Fig. 7C, D). By contrast, other bones, like the frontal, form later, in mesenchyme sparsely populated with cells amidst a collagenous matrix. In both cases, however, the mesenchyme lacks a well-defined organisation.

During fin bud development the area between the two layers of epithelium (the fin fold) is sparsely populated by mesenchymal cells, which gradually increase in number. They come to adjoin each other to form a dense core which remains separated from the basal lamina by an acellular layer, in which collagen is randomly deposited. Prior to the initiation of the lepidotrichia,
actinotrichia (slender unmineralised tapered rods of elastoidin; Géraudie & Meunier, 1980), develop in this subepidermal space, providing the initial skeletal framework for the fin (Fig. 7E).

(2) Initiation and early morphogenesis

This developmental step is characterised by the formation of papillae within the mesenchyme, whatever its level of organisation. For a number of dermal skeletal elements the dermal papillae are well delimited and close to the epithelial–mesenchymal junction. By contrast, the papillae of some other elements are poorly defined and form at a distance from the epithelium.

(a) Well-delimited dermal papillae

This category includes the dermal papillae of the odontodes, teeth, denticles, and elasmoid scales (Fig. 8).
Fig. 8. A well-delimited dermal papilla during early morphogenesis of: (A) an odontode in a chondrichthyan, the skate *Leucoraja erinacea* (after Miyake et al., 1999); (B, C) teeth on the mandible in the cichlid *Hemichromis bimaculatus*; (D, E) a denticle in the callichthyid *Corydoras aeneus*; (F, G) an elasmoid scale in a cyprinid, the zebrafish *Danio rerio*. The arrows point to the epidermal-dermal boundary. 1-μm-thick sections (A, B, D, F) and transmission electron micrographs (C, E, G). d, dermis; dp, dermal papilla; eo, enamel organ; ep, epidermis; m, muscle; Mc, Meckel’s cartilage; me, mesenchyme. Scale bars: A, D = 50 μm; B = 10 μm; C = 5 μm; E = 2 μm; F = 3 μm; G = 500 nm.
The first obvious morphological indication announcing the subsequent formation of an odontode, a tooth or a denticle is either a thickening of the entire epithelium or, more frequently, of the basal layer of the epithelium at the presumptive site of organogenesis. The differentiated basal epithelial cells will form the dental lamina, a well-delimited cell population facing cells in the upper region of the mesenchyme. The latter do not usually show any sign of condensation yet.

Prior to elasmoid scale initiation, there is neither a thickening of the basal region of the epithelium nor a well-delimited differentiated mesenchymal cell population. However, at a given moment, the epithelial basal layer cells look differentiated on the entire surface of the prospective scale region. The accumulation of differentiated fibroblast-like cells in the upper part of the stratum compactum, close to the epithelial–mesenchymal boundary, is the only clear indication that scale morphogenesis has begun. At regular intervals within this mesenchymal cell population, the cells adjacent to the lamina densa of the basement membrane show evidence of differentiation. Facing these differentiating fibroblast-like cells, but not elsewhere, the epithelial basal layer cells remain well differentiated.

During the initial steps of odontode, tooth and denticle morphogenesis, mesenchymal cells accumulate in the upper region of the mesenchyme facing the differentiated basal epithelial layer (Fig. 8A–E). Although they are not conspicuously aggregated at first, these mesenchymal cells form a distinct papilla once invagination of the epithelium has started. Tooth morphogenesis is characterised by the invagination of epithelial cells into the mesenchyme (Fig. 8B, C). Conversely, in odontodes and denticles, the well-delimited dermal papillae invaginate slightly into the differentiated basal region of the epithelium (Fig. 8A, D, E). The denticle papillae form only when the bone support (either a cranial dermal bone, a fin spine or a scute) is forming or has already formed. In odontodes, teeth and denticles, the differentiated epithelial region, now called the dental organ, is adjoined at its basis by a well-delimited population of mesenchymal cells, called the dental papilla. The dental papilla cells, through their compact organisation, are distinctly separated as a whole from the surrounding mesenchymal cells, usually by a narrow but distinct acellular zone. The dental papilla cells are organised in two populations; one forming the dental papilla proper, immediately facing the polarised cells of the dental organ, the other forming a dental sac surrounding the dental organ.

The well-delimited, dense dermal papillae of the elasmoid scales appear at precise sites in the upper region of the mesenchyme, i.e. in regions located above the myosepta. The papillae originate from the population of fibroblast-like cells that initially accumulated along the epithelial–mesenchymal boundary. Each papilla seems to invaginate over its entire surface into the epithelium in such a way that the scale papilla appears to belong to the basal region of the epithelium when observed at low magnification (Fig. 8F). Observations with the transmission electron microscope, however, reveal that the scale papillae are clearly separated from the epithelial basal layer by a basement membrane (Fig. 8G). At first, the scale papillae are composed of two or three layers of large cells, the upper layer being closely apposed to the epithelial–mesenchymal boundary. The cells of the epithelial basal layer that face the scale papilla are cuboidal and well differentiated as suggested by the amount of organelles they contain.

The dermal papilla cells of these four dermal elements are densely packed with very few intercellular spaces. Although information is lacking on the initial stages of ganoid scales in polypterids and lepisosteids, subsequent stages allow us to infer that mesenchymal cells accumulate in the upper (probably vascularised) layer of the mesenchyme, above the stratum compactum. Further data on young polypterids are however needed to confirm the localisation of scale initiation close to the epithelial surface and to reveal the way in which the relation with the rich, superficial, vascularised network is established.

(b) Poorly defined papillae

This category includes the cranial dermal bones in teleosts, the scutes in armoured catfish, the postcranial dermal plates in various gasterosteiforms, and the fin rays (Fig. 9).

The papillae of the two bones studied most thoroughly, the frontal and dentary bones, are hardly distinguishable as such, having poorly defined edges. Both develop close to a cartilage of the chondrocranium, the taenia marginalis for the frontal, Meckel’s cartilage for the dentary. The outer surface of the papilla is separated more distinctly from the overlying epithelium than from the nearby cartilage (Fig. 9A, B). Along this side, the papilla merges with the perichondrial cell population in both elements. There is hardly any morphological evidence in the basal epithelial layer suggestive of possible epithelial–mesenchymal cell interactions (neither cell–cell contacts nor evidence of cell differentiation).

The first indication that the morphogenesis of a scute or of a dermal plate has begun is a local thickening of the stratum compactum of the mesenchyme accompanied by an accumulation of cells (both flattened
Fig. 9. A poorly-defined dermal papilla during early morphogenesis of: (A, B) a cranial dermal bone (frontal) in the cichlid *Hemichromis bimaculatus*. The arrow points to the dermal papilla; (C, D) a scute in the callichthyid *Corydoras arcuatus*. The arrow indicates the dermal papilla; (E, F) a fin ray in a cyprinid, the zebrafish *Danio rerio*. 1-µm-thick sections (A, C, E) and transmission electron micrographs (B, D, F). d, dermis; ep, epidermis; m, muscle; me, mesenchyme; pc, pigment cell; tm, *taenia marginalis*. Scale bars: A, E = 10 µm; B, D = 2 µm; C = 25 µm; F = 3 µm.
Fig. 10. A close relationship with the epithelial cells during differentiation of: (A) an odontode in a chondrichthyan, the catshark *Scyliorhinus canicula*; (B, C) teeth in the callichthyid, *Hoplosternum littorale*; (D, E) a denticle in the callichthyid *Corydoras aeneus*; (F, G) an elasmoid scale in a cyprinid, the zebrafish *Danio rerio*. The arrows point to the anterior and posterior region.
fibroblast-like cells and plump, differentiating cells = pre-osteoblasts) in the region where organogenesis will start. Scute morphogenesis is initiated in the mid-region of the mesenchyme, at a distance from the epithelial surface and above the myosepta (Fig. 9C). The dermal papilla is constituted of a population of pre-osteoblasts with numerous prolongations, which surround randomly disposed bundles of entrapped collagen fibrils of the stratum compactum. This arrangement breaks up the regular, plywood-like organisation in this area. As a result, the limits of the dermal papilla are ill-defined (Fig. 9D). Although data are lacking for the developing ganoid scales of the lepisosteids, observations on the initial stages of scale regeneration (Sire, 1994) allow us to deduce that the scale papillae probably form in the same way. Further observations are however needed to confirm this statement.

The dermal papilla of the lepidotrichium appears to be constituted by the mesenchymal cells that face the acellular, collagen-containing space between the epithelium and the mesenchyme, but the limits of the papilla are poorly defined (Fig. 9E, F).

(3) Late morphogenesis and differentiation

This developmental step is characterised by the differentiation of the cells and the subsequent synthesis of the different matrices constituting the dermal skeletal elements. Some skeletal elements retain an intimate relationship with the epithelial cells throughout their development; others do not, at least not during the first steps of differentiation.

(a) A close relation with the epithelial cells

This category encompasses the odontodes, teeth and denticles, the elasmoid scales of teleosts, the ganoid scales of polypterids, and fin rays (Fig. 10). The description given below is for first-generation teeth but holds for odontodes and denticles as well because late morphogenesis and differentiation stages are very similar (Fig. 10A–E).

(i) Odontodes, teeth and denticles

The proximal end of the dental lamina folds around the dermal papilla (to produce the so-called bell stage) and comes close to the fibrous layer of the mesenchyme. This infolding means that the dental organ is usually composed of two layers surrounding the well-organised dental papilla. (The terms ‘dental organ’ and ‘dental papilla’ pertain to teeth rather than to odontodes and denticles, but we use them here because there is no equivalent for odontode). The layer immediately adjacent to the dental papilla forms the inner dental epithelium (IDE). This layer is bordered by an outer dental epithelium (ODE). The proximal limit of the dental organ constitutes the cervical loop. The cells of the IDE differentiate into polarised ameloblasts, slightly cylindrical, with their long axis perpendicular to the epithelial–mesenchymal interface. By contrast, the cells of the ODE are rectangular, with their long axis parallel to the contour of the germ. The most differentiated ameloblasts are located at the tooth tip; the state of differentiation diminishes towards the cervical loop.

At this stage the mesenchymal cells of the papilla are densely packed with little extracellular matrix in between. The cells that are located against the ameloblasts differentiate into pre-odontoblasts while the centre of the dermal papilla becomes loosely organised. Immediately prior to enameloid matrix formation the pre-odontoblasts differentiate into odontoblasts. The space separating them from the ameloblasts contains numerous and distinct odontoblastic prolongations surrounded by small amounts of fibrillar extracellular matrix, which represent the first deposits of the enameloid. Some of the cell processes contact the lamina densa of the basement membrane below the ameloblasts. The first enameloid matrix is composed of a loosely arranged network of collagen fibrils 20–30 nm in diameter, typically with 66 nm cross striations, and free of interfibrillar background substance. Opposite this newly synthesised enameloid matrix the ameloblasts are slightly columnar and polarised. At the periphery of the enameloid matrix, the fibrils are arranged predominantly parallel to the tooth axis and some of them appear to anchor into the lamina densa of the basement membrane. Cytoplasmic prolongations from the distalmost odontoblasts penetrate the enameloid matrix.

In a more advanced stage, the number of collagen fibrils has increased and the enameloid matrix is denser of the scale anlage; (H) a ganoid scale in the polypterid Polypterus senegalus. The arrows point to the epidermal basal layer cells that are differentiating into ameloblasts; (I, J) a fin ray in D. rerio. The arrows point to the lepidotrichium anlage and the arrowhead to an actinotrichium. 1-μm-thick sections (A, B, D, F, H, I) and transmission electron micrographs (C, E, G, J). am, ameloblast; d, dermis; de, dentine; em, elasmoblast; en, enameloid; eo, enamel organ; ep, epidermis; le, lepidotrichium; m, muscle; ob, osteoblast; od, odontoblast; pd, predentine; me, mesenchyme; s, scale. Scale bars: A, C = 5 μm; B, F = 25 μm; D, H = 50 μm; E, G = 2 μm; I = 10 μm; J = 3 μm.
than before, mainly because of the presence of a thin fibrillar material. The basement membrane is no longer present between the ameloblasts and the enameloid surface, and mineralisation starts in the enameloid. Short cytoplasmic extensions of the ameloblasts contact the mineralised enameloid matrix. At this stage, predentine is already deposited against the enameloid matrix. The predentine consists of collagen fibrils of various diameters, depending on the teleost species considered (approximately 80–100 nm across in the teeth of Hemichromis bimaculatus, 30–40 nm in those of Danio rerio and 80 nm in the denticles of Corydoras aeneus). These fibrils are larger than the fibrils of the enameloid and are orientated parallel to the longitudinal axis of the tooth. In odontodes of the sting rays (Dasyatis akajei and Urolophus australiacus), predentine is lined by two layers of odontoblasts (Sasagawa, 1995) instead of one as in teleost teeth and denticles. In teleosts, predentine mineralises first at the tip of the tooth and the ameloblasts facing this region are still polarised but appear foamy. The mineralisation of the predentine matrix progresses centripetally towards the odontoblast layer, thereby turning predentine into dentine. In first-generation teeth and in small denticles, the odontoblastic processes are no longer observed within the dentine matrix at a distance from the cell body. In large teeth, large denticles and in skate odontodes, the odontoblastic processes persist and are housed in dentine tubules, classically described in mature dentine (ortho dentine).

During the stages that precede the attachment of the dental elements to their supports, the enameloid enters its maturation phase. It becomes ever more mineralised whilst the organic matrix is progressively removed. The dentine continues to be deposited by the odontoblasts and to mineralise from the tip downwards and from the periphery inwards. In teeth and denticles, bone of attachment is formed at the surface of the bone support facing the base of the dentine. In particular cases, the bone of attachment forms in the absence of a supporting bone and constitutes, by itself, the bone support through fusion of separate anlagen (Huysseune, 1983). The dentine base is linked to the attachment bone by ligaments that either do or do not mineralise. In skate odontodes, while the dentine matrix is deposited, the mesenchymal cells at the base of the papilla merge with those of the underlying fibrous layer of the stratum compactum, which is now organised into a plywood-like structure. These mesenchymal cells, probably osteoblasts, deposit the basal tissue that extends beyond the limits of the dental organ and becomes the attachment bone of the odontode.

(ii) Elasmoid scales
The elasmoid scale differentiates within a central elongated space that is created between the papilla cells, which form a bag around it. This bag shows two different topographical regions: a superficial region, against the epithelial–mesenchymal boundary, where the cells are roughly globular, and a deep region, thicker than the superficial one, composed of cells of various shapes. Marginal cells connect these two regions. As a consequence the scale matrix to be deposited will be completely enclosed. All the cells that surround the central space have differentiated into so-called elasmoblasts and are actively involved in the synthesis of the first scale material (Fig. 10F, G). This matrix is composed of collagen fibrils (20–30 nm in diameter) organised in a random fashion and embedded in a homogeneous electron-dense background substance. This first matrix constitutes the anlage of the external layer. At first the scale increases in surface only by the extension of the external layer, due to the high secretory activity of the cells located at its margin. The woven-fibred matrix of the external layer rapidly mineralises. The cells located at the upper surface of the scale, close to the epithelium, flatten and lose their activity. By contrast, once the scale has become sufficiently large, the elasmoblasts located at its deep surface become rectangular and start to lay down elasmodine against the external layer. Elasmodine (formerly called isopedine) is a tissue composed of parallel, 60–80 nm diameter collagen fibrils, organised in layers and with an orientation that changes from one layer to another, constituting a plywood-like structure. In young scales most of the elasmodine is unmineralised. It mineralises only slowly (or remains unmineralised, as in coelacanth scales; Giraud et al., 1978) from the deep surface of the external layer downwards.

Slightly later, the orientation of the scale in the mesenchyme has changed a little. It is now obliquely orientated, with the anterior region sinking deeper into the mesenchyme. The posterior region remains superficial, continues to extend in surface and comes to overlap the anterior region of a more caudal scale. The epithelium starts to fold around the posterior region and the epithelial basal layer cells either come to lie in direct contact with the scale surface (as in Danio rerio) or remain at a short distance (as in Hemichromis bimaculatus). From now on, a thin layer of matrix, called the limiting layer, is deposited periodically on that area of the scale surface immediately covered by the epithelium. The organic matrix of the limiting layer contains thin fibrillar and granular material and is devoid of collagen fibrils. It mineralises rapidly and heavily, and it is thought to contain substances of epithelial origin.
Ganoid scales of polypterids

Because polypterids are hard to rear in artificial conditions, information on the early stages of formation of their ganoid scales is still lacking. Young scales in *Polypterus senegalus* have, however, been shown to be of the elasmoid type. They lie in the upper part of the mesenchyme, close to the epithelial surface. Each scale is composed of an unmineralised, collagenous, basal region organised into a plywood-like structure (and therefore justifiably elasmodine), ornamented superficially with numerous patches of a well-mineralised woven-fibred matrix. Some cells are entrapped within the elasmodine. The young scale is surrounded by a layer of flattened cells at its outer surface and by a layer of rectangular cells, the elasmoblasts, at its deep surface. Numerous capillary blood vessels form two networks, one located above and one below the scale. In contrast to teleost elasmoid scales, where the external layer does not thicken once deposited, the outer layer of even well-formed polypterid scales thickens during an apparent second growth phase. Cells located close to the superficial ornamentation are next reactivated and deposit a woven-fibered collagen matrix around each capillary blood vessel, thus forming vascular canals. This superficial, vascularised matrix is acellular and constitutes a dentine layer. The lining cells are not entrapped but they leave cytoplasmic extensions within the matrix. These cells have clearly become differentiated into odontoblasts, and through their secretory activity, they contribute to the centripetal closure of the vascular canals (to constitute denteons) and to the thickening of the dentine layer. Once this layer has thickened so much that it has come to lie close to the epithelial covering, the lining odontoblasts disappear. The well-differentiated, cuboidal basal cells of the epithelium now come into contact with the dentine surface (Fig. 10H). These epithelial cells subsequently deposit the ganoin matrix, i.e. true enamel, at the scale surface and the cells are therefore clearly ameloblasts. Meanwhile, at the deep surface of the scale, elasmodine has thickened by apposition of a dozen layers. At a given moment, the organisation of the collagen matrix changes from the regular arrangement of the elasmodine to that of a woven-fibred bone. Elasmoblasts have been replaced by osteoblasts. In this region too, the new bone matrix is deposited around capillary blood vessels. The bone matrix thickens rapidly, then its deposition slows down and parallel-fibred bone is formed. Together, these layers of woven-fibred and parallel-fibred bone constitute the bony plate. During the formation of the bony plate numerous collagen bundles of the stratum compactum of the mesenchyme are entrapped in the scale matrix. They will persist to become the so-called Sharpey’s fibres, which anchor the scale tightly into the mesenchyme.

Fin rays

A lepidotrichium is composed of two symmetrical elements, which simultaneously produce the hemirays. They are embedded in a loose, vascularised, and innervated mesenchyme, and are oriented parallel to the long axis of the fin bud. They are surrounded by a multilayered epithelium that is thicker adjacent to the developing lepidotrichium than elsewhere in the fin. The basal epithelial cells opposite a forming lepidotrichium show manifest features of differentiation indicative of epithelial–mesenchymal interactions. The absence of secretory vesicles and the presence of an uninterrupted basement membrane nevertheless suggest that these epithelial basal cells do not directly participate in the production of the lepidotrichium matrix. The first outline of the hemirays is discernible within the acellular interface between the epithelium and the underlying mesenchymal cells (Fig. 10I). It consists of a long and thin shaft located in the collagenous network of the basal lamella underlying the epithelial–mesenchymal interface. The lepidotrichium anlage is composed of a woven-fibred matrix, with an electron-dense central region and electron-lucent peripheral regions, facing the epithelial basal cells on one side and the mesenchymal cells on the other side (Fig. 10J). The matrix is acellular and not penetrated by cell processes. It mineralises rapidly, from the central region outwards. Towards its distal end the hemiray narrows and consists of collagen fibrils orientated largely parallel to the long axis of the fin. The mesenchymal cells associated with the forming lepidotrichium constitute a continuous subepidermal sheet actively involved in protein synthesis. As the fin bud grows, the lepidotrichium matrix becomes progressively separated from the epithelial surface by a single layer of mesenchymal cells, which has infiltrated the epithelial–mesenchymal interface. Once they cover the hemirays surface these cells appear to be involved in protein secretion. Later during fin development numerous additional layers of mesenchymal cells isolate the lepidotrichium from the epithelium.

No relation with the epithelial cells

This category includes the cranial dermal bones, the scutes of the armoured catfish, the postcranial dermal plates of the gasterosteiforms, and the ganoid scales of lepisosteids (Fig. 11). The cranial dermal bones studied in detail so far, the dentary and frontal bones, differ from postcranial dermal elements, such as dermal
Fig. 11. No relation with the epithelial cells during differentiation of: (A) a cranial dermal bone (frontal bone, arrows) in the cichlid *Hemichromis bimaculatus*; (B) a scute in the callichthyid *Corydoras arcuatus*; (C, D) a postcranial dermal plate in the gasterosteiform *Gasterosteus aculeatus*; (E, F) a ganoid scale in the lepisosteid *Lepisosteus oculatus*. 1-μm-thick sections (A, B, C, E) and transmission electron micrographs (D, F). b, brain; d, dermis; e, eye; ep, epidermis; m, muscle; ob, osteoblast; pc, pigment cell; tm, *taenia marginalis*. Scale bars: A = 10 μm; B, E = 50 μm; C = 25 μm; D, F = 2 μm.
plates, scutes and lepisosteid scales, in that they form in an ill-defined mesenchyme.

(i) Cranial dermal bones

The anlage of the frontal as well as of the dentary bone is not sharply delimited from the surrounding tissues. At the side facing the epithelium, the anlage is covered by osteoblasts forming a more or less distinct single layer. This layer is separated from the epithelium by a mesenchymal space containing a network of interwoven collagen fibrils and some mesenchymal and pigment cells (Fig. 11A). At the opposite side, the anlage is separated from the cartilage by osteoblasts that are not clearly delimited from the perichondrial cells. In the frontal bone, which develops later than the dentary, many bundles of parallel collagen fibrils are interspersed among the perichondrial cells and the osteoblasts. Some of these lie close to the anlage. In *Hemichromis bimaculatus* the initial matrix of the frontal and dentary bones consists of a woven-fibred, acellular collagen network (with fibrils of approximately 20 nm in diameter) embedded in a fine granular, electron-dense background substance. This matrix mineralises soon after its deposition. Later, parallel-fibred matrix is deposited on both surfaces of the bone. Some collagen bundles located in the mesenchyme below the frontal bone merge with the bone matrix proper.

(ii) Scutes, postcranial dermal plates and lepisosteid scales

The differentiation and growth of the scutes (Fig. 11B), the postcranial dermal plates (Fig. 11C, D), and the ganoid scales in lepisosteids (Fig. 11E, F) present the same overall features and are described together.

In contrast to the elasmoid scales, the dermal papillae of these elements are not clearly delimited from the surrounding layers of the stratum compactum. The first extracellular matrix to be enclosed in the dermal papillae is randomly disposed collagen bundles originally part of the pre-existing mesenchyme. These bundles are surrounded by cytoplasmic extensions from the rounded osteoblasts located in the centre of the papilla. A new collagenous matrix is deposited first in the very centre of the papilla. This matrix is composed of patches of randomly disposed, thin, collagen fibrils (on average 15 nm in diameter *versus* 60 nm for the pre-existing fibrils of the mesenchyme). These patches of new matrix constitute the first true anlage of the dermal element. An electron-dense background substance is first deposited within this newly synthesised collagen material, then invades the adjacent, previously entrapped collagen bundles. Next, the osteoblasts located at the periphery of the papilla become more regularly arranged and so delimit the anlage more clearly. In the central region of the papilla, the mineralisation first starts within the woven-fibred, newly synthesised bone matrix, and then the mineral crystals also invade the pre-existing collagen bundles. The scutes are orientated obliquely in the mesenchyme; the dermal plates and the lepisosteid scales lie parallel to the skin surface. During further growth, the dermal element is covered on its upper and deeper surfaces by a layer of roughly rectangular osteoblasts. These lay down parallel-fibred bone (20–30 nm diameter fibrils) on both surfaces. In addition, numerous collagen bundles of the adjacent stratum compactum of the mesenchyme are incorporated in the deep region. These bundles will constitute the Sharpey’s fibres. They contribute to a strong anchoring of these dermal elements in the subjacent mesenchyme.

This organisation, i.e. a core of woven-fibred bone surrounded by layers of parallel-fibred bone, remains unchanged during growth of the dermal plates of the gasterosteiforms, even when their upper surface reaches the epithelial cover. By contrast, when the upper part of the ganoid scales in lepisosteids reaches the epithelial–mesenchymal boundary, the osteoblasts disappear from the outer scale surface. In this way, the epithelial basal layer cells come into contact with the entire bony surface, differentiate into ameloblasts and deposit a layer of ganoine (enamel) at the scale surface in the way described for the ganoid scales of polypterids. In the armoured catfish, on the other hand, when the upper part of the scute reaches the epithelial–mesenchymal boundary (yet without ever coming into contact), an entirely new tissue is deposited. This tissue, called hyaloine, is devoid of collagen fibrils; it is rich in thin fibrillar and granular material, and mineralises as heavily as enamel. However, the outer surface of the scute never becomes directly covered by the epithelium.

IV. DEVELOPMENTAL RESEMBLANCES AND DIFFERENCES IN ELEMENTS OF THE DERMAL SKELETON

This overview, which highlights the developmental features of each dermal skeletal element, reveals a number of similarities and differences (summarised in Table 2), the meaning of which is discussed below.

(1) Organisation of the mesenchyme: well-structured versus unstructured mesenchyme

A common feature of all the dermal skeletal elements is that they form in a more or less organised mesenchyme
(dermis) which itself is covered by a well-differentiated epithelium (epidermis). The comparative analysis of the mesenchymal organisation prior to the initiation of these dermal elements has revealed that, despite important differences in the state of differentiation of the mesenchyme, the common denominator is the presence of a support. This support can be either a well-structured mesenchyme itself (and especially a well-developed stratum compactum) or the presence of bone, cartilage or another support, be it well formed or in the course of formation. As a consequence, the time of initiation of a dermal element, i.e. early or late in ontogeny, will depend on the state of differentiation of the support to which it is related rather than on the type of element itself. For instance, in the armoured catfish, the sequence of appearance of denticles (teeth forming in extra-oral positions) is first on the jaw bones, then on the dermal bones of the cranium, then on the fin rays and finally on the scutes (Sire & Huysseune, 1996). This sequence reflects the sequence of formation of the underlying bones.

For those elements of the dermal skeleton that need a bony support (such as most teeth and denticles) the presence of a well-structured mesenchyme is not necessary. By contrast, odontodes, elasmoid and ganoid scales, scutes and postcranial dermal plates, all need a well-structured stratum compactum, in which they firmly anchor due to the incorporation of numerous collagen bundles originally present in the mesenchyme. Since the stratum compactum forms slowly during skin ontogeny, these dermal skeletal elements also appear late in ontogeny. The initiation of these elements certainly also depends on an appropriate state of differentiation of the epithelial basal layer cells (Quilhac & Sire, 1999).

In conclusion, the similarities or differences observed in the organisation of the mesenchyme prior to initiation of the various elements of the dermal skeleton are not indicative of any degree of homology (or absence thereof), but reflect the need for an appropriate state of differentiation of the support.

(2) Delimitation of the dermal condensations: well-delimited versus poorly defined dermal papilla

The organisation of the dermal papilla itself and its location with regard to the covering epithelium are, to our opinion, the most important developmental features allowing inference of a phylogenetic relationship between certain elements.

The above comparative analysis clearly demonstrates that all the dermal elements fall into one of the two following categories: on the one hand, those elements that develop from a well-delimited papilla, i.e. a dense population of mesenchymal cells with hardly visible intercellular spaces, set off well against the surrounding mesenchyme, and, on the other hand, the dermal elements that form within an ill-defined papilla, i.e. a loose population of mesenchymal cells with many intercellular spaces and not distinct from the surrounding mesenchyme. The former are always located close to the epithelial–mesenchymal boundary, while the latter are situated deep in the mesenchyme, or near a forming cartilage, but always at a distance from the epithelium. The epithelial basal layer cells that are facing

| Table 2. Comparison of the ten categories of dermal skeletal elements at three steps of their ontogeny |
|---|---|---|---|---|---|
| Mesenchyme before initiation | Well-structured | Unstructured | Papilla | Well-delimited | Poorly defined | Epithelium | Close relation | No relation |
| Odontodes | X | | X | X | X |
| Teeth | X | | X | X | X |
| Denticles | X | | X | X | |
| Cranial dermal bones | X | | X | X | |
| Scutes | X | | X | X | |
| Postcranial dermal plates | X | | X | X | |
| Ganoid scales of polypterids | X* | | X | X | |
| Ganoid scales of lepisosteids | X* | | X | X | |
| Elasmoid scales | X | | X | X | |
| Fin rays | X | | X | X | |

* Inferred from older stages.
the well-delimited papillae always show indications of differentiation suggestive of epithelial–mesenchymal interactions, while there are no such indications in the epithelial regions covering the poorly defined papillae.

The papillae of the odontodes, teeth and denticles fall into the first category (that of the well-delimited papillae). These three types of dermal elements have a similar organisation, similar tissues, similar developmental processes, and are inferred to have a similar evolutionary origin (see Section V.I). The tissues that result from the activity of the papilla cells are dental tissues: enamoid (partially if we consider the likely involvement of the epithelial cells), dentine and attachment bone. Therefore, we have called this type of papillae odontogenic papillae. It is noteworthy that the dermal papillae of the elasmoid scales and of the ganoid scales of polypterids are included in this category. This strongly suggests that the scale tissues, which are formed as a result of the activity of the differentiated cells in these odontogenic papillae, are derived from dental tissues.

The papillae of the cranial dermal bones, the scutes, the postcranial dermal plates and the ganoid scales of the lepisosteids, all fall in the second category (that of the poorly defined papillae). All these elements form deeply in the mesenchyme, and are first composed of bony tissues. As a consequence, we have called this type of papillae osteogenic papillae. It is interesting to note that during the first steps of differentiation of all these bony elements, collagen bundles of the pre-existing mesenchyme are incorporated within their matrix in addition to newly synthesised bone matrix.

The case of the lepidotrichia is somewhat problematical. On the one hand, the absence of a well-delimited papilla could place this type of element within the second category, that of the osteogenic papillae. On the other hand, there is no incorporation of pre-existing collagen bundles of the surrounding mesenchyme. The fin rays differentiate immediately below the epithelial–mesenchymal boundary, suggesting the existence of some kind of relationship with the epithelial cover. In polypterids, the lepidotrichia are covered with ganoine (Meunier, 1980). These features distinguish the developing lepidotrichium from the other elements of the osteogenic category. The lepidotrichium is the only dermal skeletal element out of ten that is formed while the support in which it develops is still growing. Indeed, at the moment the fin ray is initiated in the proximal region, the distal region of the fin is not yet differentiated. The first support of the fin ray anlage is therefore to be found in the collagen network of the basal lamella of the basement membrane, in which it is initiated.

(3) Interactions with the epithelium: close versus no relation

The way in which matrix is laid down is closely related to the nearby presence or absence of an epithelial cover and therefore suggests an interaction between the papilla cells and the basal epithelial cells. The dermal skeletal elements that are formed from odontogenic papillae show a clearly polarised matrix deposition, i.e. the first matrix is deposited on one surface of the presumptive element, and then thickens by apposition from this side onwards. In elements that form from osteogenic papillae, matrix deposition is not polarised and occurs on both surfaces.

A polarised deposition of the matrices is observed for the odontodes, teeth and denticles. The order of appearance of the different tissues is as follows: first, a loose, woven-fibred tissue, enamoid, is deposited against the epithelial–mesenchymal boundary by the differentiated dental papilla cells, the odontoblasts; then the same cells synthesise a parallel-fibred tissue, dentine, which is deposited against the enamoid surface (see Smith, 1995 for an evolutionary interpretation of enamoid versus enamel). Once the dentine starts to be laid down, the epithelial basal layer cells that have differentiated into ameloblasts probably deposit various products within the loose enamoid matrix, ensuring its high level of mineralisation.

We have shown that the elasmoid scales form within odontogenic papillae, as do the odontodes, teeth and denticles. At a short distance from the epithelial surface, the first layer of the elasmoid scale to be deposited by the differentiated scale-forming cells, the elasmodoblasts, is a woven-fibred tissue, the external layer. Then a parallel-fibred tissue, elasmodine, organised into a plywood-like structure, is laid down under the external layer by the same cells, the elasmodoblasts. Later, the epithelial basal layer cells that are in direct contact with or close to the posterior region of the scale are assumed to synthesise epithelial products that are incorporated in the so-called limiting layer covering the scale surface.

In polypterids, the young ganoid scales are of the elasmoid type. Therefore, despite the lack of data on the morphogenesis and early differentiation of the ganoid scale, the tissue organisation of young scales makes it probable that the first tissue to be deposited is the woven-fibred tissue, which takes the appearance of the numerous patches ornamenting the scale surface. The elasmodine is most likely deposited secondarily by the elasmodoblasts below the woven-fibred tissue, in...
Fig. 12. Presence, absence or polymorphy of (A) the odontodes and denticles, (B) postcranial dermal plates/scutes, and (C) elasmoid scales in the main lineages of living gnathostomes. Characters optimised using MacClade 3.01 and relationships of the living vertebrates after Lecointre (1994). (A) Odontodes were present in early jawless vertebrates (e.g. Thelodonti); they were conserved in modern chondrichthyans, coelacanths, polypterids and lepisosteids and lost in the other lineages. Denticles
a polarised manner. In a second step, not present in the elasmoid scales, the woven-fibred superficial tissue of the young polypterid scale thickens to form the dentine layer. The differentiation of the resting superficial cells into odontoblasts is possibly mediated through information (growth factors?) brought through the network of capillary blood vessels located at the scale surface. Once the dentine layer has come close to the epithelial surface, epithelial–mesenchymal interactions probably occur. These putative interactions result in the disappearance of the odontoblasts from the scale surface and in the deposition of ganoine, an enamel, by the basal epithelial cells, which have differentiated into ameloblasts. At the same time, along the deep surface of the scale, the ameloblasts have stopped producing a plywood-like matrix and have started to deposit the woven-fibred bone matrix of the presumptive bony plate. Again, this change has possibly occurred through information spread by means of the vascular network located below the elasmoid. These blood vessels are eventually incorporated, within the bony plate of the scale, in vascular canals.

The developmental study of the ganoid scale of polypterids highlights the spatial and temporal sequence of formation of the two constituents classically described, i.e. the superficial, odontogenic and the deep, osteogenic component. Two observations are of particular significance: (1) the two components do not form as separate entities but in a continuum beginning with the odontogenic component; (2) the woven-fibred external layer and the elasmoid (the basal plate of the elasmoid scale) appear early, during the sequence of formation of the odontogenic component.

The other dermal elements, which form in poorly delimited osteogenic papillae and at a distance from the epithelium (i.e. cranial dermal bones, scutes and post-cranial dermal plates, and ganoid scales of lepisosteids), show similarities in the organisation of their matrix. Their deposition is not polarised, since it occurs simultaneously on both surfaces of the growing element. The end product is a tissue which can fairly easily be identified as bone: a central part, corresponding to the fast growing initium, composed of woven-fibred matrix, and peripheral regions composed of parallel-fibred matrix deposited once growth has slowed down. In two dermal elements (the scutes of armoured catfish and the ganoid scales of lepisosteids) the outer bone surface comes to lie close to the epithelial–mesenchymal boundary and it is assumed that epithelial–mesenchymal interactions occur at this stage. This presumed late interaction leads to ganoine deposition on the surface of the ganoid scale of lepisosteids, and is probably necessary for the formation of hyaloine on the scute surface in armoured catfish. By contrast, despite having their outer surface sometimes close to the basal surface of the epithelium, the other dermal elements do not show the presence of any other tissue than bone.

The three different tissues of the elasmoid scales (external layer, elasmoinde and limiting layer) cannot, at first glance, be identified as dental tissues. Yet, (i) they are initiated within odontogenic, but not osteogenic, papillae, (ii) their matrix deposition is polarised, and (iii) the sequence of tissue formation is similar to that described for dental elements. These findings strongly suggest that the tissues of the elasmoid scales are related to dental more than to bony tissues, unlike what several authors have proposed.

V. EVOLUTIONARY RELATIONSHIPS

Having briefly reviewed the structure and development of the tissues in the various dermal skeletal elements, let us now consider the possible evolutionary routes that have been followed by the different tissues found in the dermal skeleton. The present discussion is concerned with the evolution of the dermal skeletal elements as a whole, and is not an attempt to reconstruct the phylogeny of the vertebrate skeletal tissues. Readers are referred to Ørvig (1951, 1967), Moss (1964), Poole (1967), Hall (1992), Smith & Hall (1990, 1993) and Smith (1995), for accounts of the evolution of the vertebrate skeletal and dental tissues.

Bearing in mind that homologous structures have to meet the criterion of phylogenetic continuity (Raff, 1996; Meyer, 1999), we have mapped the skeletal elements on a cladogram of the vertebrates (Fig. 12). We acknowledge the fact that a cladogram represents but one of several possible reconstructions of a phylogenetic tree (Raff, 1996), and that a different cladogram...
can seriously affect the evolutionary interpretations drawn from it. Because of the dispersed distribution of certain elements in the cladogram presented, we nevertheless predict that the interpretations presented below will not be affected by a change in the cladogram, except for one element, to be commented on further below: the elasmoid scales.

(1) A clear evolutionary sequence: odontodes, teeth and denticles

The structural resemblance of the odontode tissues in extant chondrichthyans with tooth and denticle tissues in living teleosts enables us to classify them in one single category, that of the dental tissues. Indeed, both enameloid (at least partially) and dentine originate from cells condensed first in odontogenic papillae and are characterised by polarised matrix deposition. There are however, some differences that are related either to phylogenetic distance or to the localisation of these organs in or outside the buccal cavity.

The odontodes, or similar ancestral organs, are known from jawless vertebrates that inhabited the waters of the Ordovician, Silurian and Devonian periods, from approximately 500 to 400 mya. The head and body of these early vertebrates was covered either by isolated odontodes (as e.g. in thelodonts) or by odontodes fixed on bony plates (as e.g. in some placoderms) (Janvier, 1996). In the classical view, odontodes gave rise to teeth as ectoderm with odontode forming potential migrated into the primitive stomodaeum concurrent with the evolution of jaws. This view is based largely on the developmental resemblance of shark odontodes (placoid scales) to teeth, despite the fact that they do not grade into each other (Reif, 1980). Smith & Coates (1998, 2000, 2001) propose an alternative view to this classic theory, based on the identification of different feeding strategies in agnathans that they consider to be prepatterns for gnathostome dentitions. Although we feel the arguments for this view not to be convincing, this matter is of minor relevance in the present context: irrespective of their origin either prior to the rise of the gnathostomes, as in Smith & Coates’ (1998, 2000, 2001) view, or at the agnathan–gnathostome transition, as in the classical theory, teeth were conserved in all lineages because of their adaptive value and thus contribution to the fitness of the animal (cf. Huysseune & Sire, 1998).

In a short period of time, the gnathostomes separated into chondrichthyans (the cartilaginous fish) and osteichthyans (the bony fish). Until now, and through 450 million years of vertebrate evolution, isolated odontodes were conserved in the skin of the chondrichthyans only, giving rise to the odontodes described in the present review in living sharks, rays and skates. This persistence most likely indicates that the possession of odontodes was advantageous in early chondrichthyans and that this selective advantage (probably as hydrodynamic devices) was retained in all the descendants in this lineage. In contrast to the chondrichthyan lineage, the osteichthyan lineages did not conserve the dermal skeleton of their ancestor. In the early osteichthyans, the condition of isolated odontodes found in the ancestral jawless vertebrates rapidly changed into odontocomplexes (sensu Ørvig, 1977), i.e. the odontodes progressively merged either in surface or by superposition (but see the reviews in Reif, 1982; Smith & Hall, 1990). Bony plates covered by odontocomplexes are considered the ancestor of all the elements of the dermal skeleton found in living osteichthyans. Such odontocomplexes, in which odontode units are still distinguishable, are conserved in the basal sarcopterygian, the coelacanth, and in the basal actinopterygians, polypterids and lepisosteids (Fig. 12A). At lower phylogenetic levels, numerous modifications occurred during evolution: some elements or parts of them were lost, or their structure was modified. Consequently, the isolated denticles observed in living teleosts cannot be derived directly from the ancestral odontodes, nor can they be a re-expression of such odontodes. These denticles are interpreted as teeth forming in extra-oral locations, resulting probably from a developmental accident involving some neural crest cell populations. The optimisation of this character within a cladogram of the vertebrates clearly indicates the lack of direct phylogenetical relationships between the odontodes and dermal denticles (Fig. 12A). This subject has been discussed recently (Sire, 2001).

The 450 million years of separate evolution between odontodes and teeth explains why the structure of their organic matrix is quite different (e.g. shark enameloid differs from teleost enameloid, cf. Sasagawa, 1993). By contrast, teeth and denticles in teleosts have separated more recently (approximately 100 mya), which explains why their structure is still very similar. On the other hand, the location of the dermal papillae, which slightly invaginate into the basal region of the epithelium, groups odontodes and denticles. This resemblance is interpreted as a convergence related to the extra-oral position of both elements and the similar constraints to which these organs are subjected. The fact that tooth development often requires a deep invagination of the dental epithelium within the mesenchyme is interpreted to be secondary because a deep invagination allows a better protection of the tooth germ from possible injuries provoked by food processing. Further evidence for this interpretation is seen in the
fact that so-called intraosseous replacement of teeth (which requires a deep epithelial invagination) has been claimed to be a derived character state among teleosts (Trapani, 2001). We propose that dermal papillae invaginating into the basal region of the covering epithelium could be the primitive condition, i.e. the condition that probably prevailed for the odontodes developing in the skin of early vertebrates, some 450 mya.

The odontodes, teeth and denticles are thus considered homologous organs (showing the same structure and the same evolutionary origin) and the evolutionary sequence that we propose is as follows: 1, isolated odontode units; 2, teeth; 3, denticles.

(2) A crucial element: ganoid scales of polypterids

In the recent fauna, ganoid scales of polypterids are the only representatives of those elements of the dermal skeleton, which have conserved most characters of the ancestral type of dermal skeletal element, namely the rhombic scale of early osteichthians. This type of scale, found e.g. in the genus Cheirolepis, is composed of a thick bony basal plate covered by numerous generations of more or less fused odontodes forming an odontocomplex. Indeed, although polypterid scales have been modified slightly during evolution, they have conserved a superficial region composed of dental tissues (dentine and enamel) and a deep region composed of bone.

By virtue of the well-conserved and extensive fossil record, the evolutionary sequence of the ganoid scale tissues is easy to trace. While the bony component has not changed very much when compared to the ancestral scale, the superficial region, which was initially composed of isolated odontodes, has been progressively modified into an odontocomplex (sensu Ørvig, 1977). Although the tissues of the ancestral odontode units (dentine and its covering enamel, ganoine) have themselves been conserved, they became organised into one layer of dentine covered by ganoine. These dental tissues compose the upper region of the scale and they are still easily recognisable because of their typical structure (Meunier, 1980).

We have shown that the dental tissues of the ganoid scales in polypterids probably arise from cells condensed in odontogenic papillae. The first tissues to be formed during the early stages of ganoid scale differentiation are the typical tissues of an elasmoid scale: the woven-fibred external layer and the elasmodine. As in the elasmoid scales of teleosts these tissues are synthesised by cells originating from an odontogenic papilla and, thus, belong to the mesenchymal dental tissues. In polypterid scales the superficial tissue, the external layer, further develops into a thick dentine layer, during a secondary growth phase probably related to the presence of a vascular network. This means that the external layer in the elasmoid scale is the initial of the dentine. The dentine layer in the ganoid scales is different from the classical dentine described in odontodes and teeth. An explanation may be that it derives from the juxtaposition of several odontodal units. The upper vascular canals possibly represent the remnants of the pulp cavities of the odontodal units that have merged, and by progressive obstruction have become denteons. Elasmodine, given its development within an odontogenic papilla, is considered also a mesenchymal dental tissue. The only known dental tissue with a structural organisation roughly similar to that of elasmodine is orthodentine (see discussion in Sire, 1989). However, there are no indications in the fossil record, which could enable us to understand the relationship of this tissue with orthodentine. The ganoine, above, and the bony plate, below, are deposited after the dentine and elasmodine have been completed. Ganoine, undoubtedly enamel, is composed of several layers deposited periodically.

In polypterid scales, the basal bony plate forms in the continuity of the elasmodine, but clearly is a different type of matrix (bone). It is clear that this is not a separate bony element that merges secondarily with the deep surface of the dental component. The observations suggest that the initiation of the bony plate is mediated (through signal molecules?) by the vascularisation located below the elasmodine. The vascular network of the skin seems to play a crucial role in the further growth of the dentine and of the bony plate (together constituting the main characters of the ganoid scale). Further investigations are needed to check whether two different populations of mesenchymal cells, i.e. one committed to differentiate into odontoblasts and the other into osteoblasts, are involved in the formation of ganoid scales and to understand the role played by the vascularisation.

The superficial region (odontocomplex) covering the ganoid scales of polypterids is composed of the same tissues (dentine and enamel) as in odontodes and these tissues have the same evolutionary origin. Therefore, we can consider the tissues of the odontocomplex, dentine and ganoine, homologous to those of the odontodes. The evolutionary sequence for the ganoid scales of polypterids could be interpreted as follows (see also the odontode regulation theory proposed by Reif, 1982): 1, numerous, isolated odontodes located on a thick basal bony plate; 2, juxtaposition and superposition of several generations of odontodes; 3, fusion
of the first generation of juxtaposed odontodes thereby giving rise to the dentine layer and progressive reduction of odontode superposition, giving rise to the deposition of successive layers of ganoine only.

(3) Loss of odontogenic component links cranial dermal bones, scutes, postcranial dermal plates, ganoid scales of lepisosteids and fin rays

The dermal skeletal elements composed of bony tissues find their origin in an ancestral jawless lineage some 450 mya. The postcranial dermal plates have been lost in modern chondrichthyans but conserved in various lineages of living osteichthyans (Fig. 12B). It seems parsimonious to consider that the cranial dermal bones, scutes and postcranial dermal plates of the living osteichthyans, and to a lesser degree the lepidotrichium, are derived from the deep osteogenic component of the ancestral scale while the superficial, odontogenic component has been lost. This interpretation, along with the important differences that exist between the odontogenic and osteogenic papillae and between the matrices, supports the putative existence of two ancestral mesenchymal cell populations (cf. Smith & Hall, 1990, 1993), the osteogenic population being the only one conserved in these elements. However, in the ganoid scales of lepisosteids and, probably, in the scutes of the armoured catfish as well, it appears that the epithelial cells have conserved the possibility to deposit epithelial products at the scute surface despite the fact that the mesenchymal odontogenic component, dentine, has been lost. It is probable that the loss of this superficial component has occurred independently in the lineages leading to the present-day osteogenic components.

Whereas the optimisation of this character in the cladogram of vertebrates supports a phylogenetical relationship of the basal (bony) plates of the scales in polypterids, chondrosteans (sturgeons) and lepisosteids, it also indicates the absence of a phylogenetical link for the postcranial dermal plates, spines, and scutes of teleosts (e.g. in gasterosteiforms). In addition, the evolutionary origin of the osteoderms in the anurans, reptiles, and armadillos is equivocal (Fig. 12B).

In the osteichthyans the evolutionary sequence could be: 1, an ancestral dermal skeletal element with two components (osteogenic and odontogenic) was conserved in the polypterids; 2, the odontogenic component for the postcranial dermal plates was lost in the chondrosteans and in the ganoid scales of lepisosteids; 3, the osteogenic component was lost in basal teleosts; and 4, scutes, postcranial dermal plates and spines were re-expressed in some teleost lineages. The condition of the dermal plates (osteoderms) in the sarcopterygian lineage is equivocal, i.e. they were either conserved or they were lost and then re-expressed in anurans, reptiles and armadillos.

(4) An enigmatic element: elasmoid scales

Elasmoid scales are present in sarcopterygians (coelacanth, lungfish and Gymnophiona) and in most actinopterygian lineages. The optimisation of this character indicates either a triple acquisition (in sarcopterygians, polypterids and teleosts) or a single apparition in an ancestral osteichthyan (Fig. 12C). New data from fossils could help in this analysis.

Considering that the elasmoid scale could have derived from an ancestral rhombic scale roughly similar to the ganoid scale of polypterids, and that the young ganoid scale is an elasmoid scale, we conclude that the elasmoid scale in teleosts could derive from a rhombic scale by a phenomenon of paedomorphosis: the immature stage of the ancestral organ is conserved in the mature stage of the descendant (cf. e.g. Raff, 1996).

It is obvious that the data obtained on young polypterid scales are very helpful to resolve the problem of the evolutionary affinities of the tissues of the elasmoid scale. For instance, when comparing the tissue environment in which both scales differentiate, the main difference is the absence of capillary blood vessels in the mesenchyme surrounding the developing elasmoid scales in teleosts. This lack of vascular network surrounding the scale could explain why the teleost scale does not develop a thick dentine layer at its outer surface or a thick bony plate at its deeper surface (as is the case in polypterid scales). Another important observation, which helps in tracing the evolutionary sequence of the elasmoid scale tissues, is that the external layer is probably the initium of the dentine layer, and that the limiting layer is probably derived from the ganoine. By contrast, as already said above, it is much more difficult to trace the origin of the elasmodine. Except for the fact that elasmodine is probably derived from a dental tissue, its plywood-like structure is enigmatic in terms of evolutionary relationships.

VI. CONCLUSIONS

(1) In this review, we hope to have provided a few examples of how studies on the development of particular dermal skeletal elements in ‘fish’ have contributed to our understanding of the structural relationships of their tissues to other known tissues, and have provided
insights into the evolutionary history of the elements concerned.

(2) Developmental studies at the tissue level of all the dermal skeletal elements found in present-day aquatic vertebrates indicate that these elements can be assigned to either odontogenic or osteogenic categories on the basis of the place of formation of their dermal papillae and of the way of deposition of their tissues. The pivotal role of cell condensations in the development of skeletal tissues, and as a substrate for modification of skeletal morphology during evolution, was recognised previously by Hall & Miyake (1992, 2000).

(3) Our studies support the evolutionary affinities (a) between odontodes, teeth and denticles, (b) between the ganoid scales of polypterids and the elasmoid scales of teleosts, and (c) to a lesser degree between the different bony elements.

(4) There is now ample evidence to ascertain that the tissues of the elasmoid scale are derived from dental and not from bony tissues. Further investigations are needed to endorse this hypothesis. One way is to search for tissue-specific proteins in the different tissues involved. Studies are now underway aimed at revealing enamel protein expression in the limiting layer of the elasmoid scales, and in the hyaloine of the scutes of armoured catfish. Similarly, a study of the expression of dentine-specific proteins (e.g. dentine sialoprotein and dentine phosphoprotein) could be envisaged to test the hypothesis that the external layer of elasmoid scales, as well as the elasmodine, is derived from dentine.

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VIII. REFERENCES


