# The Eel

## *Third edition*

**F.-W. Tesch**

*With contributions from*
P. Bartsch, R. Berg, O. Gabriel, I.W. Henderson,
A. Kamstra, M. Kloppmann, L.W. Reimer, K. Söffker
and T. Wirth

*Translated from the German by* R.J. White

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# Preface

Demand for the German editions and for the English translation of this book on eels has made it necessary to publish a further English edition. It is based on the third German edition (1999) and contains further updatings. The unusually high demand for a book specialising on a single genus is due to the eel's scientific and gastronomic popularity in large areas of Europe and in Japan, and the scientific demand has expanded greatly since first publication of the book in 1973, especially in East Asia and Australia/New Zealand. Subject areas like continental ecology and aquaculture contributed to this. These have drawn in with them other topics like oceanic ecology, genetics, and parasitology: this edition contains a completely new section for genetics.

With regard to the oceans, meteorology and sea currents expanded interest in eels to specialists of those subjects. In the 1970s, the author was even asked whether knowledge of eel occurrence in the various parts of the oceans could also contribute to exploration of ocean currents. In North America, until then interest in eels was limited to the areas of its continental occurrence along the east coast. Besides the economics of the eel, its importance as an oceanographic indicator has expanded interest in this animal among other circles, especially in North America and East Asia

Accordingly, it seemed appropriate to consult with other colleagues in certain subject areas of this book, so specialists in endocrinology, genetics, aquaculture, parasitology and toxicology, among others, were brought in. The descriptions of fishing techniques also benefited from collaboration of a specialist. It became clear that almost no other fish species is caught by such a diverse range of gear, so this chapter represents almost a cross-section of general fish catching technology.

Recent population decline of some eel species created utmost economic and scientific interest. This might be equated with the diminution of other economically important food fishes and blamed on overfishing. But because the critical times of the eel's highest mortality extend over longer periods than those of other fishes, and are primarily at sea, this decline cannot be explained so simply. Therefore, in the present English edition the marine phases receive no less attention than do the continental phases of the life cycle. The data on the marine biology of the eel are increasingly important also because there are considerable deficiencies in knowledge of the Indopacific species relative to the Atlantic species, even though in recent years research activities on eels in the Pacific Ocean have far exceeded those in the Atlantic.

**Sincere thanks are due to the Fisheries Society of the British Isles whose generous financial support enabled the translation of this book to go ahead.**

Finally, I must express my grateful thanks to all those who have helped in the production of this book. I feel particularly indebted to the translator, the editor and the publisher, who have worked so conscientiously to ensure the appearance of the second English edition.

# 1

# Body structure and functions

*Updated by M. Kloppmann*

## 1.1 Introduction

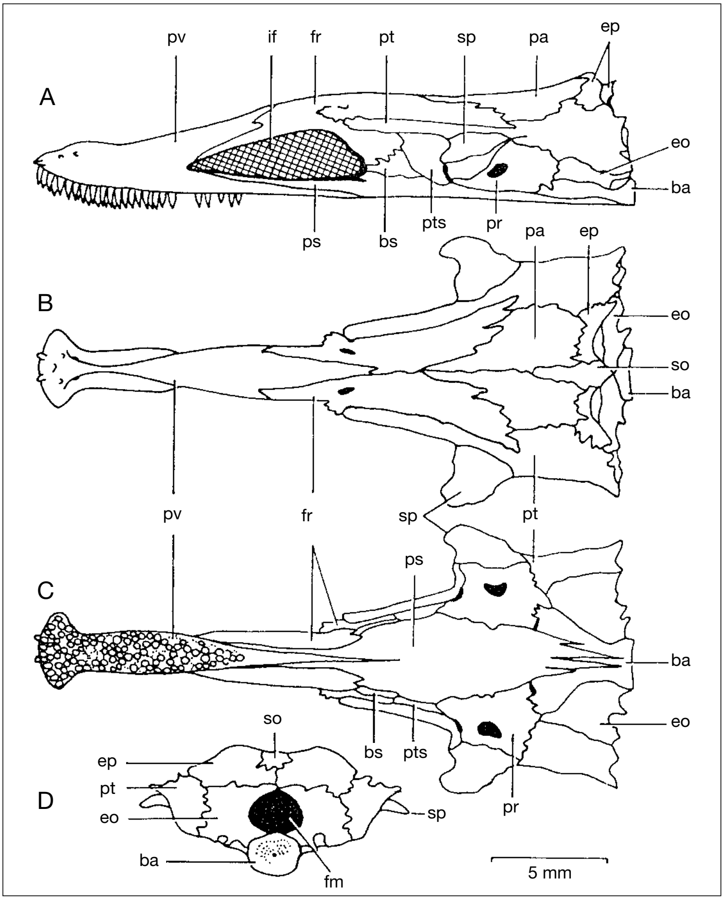
Eels (Anguilliformes) are always relatively elongated fishes. They have no ventral fin and no pelvic girdle. Some groups (e.g. Muraenoidei) exhibit reduced pectoral fins. The number of vertebrae and of myomeres can vary between 105 in some Congridae up to >300 in the meso- and bathy-pelagic Nemichthydae of the deep sea (Nielsen and Smith, 1978). The unpaired fins are confluent, and relicts of the caudal fin are distinguishable at the tail end, at least internally early in ontogenesis (Fig. 1.4). The fin rays (Lepidotrichia) always correspond functionally and numerically exactly with the pterygiophores the elements supporting their endoskeletal epineural. In accordance with its elongated body form, the eel has a rather narrow head that helps hiding in sand, mud and narrow holes. Within the head, the gill apparatus has to be accommodated to the elongated form. From its normal position in fishes below the skull it is displaced backwards almost to behind the skull. The gill construction is, therefore, very long; the pectoral girdle is disconnected from the skull and the post-temporal is reduced. There are no gillrakers and no mesocoracoid in the pectoral girdle. In particular, the skull shows a number of reductions and characteristic peculiarities that are described below. The alimentary tract of the Anguilliformes probably always lacks pyloric appendices (Robins, 1989). The female gonads have no separate outlet and the eggs are expelled through the abdominal pore. As far as we know, the Anguilliformes are monocyclic, which means that the parents die after the first spawning. The strange leptocephalus larvae of the Anguilliformes always have pectoral fins, even in those groups where the adults have none. In early developmental stages they also have a rounded caudal fin that develops in connection with the dorsal and anal fin and which shows no caudal fin peaks. A rostral commissure of the lateral line always exists in young developmental stages and persists usually from larval to adult stages.

From a physiological point of view the eel is a particularly popular experimental animal. This is due not only to its extremely marked resistance to experimental conditions, but also to many distinctive characteristics, namely: its hol-euryhaline osmoregulatory capacities; its phases of differential activity and behaviour patterns; its multistage metamorphosis during ontogeny; its great endurance and ability to navigate during migration; and lastly, even its unusual body shape. The range of publications in these fields of study increased greatly over the past few decades. In the morphological and physiological parts of this chapter, particular reference will be made to those publications that are in some way connected with the ecology of this interesting fish.

## 1.2 Skeleton

### *1.2.1 Skull (updated and revised by P. Bartsch)*

The structure of the eel's skull will be described using Matsui and Takai's (1959) clear description of the skull of the Japanese eel (*Anguilla japonica*) (Figs 1.1 and 1.2). The skull and other parts of the adult eel's (*A. anguilla*) skeleton, as well as that of other Anguilliformes (*Muraenesox cinereus*), were described adequately, and partly compared, by Törlitz (1922) and Takai (1959). Smith and Castle (1972) made similar studies on *Anguilla*, *Neoconger vermiformes*, *Moringua edwardsi* and *Phytonichthys*, McCosker (1977) on several Ophichthidae, and Smith (1989a) on *A. rostrata*. Detailed monographs on the develop-



| | |
|---|---|
| A | From the side |
| B | From above |
| C | From below |
| D | From behind |
| ba | Basioccipital |
| bs | Basisphenoid |
| eo | Exoccipital |
| ep | Epiotic |
| fm | Foramen magnum |
| fr | Frontal |
| if | Interorbital window |
| pa | Parietal |
| pr | Prootic |
| ps | Parasphenoid |
| pt | Pterotic |
| pts | Pterosphenoid |
| pv | Premaxillo-ethmovomerine bloc |
| so | Supraoccipital |
| sp | (Auto)Sphenotic |

**Fig. 1.1** Skull (Neurocranium and upper exocranium) of *A. japonica* (after Matsui and Takai, 1959, modified)

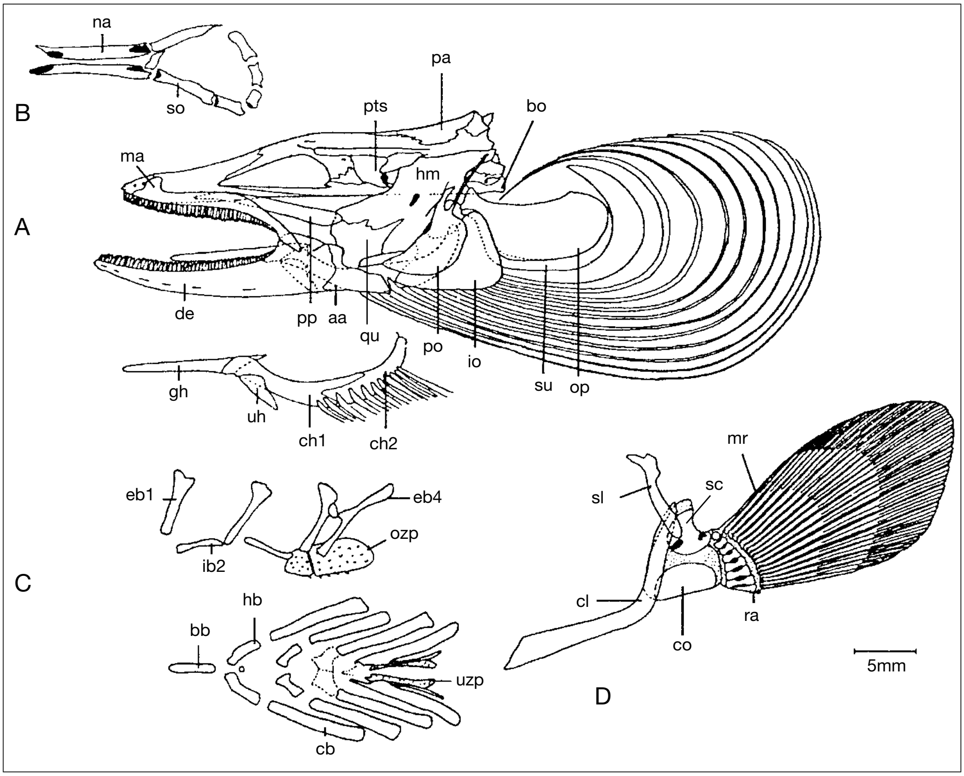
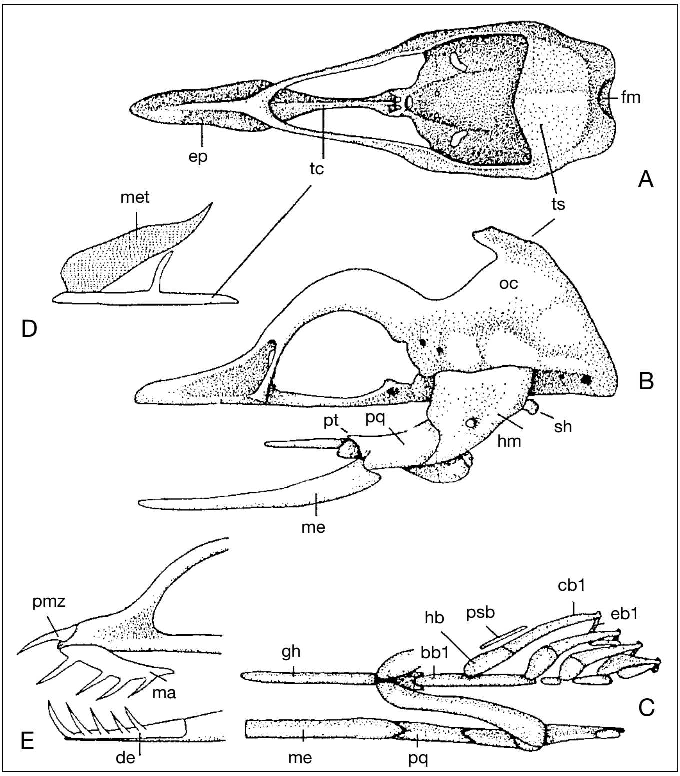


**Fig. 1.2** Cranial skeleton and pectoral girdle of the eel (partly after Matsui and Takai, 1959 and Smith, 1989)

| | |
|---|---|
| A | Cranial skeleton with suspensorium and jaws of *A. japonica* |
| B | Ossifications of lateral line organs (*A. anguilla*) |
| C | Inferior hyoid arch of *A. japonica* |
| D | Pectoral girdle |
| aa | Angulo-Retro-Articular |
| bb | Basibranchial |
| bo | Basioccipital |
| br | Branchiostegal rays |
| cb | Ceratobranchials |
| ch1/ ch2 | Ceratohyal 1 and 2 |
| cl | Cleithrum |
| co | Coracoid |
| de | Dental |
| eb1 | Epibranchial 1 |
| eb4 | Epibranchial 4 |
| gh | Glossohyal |
| hb | Hyperbranchial |
| hm | Hyomandibular |
| ma | Maxilla |
| mr | Marginal pectoral ray |
| Na | Nasal |
| op | Operculum |
| ozp | Upper dental plate |
| pa | Parietal |
| po | Preoperculum |
| pp | (Ecto-)Pterygoid |
| pts | Pterosphenoid |
| qu | Quadrate |
| ra | Radial |
| sc | Scapula |
| sl | Supracleithrum |
| so | Supraoccipital |
| su | Suboperculum |
| uh | Urohyal |
| uzp | Lower dental plate |

ment of the skull of *A. anguilla* larvae were published by Norman (1926) and, on the congrid larva of *Ariosoma balearicum* by Hulet (1987). The skull of the European eel leptocephalus (Fig. 1.3) is quite different in its components and proportions from that of the adults (Fig. 1.1). Also, the proportions of the skulls differ between the two ecological varieties of broad- and narrow-headed European eels (Törlitz, 1922; see Section 3.3.1.4).

Generally, the anguilliform skull differs significantly from that of other groups of genuine bony fish (Teleostei). In the upper jaw a stable, fused bone is formed that is derived from the dentated upper bony elements – the premaxillary, the vomer, and the so-called mesethmoid bone. The latter in eels does not seem, at least in parts, to be a cartilaginously



| | |
|---|---|
| A | Chrondrocranium without branchial skeleton (total length of the larva: 31 mm) |
| B | Chrondrocranium from the side |
| C | Chrondrocranium visceral skeleton from below |
| D | Rostral region with mesethmoid bone (total length of the larva: 70 mm) |
| E | Teeth of an early larva (total length of the larva: 11 mm) |

| | |
|---|---|
| bb1 | Basibranchial 1 |
| cb1 | Ceratobranchial 1 |
| de | Dentary |
| eb1 | Epibranchial 1 |
| ep | Epiotic |
| fm | Foramen magnum |
| gh | Glossohyal |
| hb | Hyperbranchial |
| hm | Hyomandibular |
| ma | Maxilla |
| me | Meckel's cartiledge |
| met | Mesethmoid |
| oc | Ear capsule |
| pmz | Premaxillar tooth |
| pq | Palatoquadrate |
| psb | Pseudobranchial arch |
| pt | Pterygoid process |
| sh | Stylohyal |
| tc | Trabecula communis |
| ts | Synotic tectum |

**Fig. 1.3** Cranial skeleton of different stages of leptocephalus larvae (after Norman, 1926)

preformed bone. More probably it originates as an independent, immediate ossification (Norman, 1926: *A. anguilla*) or, it could arise from a ventral excrescence of a covering-bony dermethmoid (Leiby, 1979: *Myrophis punctatus*, Ophichthidae), following the disappearance of the mesethmoid cartilage of the leptocephalus (see also Jollie, 1986; Patterson, 1975, 1977: Teleostei). This 'premaxillo-ethmo-vomerine-block' (Fig. 1.1) limits the mobility of the bordering elements of the upper jaw. It seems to assist an excellent grasping and holding ability (see also Gregory, 1933), which corresponds with a considerable mass of the adductor musculature of the jaw and its extension to the vault of the cranium.

The maxilla in the upper jaw articulates movably with the ethmoidal region. Inwards, it forms a broad flank, leaning on the 'pterygoid' or 'palatopterygoid' bone. However, considering position and genesis of this bone, it seems to represent the ectopterygoid of other groups of the Teleostei only; its cartilaginous processus pterygoideus of the palatoquadratum is reduced or not developed at all, early in ontogeny.

Compared, for example, with the Muraenidae, the mouth opening of the Anguillidae is comparatively short and the suspensorium (movable suspension of the upper jaw on the neurocranium by the hyomandibula, Fig. 1.2) is tilted forward considerably. The hyomandibula articulates with the ear capsule of the neurocranium by means of a rather elongated hinge joint; the joint pit is situated in the pteroticum and is, in the forepart, considerably extended, roundish, into the autosphenoticum. On the ventral side the hyomandibula is connected with the quadratum (Fig. 1.2) by a stable, closely toothed suture. Normally, this connection is mediated by an independent bone, the sympleticum. In the eel this bone cannot be distinguished. But, the eel larva has a distinct cartilaginous processus sympleticus of the hyomandibula. Therefore, it is suggested that it has been ossified continually together with the hyomandibula or, connected with the quadratum (Leiby, 1981). The lower elements of the hyoid arch are suspended on the inner side of the hyomandibula by a ligament only and not by a separate bone that is present in actinopterygians showing a rod-shaped stylo- or interhyal (Fig. 1.2). In the Ophichthidae, a similar element consisting of cartilaginous matter supposedly occurs in its leptocephalus (Leiby, 1981). The ceratohyalia 1 and 2 (the latter sometimes called epihyal) constitute a paired, robust, rounded bone element that bears about 10-11 branchiostegal rays. In the forepart, the ceratohyalia of both sides are connected by an elongated unpaired geniohyal (basihyal). Ventrally, between the hyoid arch branches, there is a urohyale, which is triangular in side view and flat on the lower side. It is embedded in the connective tissue of the paired retractor muscles (Mm. sternohyoidei) of the hyoid arch (Kusaka, 1973, 1975; Arratia and Schultze, 1990).

The articulare, ossifying in the posterior section of the Meckel’s cartilage, together with the quadratum, forms the jaw articulation. For the major part, the lower jaw branch is occupied by the extensive dentary that surrounds the Meckel’s cartilage and its substituting ossification (‘mento- and corono-Meckel’s’ bone). In the grown eel, neither a separate angular nor a retroarticular is visible. They generally fuse to form a uniform bone element, first the angulare with the retroarticulare (cf. Nelson, 1973 in the Elopiformes; Leiby, 1981 in the Ophichthidae), and fuse later on in ontogeny with the articulare. The mandibular lateral line canal runs enclosed in the dentary, opening outwards by several pores.

As in other teleost fishes, the upper skull has an extraordinarily complicated structure. It is composed of neurocranial elements inserted into each other (endoskeleton) and covering bony (exoskeleton) elements. The narrow base of the skull is supported essentially by the vomer part, which is elongated caudally, and by the parasphenoid (covering bony elements of the palatal cover, Fig. 1.1). In the backward cephalic area, this is indented with the basioccipital, which is the ossification of the hindmost base of the neurocranium. A small basisphenoid sits rostrally on the parasphenoid forming the bony backward limitation of the membranic interorbital septum, by a downward extending appendix of the frontal. A separate opisthoticum or intercalar is absent in adult eels at least. On the other hand, the pteroticum extends far behind and forms, with the exoccipital, the sharp outside edge of the backward part of the head. In *Anguilla*, lacrimal, nasal, suborbitals and postorbitals, are represented merely by thin shell-shaped lateral line canal ossifications, which are situated superficially in the connective tissue; they are omitted in many representations of the skeleton (Fig. 1.2B).

In the Anguillidae, the ossifications of the gill cover are quite large and very completely developed which contrasts with most other families of the Anguilliformes. The preopercular is fixed by connective tissue with the backward outside edge of the hyomandibular and surrounds a great opening (foramen) for the ramus hyoideus of the facialis nerve. The movable operculum articulates with the opercular process of the hyomandibular by a comprehensive socket of a joint. A narrow falciform suboperculum and a large-surface interoperculum complete the ossified operculum to the lower and to the frontal side. In its main area, however, the gill cover membrane, which in eels exhibits a largely expanded branchial space caudally, is supported by the branchiostegal rays (Fig. 1.2A).

The gill arches appear considerably more flexible than in other bony fish and they provide essential assistance in the production of positive and negative pressure during uptake of food (Alexander, 1970). Also, the gill arch elements are rather completely formed in the Anguillidae except the fifth arch that consists of ceratobranchials only supporting the lower pharyngeal tooth plates. The third and fourth epibranchials bear the corresponding upper tooth plates. These form a simple not spectacular device for ingestion at the entrance of the oesophagus (Fig. 1.2C). The fine and pointed conical teeth do not imply a function of food processing as known from the pharyngeal tooth apparatus of cyprinids and of many acanthopterygians (Nelson, 1969; Lauder and Liem, 1983; for a general view). A detailed analysis of the gill arch skeleton and of the appertaining branchial musculature is provided by Nelson (1966, 1967). These studies have also displayed an anagenetic sequence of progressing reduction from *Conger marginatus* (Congridae) through *A. rostrata* (Anguillidae) and *M. javanica* (Ophichthidae), *Kaupichthys diadonotus* (Clopsidae), *Uropterygius knighti* to *Gymnothorax petelli* (Muraenidae).

### 1.2.2 Vertebral column

The vertebral column in eels (Anguilliformes) is particularly interesting from the morphological, functional and systematic points of view. Hardly any vertebrate order is as polymorphic in this respect as are eels. Often it is used for species determination that is favoured by radiographic determination; even within the family of Anguillidae, the number of vertebrae is one of the most important diagnostic features at the species level (Sections 2.2 and 2.3).

There are only a few comparative studies on the morphology of the vertebral column in the various species of *Anguilla*. But additional groups of Anguilliformes have provided comparative results on the osteology, such as Muraenesocidae (Takai, 1959), Congridae (Asano, 1962; Smith, 1989b) and *A. japonica* (Matsui and Takai, 1959), *A. rostrata*, *N. vermiformis*, *M. edwardsi* and *Phythonichthys* sp. (Smith and Castle, 1972), as well as Ophichthidae (McCosker, 1977).

The vertebral column of *Anguilla japonica* (Fig. 1.4), which has a similar number of vertebrae to the European eel (*A. anguilla*), but more than the American eel (*A. rostrata*) (Table 1.1), is subdivided as follows: total number of vertebrae 116; the 44th is the last abdominal vertebra; the 38th is situated near the anus; pleural ribs occur on the 7th to 38th vertebrae; the haemal arches begin near the region of the 45th vertebra, which then is the first caudal vertebra (Fig. 1.4); dorsal intermuscular bones (epineurals) occur on the 1st to the 86th vertebrae, ventral intermuscular bones (epipleurals) occur on the 38th to the 86th vertebrae. According to Smith and Castle (1972; see also Patterson and Johnson, 1995), the distribution of epipleurals in *A. rostrata* is slightly different, in that they occur on the 34th to the 87th vertebrae. The epineurals of the first vertebrae are always grown together with the neural arches. Moreover, the neural spines of these vertebrae, in the longitudinal axis, are strongly extended and close together, which is a normal phenomenon in the Anguillids. The axial system of the skeleton has to be considered as closely connected

| | |
|---|---|
| A | Lateral view, 1st to 5th vertebrae |
| B | Ventral view, 1st to 5th vertebrae |
| C | 1st vertebra anterior view view |
| D | 5th vertebra anterior view |
| E | last abdominal and first two caudal vertebrae (44th, 45th and 46th vertebrae) |
| F | 44th vertebra anterior view |
| G | 45th vertebra anterior view |
| H | 46th vertebra anterior view |
| I | Caudal skeleton |

| | |
|---|---|
| ar | Anal fin ray |
| ce | Centrum |
| cr | Caudal fin rays |
| dr | Dorsal fin ray |
| el | Epipleural inter muscular bone |
| en | Epineural inter muscular bone |
| ha | Haemal arch |
| hp | Haemal canal |
| hs | Haemal spine |
| hy | Hypurals |
| na | Neural arch |
| np | Neural canal |
| ns | Neural spine |
| pa | Parapophysis |
| rad | Distal radial |
| rap | Proximal radial |
| un | Uroneural |

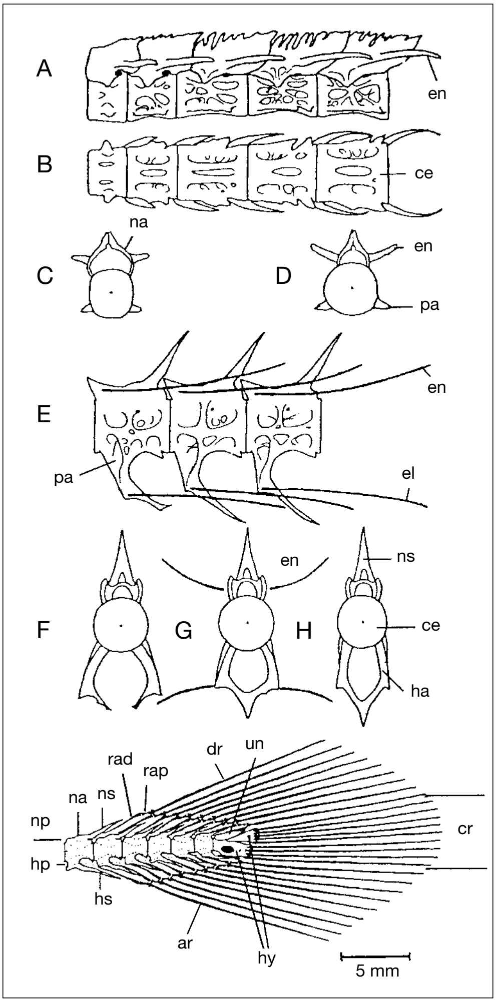


**Fig. 1.4** Spinal column of *A. japonica* (after Matsui and Takai, 1959)

functionally with myosepta and the segmental musculature (see Section 1.3.5). The number of muscle segments corresponds approximately with the number of vertebrae, the high number of these segments and the relatively long body expressing themselves in the characteristic high amplitude winding anguilliform movement, which runs uniformly along the whole body (Lindsey, 1978). Also, the eel has S-shaped transverse walls of connective tissue of the body muscle segments showing three-dimensional foldings to anterior and posterior bags; this arrangement is typical for primary aquatic vertebrates with jaws (Gnathostomata). The 'intramuscular' bones, epineuralia and epipleuralia, are embedded in corresponding collagen filaments of the myosepta (Gemballa, 1995).

Finally, it should be mentioned that the skeleton of the vertebrates is never an entirely static system, but alters continuously throughout life and with growth. Lopez *et al.* (1970) have determined the amount of crystalline apatite and amorphous calcium phosphate in the bone of the vertebral column of the European eel. With increasing maturity of the gonads, decalcification takes place resulting in a great decrease in the amount of amorphous calcium phosphate. Lopez (1970) has studied the bone structure. Deformities of the vertebral column are described in Section 7.4.1.

### *1.2.3 Pectoral girdle and fins*

Lack of connection of the pectoral girdle (Fig. 1.2D) with the skull and a reduced posttemporal are specialities that distinguish eels from other fishes; at most, connective tissue provides some association with the vertebral column (Berg, 1958). In comparison with other Anguilliformes, such as *N. vermiformes*, *M. edwardsi* and *Phytonichthys* sp. the eel (*A. rostrata*) has a relatively small supracleithrum. But the cleithrum is large, looks like a boomerang and extends cranially. It provides the base for the endoskeletal pectoral girdle with the bony scapula and coracoid as well as seven bony radialia.

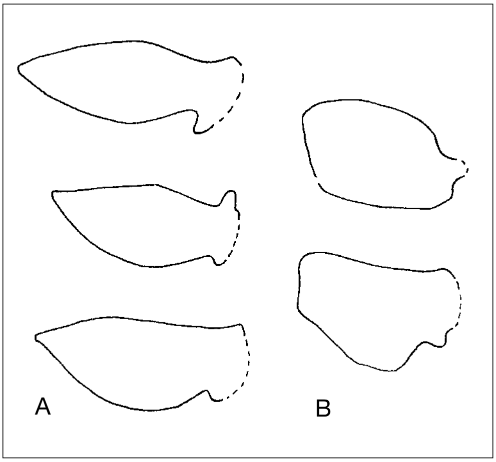
The unpaired fins, the dorsal and anal fin, are confluent with the tail fin, which really exists (Fig. 1.4). The caudal section of the vertebral column (the two consolidated ural vertebrae) clearly shows two hypural elements, which can be considered as the result of fusion of a higher number of hypuralia during larval development. These endoskeletal elements have nine unequivocal caudal finrays that are not discernible because they are included in the dorsal and caudal fin arrangement. Also, there is one uroneural, connected dorsolaterally. Therefore, one may deduce that the strongly declined symmetrical form of the caudal fin of eels may be related to an originally homocercal tail of the teleosts (Whitehouse, 1910; Schmalhausen, 1913; Monod, 1968).

The eel's only paired fins are the pectorals (pectoralis), which do not differ greatly from those of many other species of bony fish. The fin area of the pectoralis is supported by branched and grouped bony fin rays (lepidotrichia); the rays of the unpaired fins are undivided and not branched. However, the pectorals are interesting because of their change in shape during the later phases of development in adults. While the so-called yellow eel has relatively wide, spoon-shaped pectoral fins, these become long and pointed (Fig. 1.5) shortly before the gonads mature. Furthermore, differences exist between the paired fins of male and female Japanese eel, *A. japonica*: the pectoral fin in the female is shorter and more rounded than that of the male (Matsui, 1952).

## 1.3 Skin and musculature

### *1.3.1 Structure and function of the skin*

Eels survive in many diverse, and often harsh environments. Such an ability stems, at least in part, from the possession of a tough durable integument. Both the epidermis, and especially the corium, are thick. In a 20 cm long eel the total thickness of the skin was 0.15–0.18 mm and in a 56 cm long eel 0.50–0.53 mm (Hebrank, 1980). Jakubowski (1960b) compared the skin of seven teleost species, among them the eel, the flounder (*Pleuronectes flesus*) and the weather fish (*Misgurnus fossilis*). Only *M. fossilis* had an epidermis thicker than that of the eel. The epidermis of the eel is 0.263 mm thick, while that of the flounder



A Eels in advanced stages of maturity
B Yellow eels

**Fig. 1.5** Outline of the pectoral fin (after Wundsch, 1953)

is 0.036 mm (Fig. 1.6). Pfeiffer (1960) studied the skin of 10 species and found that the eel had the thickest epidermis. But in the eel, unlike other teleosts, the corium, particularly that on the head, is thicker than the epidermis. Saglio *et al.* (1988) demonstrated that the skin is thickest in the middle of the eel's body, and thinnest in the caudal area and around the pectoral fin. Also, the skin of female silver eels is thicker than that of the males. Yellow eels have thinner skins than silvery specimens.

The corium of the eel is provided intensively with collagen fibres; they run at an angle of 45° across the longitudinal axis of the fish and have tendinous stability (Hebrank, 1980). Therefore, it is likely that muscular action on the comparatively long body does not damage the skin; the torsion forces of the eel's spiral movements are not dangerous for the animal. In Scandinavia, it is said that eel skin treated with tannin is used for door-hinges. In South Korea and China, clothes and different kinds of bags made of eel skin are available.

Numerous, extremely well-developed club cells occur over the whole epidermis and apparently secrete many substances that have a protective function (Harder, 1964). Such cells may be as large as 0.150 mm by 0.025 mm in diameter in the eel (more than half the total height of the epidermis) (Pfeiffer, 1960), contrasting with species such as the armoured catfish (*Corydoras palaeatus*) in which they are about 0.025–0.035 by 0.013 mm. Henrikson and Maltotsy (1968a–c) have described the ultrastructure of the eel integument; the ontogeny from larval to silver eel stages has been studied by Aust (1936). Major changes take place in the skin during the fourth larval stage of metamorphosis (Table 1.1).

The thick epidermis, a robust protection against mechanical damage, is also relatively impermeable to water and electrolytes. Indeed, Bentley (1962) estimated that 1 ml of water would take 5 years to pass through 1 $cm^2$ of eel skin at a pressure difference of 1 atm! Transfer of eels from fresh water to brackish water results in an increased epidermal thickness (Thurow, 1957), and fish chronically adapted to fresh water have thinner skins than those adapted to brackish water; moreover, the skin made up to 8.5% of the body weight of freshwater-adapted specimens, compared with 9.4% in brackish water eels. Repeated transfer experiments produced equivocal results, however, and Thurow (1957) suggested that the induced excessive secretion of mucus eventually exhausted the cells producing

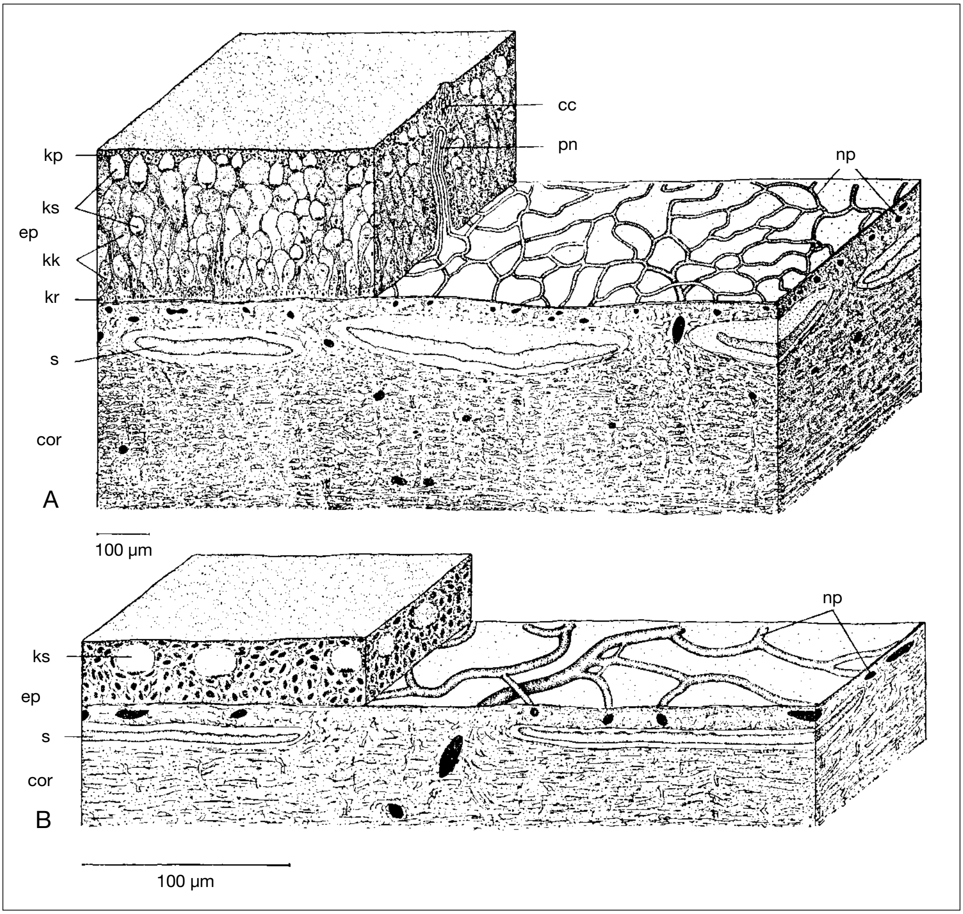


**Fig.1.6** Structure and proportions of the epidermis and the corium of the European eel and of the flounder (*Pleuronectes flesus*) (after Jakubowski, 1960a, b)

| | |
|---|---|
| A | Eel |
| B | Flounder |
| ep | Epidermis |
| cc | Sensory cell |
| cor | Corium |
| kk | Club cell |
| kp | Squamous cell |
| kr | Germinative layer |
| ks | Mucous or goblet cells |
| np | Subepithelial blood vessels |
| pn | Vascular loop |
| s | Scale |

this substance. It was suggested that the thinner skin of freshwater eels requires regeneration of mucus cells before the eel can successfully enter sea water. Other data are probably more relevant (Portier and Duval, 1922; Portier, 1938 in Remane and Schlieper, 1958): eels transferred from low to high environmental osmolarities adapted less well if the skin was rubbed with a cloth to remove the mucus. In particular, hyperosmolarity of the blood and ion imbalance occurred. It was concluded that the skin – especially its mucus secretion – acted as a barrier against fluxes of water and electrolytes along osmotic and diffusion gradients. The secretion of mucus and its relationship to *N*-acetylneuramine have been examined (Lemoine and Olivereau, 1971) and prolactin from the adenohypophysis has been implicated as a factor controlling the structure and function of the skin (Olivereau and Lemoine, 1971; see Section 1.8.3).

Another physiological aspect of the eel's integument is its possible hindrance in gaseous exchange (see Section 1.4). Jakubowski (1960a), citing Krogh (1924), and Jeuken (1957), reported that fishes such as the eel, and the equally thick skinned *Misgurnus fossilis*, can meet virtually all their oxygen needs cutaneously. Furthermore, Byczkowska-Smyk (1958), in a study of branchial respiration also concluded that a large part of the eel's respiration must be met from cutaneous respiration (see Section 1.4). Indeed in air, species such as the eel, survive far better than do purely branchial breathers (Murygin and Anokhina, 1967). Therefore, the thick epidermis does not seem to prevent gaseous exchange or small exchanges of electrolytes. Jakubowski (1960b) suggested that the secretory cells – both mucus producing and club cells – lying between the blood vessels of the dermis and epidermis, contain sufficient amounts of water to permit ready diffusion of oxygen. Bolognani-Fantin and Bolognani (1964; see also Seutter *et al.*, 1970; Asawaka, 1974; Yamada and Yokote, 1975; Saglio *et al.*, 1988) have discussed the cytological and chemical bases for the production of mucus by eel skin. Mucus is of great adaptive significance, not only when the animals are in water, but it may also prevent dehydration when the animals undertake their brief excursions on land, and may aid survival at low temperatures (Gadeau De Kerville, 1918). Stripped of mucus experimentally, eels survived up to 7 days provided the humidity of the air was normal and the temperature low. Saglio and Fauconneau (1988) considered the free amino acid content of mucus and its significance for osmoregulation as well as for recognition of sexual partners; mature silver eels exhibited more free amino acids than did yellow eels.

## *1.3.2 Scales*

Like other families in the Anguilliformes, the Anguillidae possess scales. However, these scales are rudimentary – at least in comparison with those of other species of fish. The scales are relatively well embedded in the upper layers of the corium below the epidermis (Fig. 1.6), and are not arranged in overlapping rows as they are in other fish, but are irregular, and in some places, distributed like parquet flooring. In general, one row of scales lies at right angles to the next, although the rows of scales immediately above and below the lateral line lie at an angle of approximately 45°.

In *Anguilla* species the first scales do not develop immediately after the larval stage is over – as is normal in other bony fish – but appear much later. Opuszynski (1965), Matsui (1952) and Jellyman (1979b) have shown that, in *A. anguilla, A. japonica* and *A. dieffenbachii* individuals measuring 15 cm or less do not have scales, whereas scales are present in most individuals 17 or 18 cm long. It seems likely that other species of eels also develop scales very late in ontogeny, although Pantulu (1956) reports their earlier appearance in *A. nebulosa*, where specimens of 11 or 12 cm have already developed scales. It seems likely that in *A. anguilla* the formation of scales is not an age-dependent process, and this has been demonstrated in *A. japonica* (Matsui, 1952).

As regards the region of the body where the scales develop first, it seems that there may be further differences between *A. nebulosa* and the so-called 'northern' eels of the temperate regions. In species like *A. rostrata, A. bengalensis, A. dieffenbachi* (Fig. 1.7) and *A. australis* the primary region is in the last third of the body (Smith and Saunders, 1955; Pantulu, 1956; Jellyman, 1979b), in *A. japonica* (Matsui, 1952) and *A. anguilla* (Rahn, 1957c)

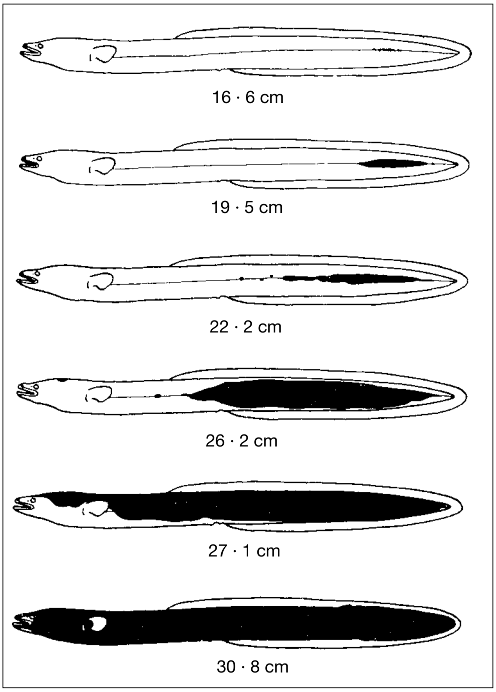


**Fig. 1.7** Position and distribution of the first scales (black areas) in *A. dieffenbachii* (after Jellyman, 1979b)

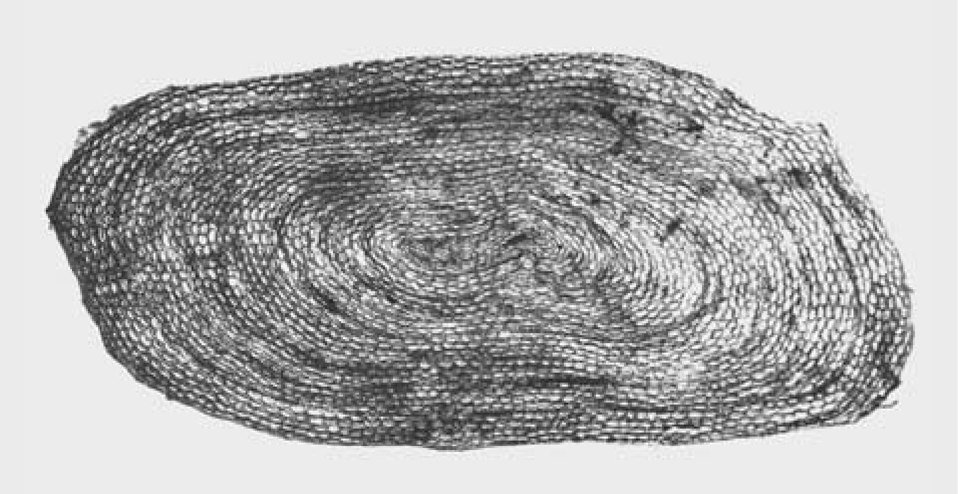


**Fig. 1.8** Photograph of an eel scale (photo: Tesch)

perhaps slightly further orally. In *A. anguilla* this primary region has been located only indirectly, by establishing which part of the body had scales with the greatest number of annual rings (Rahn, 1957c). From the anal region, the zones of scale develop and spread forwards and backwards along the lateral line as well as dorsally and ventrally; in normally developing eels 2 or 3 years may elapse between the appearance of the first and the last scales (Gemzøe, 1906; Matsui, 1952). The lips of the upper and lower jaws, the throat, and, it appears the pectoral fin bases too, all remain scaleless.

The morphology of the scales has been described in many papers on the growth of the eel. But, recently they are used rarely for age determinations (see Section 3.3.2.1). The superficial structure of the scale is rather unusual (Fig. 1.8). Its contours suggest it is cycloid, but it has a very elongate-oval shape, although there are many variations. So-called circuli (concentric lines) are also seen in the eel scale. These are not made up of smooth 'ridges' and 'grooves' but from rows of plates, which resemble small medallions.

### *1.3.3 Pigmentation*

The development of pigment provides the most useful means of recognising the different ontogenetic stages in the eel. This not only applies to subepidermal, external pigmentation but also to the internal pigment of the larval phases. During early development, as in the case of many other species of fish, the internal pigment also acts as a means of separating different species. In the leptocephalus, the first internal pigment develops along the notochord, while at the beginning of stage II (Table 1.1) it spreads in a caudo-rostral direction

**Table 1.1** Development of pigmentation in *A. anguilla* (abridged from Strubberg, 1913, and adapted from Bertin, 1956).

| Stage | Characteristics |
|---|---|
| I | Larva, fully grown leptocephalus (Fig. 2.3) |
| II | Semilarva, pigmentation on the posterior end of the spinal chord |
| III | Semilarva, pigmentation on the nerve chord becomes more extensive, skin pigment also seen at the tip of the caudal fin |
| IV | Semilarva, pigmentation on the nerve chord reaches the head |
| VA | Metamorphosis complete, eel-like in form, no external pigment (glass eel) except the caudal spot (Fig. 1.9) |
| VB | No pigment on the back, body or tail region, except for the skull, caudal spot and some rostral pigment |
| $VIA_I$ | Development of pigmentation along the whole dorsum, post-anal dorsolateral pigment develops, post-anal, no clear mediolateral pigment (Fig. 1.10a) |
| $VIA_{II}$ | No pre-anal ventrolateral pigment. Post-anal development mediolateral pigment (Fig. 1.10b) |
| $VIA_{III}$ | No pre-anal ventrolateral pigment. Clear pre-anal development of mediolateral pigment, post-anally over almost entire dorsum, pigment rows along the myosepta, and in places doubling of the mediolateral melanophores (Fig. 1.10c) |
| $VIA_{IV}$ | Clear development of pre-anal ventrolateral pigmentation. Initially, in places, a doubling of the mediolateral melanophores in the pre-anal region (Fig. 1.10d), post-anal pigment between the myosepta in the ventral region (Fig. 1.10e), and finally, similar changes in the pre-anal region (Fig. 1.10f) |
| VIB | Pigment rows along the myosepta becoming indistinct. Lateral line still recognisable, as are the individual melanophores on the head, 'cheek', behind and below the eyes and on the lower jaw (Fig. 1.10g) |

(Schmidt, 1906; Gilson, 1908). In comparison with the first, external chromatophores, which are brownish in colour, the internal chromatophores are black and relatively large. Species differences appear to exist in the ontogenetic development of the internal pigment. Pigmentation of the notochord during stage II (Table 1.1) begins posteriorly in *A. anguilla*, whereas in *A. japonica* pigmentation begins anteriorly (Egusa, 1972).

External pigment also develops during the leptocephalus stage and is visible as a dark patch on the fin rays of the tail fin during stage III. This patch remains recognisable during further development and is the only form of external pigmentation until stage VA (Fig. 1.9, Table 1.1). A characteristic of this stage is that developmental changes are largely internal; but if the temperature is raised, large numbers of melanophores appear along the whole length of the body.

The beginning, and to a certain extent the end of stage V (also called VB) is marked by the formation of the so-called 'skull spot', the appearance of which is certainly of great physiological significance; this spot can still be seen in older eels although it does become less distinct. As Gilson (1908) has shown, this pigment is not produced in the corium – as is the caudal spot and most of the pigment that appears after it – but in a sort of fontanelle. Later, this hole is occluded as a result of dermal bone formation. In older eels the skull spot is found in the meninges under the frontal and parietal bones.

Developmental differences in external pigmentation are evident in *A. japonica* and the European eel. In the Japanese eel, the caudal patch does not develop until after the beginning of stage IV, and not in stage III. In contrast, in *A. japonica*, the skull spot and a certain degree of rostral pigmentation are already in evidence in stage III (Egusa, 1972). These differences may also occur in the other Indo-Pacific species, thus making it possible to distinguish between the various metamorphic stages of the different species (Marquet, 1992).

According to studies on other fish species, the melanophores in this region of the head act as regulators controlling the amount of incoming light (Nicol, 1963). The pineal organ, the epiphysis, is photosensitive and must be protected from excess illumination. On the other hand, young fishes, including the leptocephalus, are relatively insensitive to light and receive very little protection from their melanophores (Breder and Rasquin, 1950). As research on the salmon has indicated (Hoar, 1955), the almost total absence of morphological differentiation in the pineal organ in young fish probably is partly responsible for

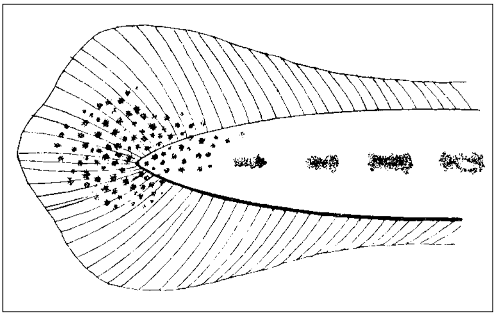


**Fig. 1.9** Tip of the tail showing the caudal spot in a glass eel at Stage VA; this spot is even more developed at stage VB (after Gilson, 1908)

this insensitivity. Leptocephali (*A. anguilla*), with increasing age and size, prefer greater depths (Schoth and Tesch, 1984), which may be connected with increasing light sensitivity of their pineal organ.

The first appearance of the skull spot indicates an important step in the life of the eel. It forms at a time when the eels arrive in the coastal waters and abandon their purely pelagic existence (Section 3.1.1). The eel's behaviour during this first phase of pigmentation indicates a marked sensitivity to light (Tesch, 1965). Melanophores then begin to develop along the entire body length and a transient phase of reduced sensitivity to light begins; from time to time glass eels even swim along the banks near the surface.

A list of characteristics can be drawn up that describes the extent of pigmentation during various advanced stages of development (Table 1.1; Fig. 1.10) (Grassi, 1913; Strubberg, 1913; see also Boëtius, 1976). According to this system, stage VI (Schmidt, 1906) has been divided into substages A and B. Essentially, VIB indicates the end of the pigmentation, and stage VII represents the fully pigmented, benthic and migrating young eel (Gilson, 1908). Thus, in stage VIB the eel loses its glass-like transparency.

In addition to the black colouring, provided by the melanophores, other pigments also begin to appear and are already in evidence towards the end of stage VIA. In particular, a green colouration becomes recognisable as a result of the formation of yellow pigment. Heldt and Heldt (1929a) attribute this to the beginning of food intake (see Section 3.3.1), whereby lipoids are formed, thus providing the basis for the yellow colour. Water-soluble flavones are particularly involved in the formation of yellow pigment in the eel – a characteristic that distinguishes the eel from other, less euryhaline fishes (Fontaine and Busnel, 1939).

Stage VIA is further divided into a number of subsections of which only the main divisions, $\mathrm{VIA}_{\mathrm{I}}$–$\mathrm{VIA}_{\mathrm{VI}}$ are given in Table 1.1. According to Strubberg (1913), each of these four subsections is made up of a further one to four subdivisions; this system is based on the fact that pigmentation starts caudally and dorsally and proceeds rostrally and ventrally. In German, regardless of the degree of pigmentation, young eels are referred to as 'Aalbrut', 'Montée' or, if they are not too darkly coloured, as 'Glasaal'. In French, they are called 'civelles'. In English, however, unpigmented young are referred to as 'glass eels', while pigmented ones are called 'elvers'. When pigmentation is complete the yellow eel stage is reached; there are no major external changes after this until the eel returns to the sea. In German, the small, fully pigmented eels, which are not yet suitable for marketing, are called 'Satzaale'. Strictly speaking, the name 'yellow eel' is not correct, because, although many eels do vary from yellow to white on the underside, a large number have almost completely white bellies that change to a light grey on the flanks. However, the term 'yellow eel' has now been adopted universally and is used to distinguish this stage from the silver eel stage. The yellow eel's dorsal surface varies from dark green or brownish-green to black, the former colours giving rise to the term 'Grünaal' or 'green eel'. A similar duality of terms occurs in France; both 'anguille jaune' and 'anguille verte' are frequently used; the use of 'green' or 'vert' might also imply immaturity. In English, the term 'yellow eel' is commonly used, but from time to time one comes across the expression 'golden eel'. However, this use of metallic colour terms can be misleading because a metallic shimmer is the distinguishing characteristic of the 'Blankaal' ('silver eel' or 'bronze eel') or of eels without black pigment (xanthochromatism) (Section 7.3).

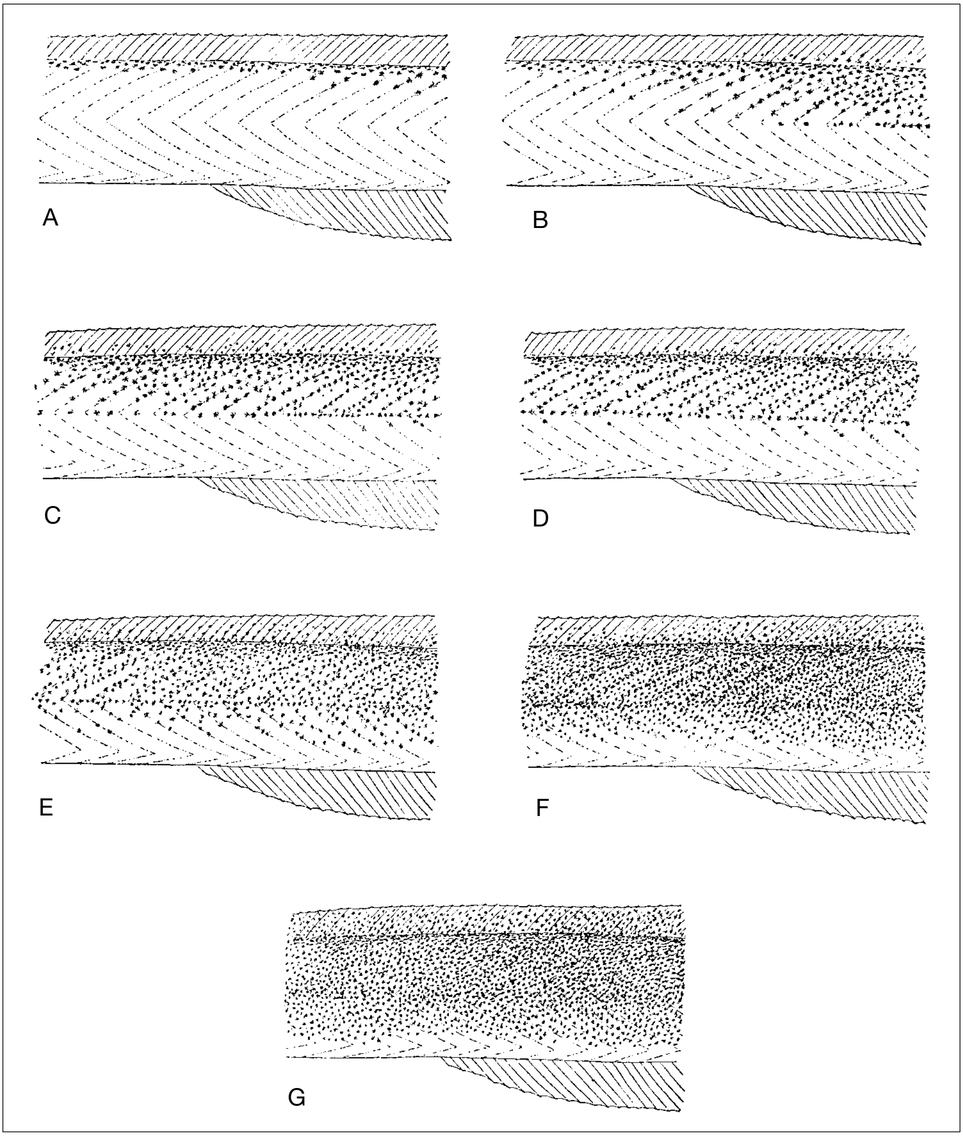


**Fig. 1.10** Development of the subepidermal pigment in the glass eel (after Strubberg, 1913)

A Stage VIA$_{\text{I}}$ B Stage VIA$_{\text{II}}$ C Stage VIA$_{\text{III}}$ D,E,F Stage VIA$_{\text{IV}}$ G Stage VIB

Naturally, colour in eels from various biotopes can be very different and must depend to a great extent on the background. Fishermen involved in marking and transplanting eels in the North Sea have reported (Tesch, 1967a) that transplanted eels recaptured outside their original habitats were a quite different colour from those that normally lived in the area. Thus, these eels had retained their colour for days, weeks even, without showing adaptation to their new environment. Experimental studies by Neill (1940) and Odiorne (1957) have also shown that eels take a very long time to change colour; as many as 20 days may elapse before one extreme condition of the melanophores will change to another. In