

The Development of Squamation in Four Teleostean Fishes with a Survey of the Literature

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Abstract The development of squamation is described in four teleost species, *Cichlasoma octofasciatum* (Cichlidae), *Poecilia reticulata* (Poeciliidae), *Barbus barbus* (Cyprinidae) and *Corydoras arcuatus* (Callichthyidae). These observations are compared to previous descriptions of the squamation development in other species (mainly teleosts) known from the literature. Among teleosts, 7 different regions can be delimited on the body, each containing the sites of the first scale appearance. Some species have only one site (generally located on the caudal peduncle) whereas others have two or more. The possibility of the involvement of epigenetic factors to explain the existence of several sites of scale appearance and their localization on the body surface is discussed.

The formation of the squamation pattern during the ontogeny of fishes have interested many ichthyologists since Klaatsch (1890) as demonstrated by more than eighty publications listed in Table 1. Numerous data are included in general biological (Oosten, 1957; Reed, 1971; Park and Lee, 1988) or osteological (Jollie, 1975; Potthoff and Kelley, 1982) publications, but several works are solely devoted to squamation development. The latter were commonly undertaken to investigate possible use for systematics (Potthoff, 1974) or fish ageing (Priegel, 1964, 1966; Jellyman, 1979). To our knowledge, no study deals with the development of the squamation itself, and the factors that can influence the localization of the site of the first scale appearance. Although the caudal peduncle is the main site of the first scale appearance in teleosts, numerous species show scales first either in another site (head, belly, or pectoral peduncle) or in several sites (Table 1). The present study has been undertaken in order to investigate the influence of fish shape, scale type and also ovoviviparity on the localization of the first site of scale appearance using four teleosts. The results have been added to and compared with the data in the literature in the aim of understanding which factors might control the initiation and organization of the squamation development in fishes.

Material and methods

The four teleost species studied were: *Cichlasoma octofasciatum* (Perciformes, Cichlidae), *Poecilia re-*

ticulata (Cyprinodontiformes, Poeciliidae), *Barbus barbus* (Cypriniformes, Cyprinidae) and *Corydoras arcuatus* (Siluriformes, Callichthyidae). These species were chosen for the following reasons: 1) *C. octofasciatum* is a short-shaped species with ctenoid scales, in contrast with other cichlids for which the data available were mainly obtained in species with cycloid scales. 2) *P. reticulata* is an ovoviparous species and, to our knowledge, the chronology of the scale formation has not been described in an ovoviparous teleost. 3) *B. barbus* has an elongated shape and belongs to Cyprinidae in which the first scales have been reported to appear in two opposite regions in different species. 4) *Corydoras arcuatus* is covered with dermal plates (scutes), the organization and structure of which differ from those of the elasmoid scale (Bhatti, 1938).

C. octofasciatum, *P. reticulata* and *C. arcuatus*, were bred in aquaria where the temperature was adjusted at $25 \pm 1^\circ\text{C}$. Fry of *B. barbus* were obtained from the "Laboratoire de Morphologie fonctionnelle, Institut de Zoologie, Liège", Belgium.

The appearance of the first scales has sometimes been related to the age of the fish (Ward and Leonard, 1954; Cooper, 1971). However, in the present species it appeared to be more related to length (SL or TL) than to age as Armstrong (1973) and Sire (1981) reported. For this reason our results will consider only the standard length (SL).

The fry of *C. octofasciatum* (30 specimens) were from 7.3 mm to 18.5 mm SL, *B. barbus* (30) from 10.0 mm to 32.0 mm SL, *C. arcuatus* (13) from 8.0

mm to 19.2 mm SL and *P. reticulata* (40) from 3.0 mm to 9.0 mm SL. In the latter, the first stages (from 3.0 mm to 7.0 mm) were obtained by dissection of gravid females.

Fishes were killed in MS 222 (1/1,000), then fixed for 2 days in a mixture of 70% ethyl alcohol and 10% neutral formalin (9.5 v/0.5 v). They were bleached with H₂O₂ to remove pigments that pre-

vented the observation of the scales. After a short rinse in distilled water, they were stained for 24 hours in a solution of alizarin red S (15 mg% in 1% KOH) and cleared in glycerol/0.5% KOH (1 v/1 v) mixture, then stored in pure glycerol (after Simmons and Van Horn, 1971).

Table 1. Sites of scale appearance in teleost fishes. Data compiled from the literature. For one species, 2 or 3 sites indicate that scales are formed independently in 2 or 3 regions of the body. Generally, the first named is the site in which the scales appear first but sometimes scales can be formed simultaneously in 2 sites. Classification after Nelson (1984). For the localization of the sites on the fish body, see Fig. 5.

Order	Family	Genus and species	Site	References
Anguilliformes	Anguillidae	<i>Anguilla dieffenbacki</i>	1-6	Jellyman (1979)
		<i>A. australis</i>	1-6	Jellyman (1979)
Clupeiformes	Clupeidae	<i>Alosa kessleri</i>	1	Braginskaja (1957)
		<i>Brevoortia patronus</i>	4	Chapoton (1967)
		<i>Clupenodon punctatus</i>	1	Yoshida (1937)
		<i>Clupea harengus</i>	1-3-4	Huntsman (1918)
		<i>Pomobolus pseudoharengus</i>	1-4-5	Huntsman (1918)
		<i>Sardinops melanostica</i>	1	Kubo et al. (1949)
		<i>S. sagax</i>	1	Kubo et al. (1949)
		<i>Engraulis mordax</i>	1	Miller (1955)
	Engraulididae			
Cypriniformes	Cyprinidae	<i>Abramis ballerus</i>	3	Balon (1959b)
		<i>A. brama</i>	1	Segerstrale (1932)
		<i>Acheilognathus lanceolata</i>	1	Okada and Seishi (1936b)
		<i>Barbus barbus</i>	1	Present work
		<i>Blicca bjoerkna</i>	1	Frank (1956)
		<i>Brachydanio rerio</i>	1	Waterman (1970)
		<i>B. rerio</i>	1-5	Armstrong (1973)
		<i>Carassius auratus</i>	3	Hase (1907); Dmitrijeva (1957)
		<i>C. carassius</i>	3	Hase (1907); Dmitrijeva (1957)
		<i>Cyprinus carpio</i>	3	Nozawa (1941); Balon (1958); McCrimmon and Sweet (1966)
		<i>Idus idus</i>	1	Cala (1971)
		<i>Leucaspis delineatus</i>	1	Balon (1959a)
		<i>Notropis cornutus</i>	1-4	Brancamp (1938)
		<i>Pimephales promelas</i>	1	Andrews (1970)
		<i>Pseudorasbora parva</i>	3	Okada and Seishi (1936a)
		<i>Rhodeus sericus</i>	3	Balon (1959a)
		<i>Rutilus rutilus</i>	1	Balon (1955); Vasnecov et al. (1957); Cala (1971)
		<i>Semotilus corporalis</i>	1	Reed (1971)
		<i>Zacco platypus</i>	3	Okada and Seishi (1936c)
	Catostomidae	<i>Minytrema melanops</i>	1	White (1977)
Siluriformes	Loricariidae	<i>Plecostomus plecostomus</i>	1-4	Bhatti (1938)
	Callichthyidae	<i>Corydoras arcuatus</i>	1-3	Present work
Salmoniformes	Esocidae	<i>Esox americanus</i>	2-5	Jollie (1975)
		<i>E. lucius</i>	2	Francklin and Smith (1960)
	Osmeridae	<i>Hypomesus olidus</i>	1	Amemiya and Hiyama (1940); Shiraishi et al. (1955)
		<i>Osmerus eperlanus</i>	1	Bayrakci (1936)
	Plecoglossidae	<i>Plecoglossus altivelis</i>	1	Nakai and Matsui (1936)

(Table 1, continued)

Order	Family	Genus and species	Site	References	
	Salmonidae	<i>Coregonus artedii</i>	1	Hoagman (1970)	
		<i>C. kivi</i>	1	Hoagman (1970)	
		<i>Oncorhynchus keta</i>	1	Matsui and Kogure (1941); Sano and Kobayashi (1952)	
		<i>O. nerka</i>	1	Koo (1955)	
		<i>Salmo salar</i>	2	Warner and Havey (1961)	
		<i>S. clarkii</i>	1	Robertson (1947); Brown and Bailey (1952)	
		<i>S. irideus</i>	2	Yamada and Saito (1952); Kassner (1963)	
		<i>S. trutta</i>	2	Paget (1920); Parrott (1934); Setna (1934); Neave (1936)	
		<i>Salvelinus fontinalis</i>	1	Elson (1939); Cooper (1971)	
		Cyprinodontiformes	Aplocheilidae	<i>Aplocheilus latipes</i>	1
Cyprinodontidae	<i>Rivulus marmoratus</i>		6-1-7	Park and Lee (1988)	
Poeciliidae	<i>Poecilia reticulata</i>		1-6	Present work	
Gasterosteiformes	Gasterosteidae	<i>Gasterosteus aculeatus</i>	3-1	Igarashi (1970)	
		<i>Pungitius pungitius</i>	1-3	Igarashi (1968)	
		<i>Pungitius</i> sp.	1	Igarashi (1968)	
Scorpaeniformes	Hexagrammidae	<i>Hexagrammos otakii</i>	3-1	Fukuhara and Fushimi (1984)	
Perciformes	Percichthyidae	<i>Lateolabrax japonicus</i>	1	Kobayashi and Miwa (1964); Fukuhara and Fushimi (1982)	
		Centrarchidae	<i>Lepomis macrochirus</i>	3	Potter (1924)
			<i>L. pallidus</i>	3	Potter (1924)
			<i>Micropterus dolomieu</i>	1	Everhart (1949)
			<i>Pomoxis annularis</i>	1	Siefert (1965)
			<i>P. nigromaculatus</i>	1	Ward and Leonard (1954); Oosten (1957)
			<i>P. nigromaculatus</i>	1-4-3	Cooper (1971)
		<i>Centrarchus macropterus</i>	2	Conley and Witt (1966)	
		Percidae	<i>Lucioperca lucioperca</i>	1	Mohr (1916); Konstantinov (1957); Dmitrijeva (1957)
			<i>Perca flavescens</i>	1	Pycha and Smith (1955)
			<i>Perca fluviatilis</i>	1	Segerstrale (1933); Konstantinov (1957)
	<i>Stizostedion vitreum</i>		1	Priegel (1964); Glenn and Mathias (1985)	
	Pomatomidae	<i>Pomatomus saltatrix</i>	1	Silverman (1975)	
	Carangidae	<i>Caranx crysos</i>	1	Berry (1960)	
		Sparidae	<i>Chrysophrys major</i>	2	Fukuhara (1976)
	<i>Evyinnis japonica</i>		2	Fukuhara and Fushimi (1981)	
	<i>Mylio macrocephalus</i>		2	Fukuhara (1977)	
	Sciaenidae	<i>Aplodinotus grunniens</i>	1	Butler and Smith (1950); Priegel (1966)	
		<i>Cynoscion regalis</i>	1	Huntsman (1918)	
	Oplegnathidae	<i>Oplegnathus fasciatus</i>	3-1	Fukuhara and Ito (1978)	
	Cichlidae	<i>Astatotilapia burtoni</i>	1-5-6	Sire and Arnulf (1989)	
		<i>Cichlasoma octofasciatum</i>	1-5-6	Present work	
		<i>Hemichromis bimaculatus</i>	1-5-6	Sire (1981)	
		<i>Herichthys cyanoguttatus</i>	1	Balon (1959 a)	
		<i>Tilapia macrocephala</i>	1	Fishelson (1966)	
		<i>T. nilotica</i>	1	Fishelson (1966)	
		<i>T. sparrmani</i>	1	Fujita (1971)	
		<i>T. tholloni</i>	1	Fishelson (1966)	
		Mugilidae	<i>Mugil saliens</i>	2	Burdak (1969)
			<i>M. so-fuy</i>	1-4-6	Gongzhao et al. (1985)
	Scombridae	<i>Thunnus</i> sp.	5	Potthoff (1974)	
	Xiphiidae	<i>Xiphias gladius</i>	2	Potthoff and Kelley (1982)	
	Pleuronectiformes	Bothidae	<i>Paralichthys olivaceus</i>	1	Seikai (1980)

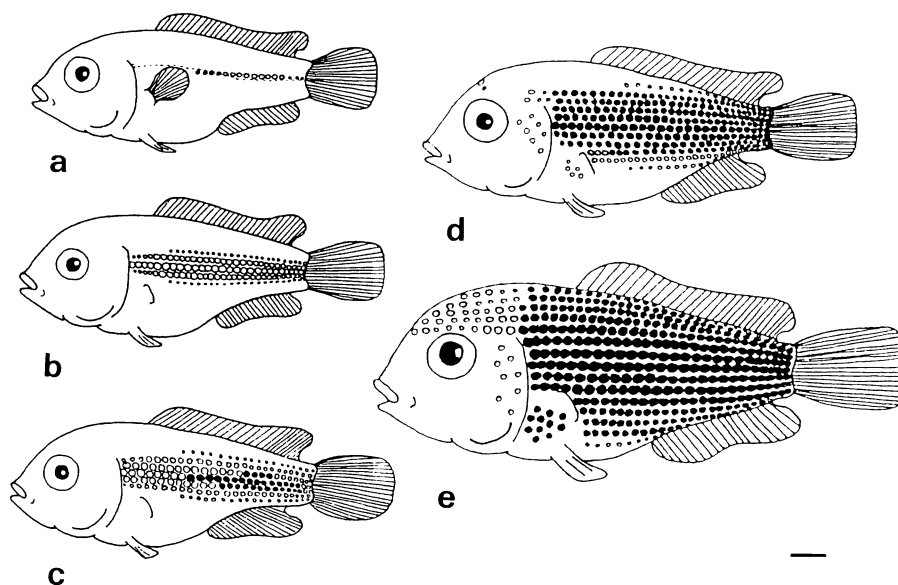


Fig. 1. Pattern of squamation development in *Cichlasoma octofasciatum*. a, 9.0 mm-SL fry; b, 9.5 mm; c, 10.0 mm; d, 12.0 mm; e, 14.0 mm. Black dots: ctenoid scales. Dotted line in a = lateral-line. Bar = 1 mm.

Results

Cichlasoma octofasciatum: Fry smaller than 8.5 mm SL (8 specimens) have no scales; between 8.5 and 10.0 mm (8 sp.) scales are generally forming but 2 specimens (9.0 and 8.5 mm) lack scales; from 10.0 mm to 14.0 mm (6 sp.) squamation spreads on the body; from 14.0 mm (8 sp.) the body is completely covered. Scales appear first on the caudal peduncle (Fig. 1a). These scales constitute the beginning of the first row located at the level of the horizontal septum. The posterior scales of this row belong to the lateral-line scales. The first scales have 1 or 2 circuli but no ctenial spines. When other scale rows are formed on the flank (Fig. 1b), the first row has extended anteriorly, following the horizontal septum, and reached the pectoral region. When these rows are nearly complete, other rows form, until the body is entirely covered (15 rows) (Fig. 1e). In 10.0 mm fry, 2 or 3 ctenial spines are visible on the posterior region of the scales belonging to 3 rows. These ctenoid scales are located on the middle part of the caudal peduncle (Fig. 1c). In 12.0 mm fry, the ctenial spines are present on the scales of 8 rows, occupying a large part of the flank (Fig. 1d).

Before the squamation of the body is complete, scales are formed on the pectoral peduncle and on the head (gill cover and cranial vault) of 12.0 mm fry

(Fig. 1d). These additional sites of scale appearance are independent of the horizontal rows of the body. The squamation of the pectoral peduncle extends first around the site of the scale appearance, then, posteriorly, joins the horizontal rows.

Poecilia reticulata: Fry smaller than 5.0 mm SL (6 specimens) have no scales; between 5.0 and 6.0 mm (12 sp.) scales are generally forming except in 2 specimens where they are lacking; from 6.0 to 8.0 mm (18 sp.) the squamation develops; from 8.0 mm (4 sp.) the body is entirely scaled. The first scales appear on the posterior region of the caudal peduncle at the level of the horizontal septum (Fig. 2a). At this step the fry are still in the body of the female and are coiled round their yolk sac. Eight scales which belong to the lateral-line scales arise simultaneously, constituting the first row located above the horizontal septum. The squamation spreads anteriorly following a V pattern (Fig. 2b). The body is entirely scaled (6 rows of scales), approximately 2 weeks after birth. The pigment pattern of the skin of the fry is clearly marked, underlying the connective tissue septa and outlining hexagons in the site of which each scale forms (Fig. 2a). In fry of 8.0 mm, before the body is completely covered, 2 large scales are present on the cranial vault and 3 on the operculum (Fig. 2c).

Barbus barbus: Fry smaller than 18.0 mm SL (8 specimens) have no scales; between 18.0 and 21.0

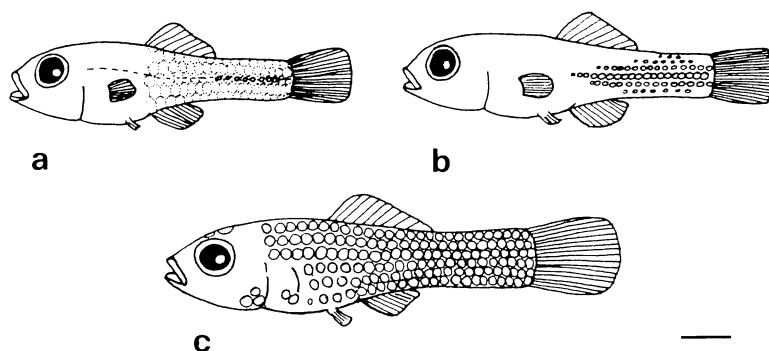


Fig. 2. Pattern of squamation development in *Poecilia reticulata*. a, 6.0 mm-SL fry showing the organization of the pigment pattern on the skin; b, 6.5 mm; c, 8.0 mm. Bar = 1 mm.

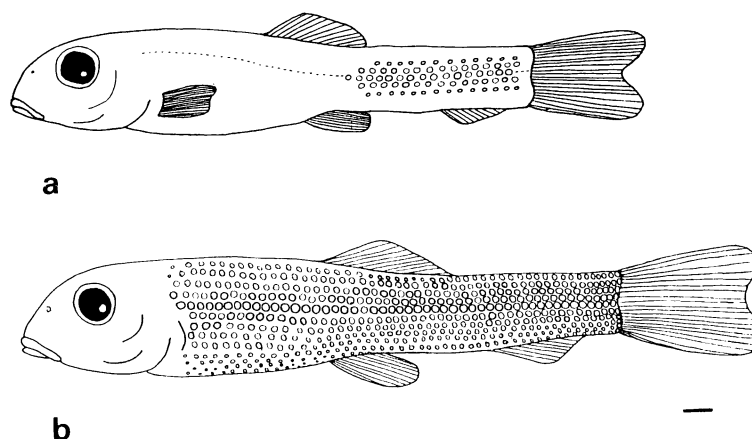


Fig. 3. Pattern of squamation development in *Barbus barbatus*. a, 18.0 mm-SL fry; b, 21.0 mm. Bar = 1 mm.

mm (11 sp.) scales are generally forming but they are lacking in 4 specimens; from 21.0 mm (11 sp.) the squamation is nearly complete on the body. Scales appear first (several rows simultaneously) in the middle region of the caudal peduncle (Fig. 3a). The scales are coloured lightly by alizarin red indicating that the surface has poorly-developed mineralized ridges; they are interrupted by uncalcified radii in the posterior region. The squamation spreads anteriorly, dorsally and ventrally, except along the dorsal fin (Fig. 3b). Until 32.0 mm, the largest fry we examined, 13 rows of scales are visible on the caudal peduncle but no scales are present on the head or on the dorsal region.

Corydoras arcuatus: The squamation of *C. arcuatus* is composed of only two rows of large dermal bony plates (scutes) bearing little spines (denticles or dermal teeth), as in other species of Callichthyidae (Bhatti, 1938). The rows are located above and

below the horizontal septum and only a few of the scutes overlap each other. Fry smaller than 11.5 mm SL (3 specimens) have no scutes; between 11.5 and 15.0 mm (6 sp.) the scutes are generally forming (Fig. 4a, b) but they are lacking in one specimen; from 15.0 mm (4 sp.) all the scutes are present on the body but they only cover a small surface of the flank (Fig. 4c). The first scutes (5 dorsal and 4 ventral) appear on the posterior region of the caudal peduncle (Fig. 4a). These scutes bear only one or two spines on their posterior region. The scute formation progresses from the posterior to the anterior region of the body but precocious dermal ossifications appear surrounding the lateral-line canal in the anterior region of 13.5 mm fry (Fig. 4b). The body is completely scuted in fry larger than 19.0 mm in which the dorsal anterior scutes extend over the posterior region of the head.

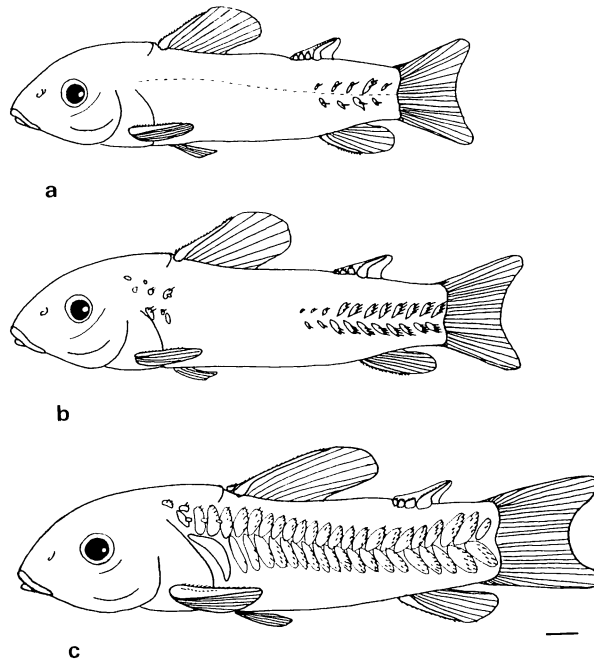


Fig. 4. Pattern of squamation development in *Corydoras arcuatus*. a, 12.0 mm-SL fry; b, 13.5 mm; c, 15.0 mm. Bar = 1 mm.

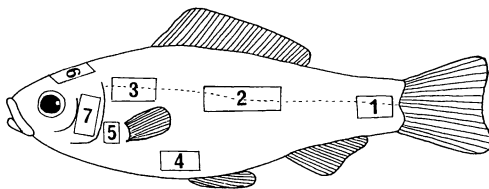


Fig. 5. Localization of the different sites of the first scale appearance in a teleost fish. 1, medial region of the caudal peduncle; 2, middle region of the flank; 3, anterior region of the body near to the lateral line; 4, belly between pectoral and pelvic fins; 5, pectoral peduncle; 6, cranial vault; 7, opercular region.

Discussion

Table 1 shows that, among teleosts, the squamation develops in different ways, that can vary within orders or families. For instance, in cyprinids the first site of scale appearance can be located either on the caudal peduncle (site 1) or on the anterior part of the body (site 3). Generally, the squamation spreads from the primary site but sometimes secondary sites appear before the body squamation is completed. Seven sites of squamation can be dis-

tinguished among teleosts: site 1, on the caudal peduncle; site 2, on the middle region of the flank; site 3, on the anterior region of the body; site 4, on the belly; site 5, on the pectoral peduncle; site 6, on the cranial vault, and site 7, on the opercular region (Fig. 5). First to fifth sites can be considered primary sites of scale appearance, and site 7 is always a secondary site which appears always after the squamation is developed on the body. The primary site of scale appearance for one species can be a secondary site for another.

Several authors have not mentioned the squamation development on the head. Consequently, the importance of sites 6 and 7 is undoubtedly underestimated in the compilation in Table 1.

To our knowledge, the squamation development has not been reported in fishes other than teleosts except in the extinct acanthodian, *Acanthodes* sp. (Zidek, 1976) and in a shark *Scyliorhinus canicula* (Reif, 1980), and in two holosteans, *Lepisosteus* and *Amia calva* (Jollie, 1984a, b). In *Acanthodes* sp., minute rhomboid scales appear first on the extremity of the caudal peduncle. This pattern is similar to the squamation development from site 1 in teleosts. In embryos of *S. canicula*, placoid scales appear first in the anterior region of the body (like site 3 of tele-

osts). In *Lepisosteus* ganoid scales appear first on the tail (=site 1 in teleosts) and in *Amia* elasmoid scales appear first on the anterior part of the body (=site 3).

Table 1 shows clearly that the squamation most commonly develops from the posterior region of the caudal peduncle (site 1) (61 species out of 85, 74% of the teleosts examined). In 25 species (29%), scales appear first in other regions of the body: site 2 in eleven species, site 3 in thirteen species, site 4 in one species, site 5 in one species and site 6 in one species.

In 20 species out of 85, more than one site of scale appearance has been observed in the same fish. In 83 species, the first scales are close to the lateral line (sites 1, 2 and 3) but sites 1 and 2 also relate to the position of the horizontal septum and are the locations of the first scales in 71 of these species.

In two species, *Brachydanio rerio* and *Pomoxis nigromaculatus*, the results differ slightly according to authors (Table 1).

First scale appearance. In the present species, several scales (sometimes distributed in several rows) were observed appearing simultaneously on the body of the smallest scaled fry. This confirms the findings of Balon (1959a) and Fishelson (1966). There is no single point of scale initiation but a site (or locus) where several scales appear.

The length of the fry at scale formation is generally constant (within a range of 1 mm or less) in the present species, but it differs largely among species within a family. This difference may be explained by the minimal length for scale formation as a consequence of the adult specific length (Oosten, 1957; Sire, 1981). The case of *Anguilla*, in which the first scales are formed late during ontogeny (Jellyman, 1979), appears to be an exception.

In the present species, the squamation develops first from site 1 (caudal peduncle), the major site of the first scale appearance in teleosts. Moreover, this site of squamation development is reported in species with different types of scales, as in *Cichlasoma octofasciatum* with elasmoid scales and in *Corydoras arcuatus* having osseous plates, or as in *C. octofasciatum* or *Poecilia reticulata* with large scales and *Barbus barbus* with relatively small scales.

Consequently, the localization of the first site of scale formation does not appear to be related to the type of scale, the fish shape, or the ovoviparous condition for the four species studied.

Development of squamation in fishes—phylogeny and systematics. The literature is poorly documented on the development of squamation in fishes other than teleosts except in the primitive actinopterygian fishes, the holosteans *Lepisosteus* and *Amia* (Jollie, 1984a, b). This lack of information is probably due to the difficulty of breeding dipnoans or polypterids. Studies on scale development are available on dipnoans (Brien, 1962) and on *Polypterus* (Sewertzoff, 1932) but the authors do not comment on the order of scale development. In *Lepisosteus*, the scales appear first along the lateral line in the tail region (=site 1), then the squamation spreads anteriorly (Jollie, 1984a). In *Amia calva*, the scales appear at the lateral line just behind the pectoral girdle (=site 3), then the squamation extends posteriorly (Jollie, 1984b). In the absence of other data on the development of the squamation in primitive osteichthyan fishes, it is difficult to discuss the phylogenetic implications of the pattern of squamation development in fishes. Nevertheless, in closely related fishes such as *Lepisosteus* and *Amia*, the scales appear first in two opposite regions. Moreover, we can note that the squamation developed in an extinct osteichthyan, *Acanthodes* sp. followed a pattern (=site 1) similar to that of the majority of teleosts (Zidek, 1976). The squamation development differs within orders and families of teleosts, and it appears similar in families as phylogenetically distant as Callichthyidae and Cyprinidae (Ostariophysi), and Poeciliidae and Cichlidae (Acanthopterygii). Thus the localization of the first site of scale formation and the development of the squamation cannot be linked to primitive or evolved condition. Nevertheless, the overwhelming preponderance of site 1 seems to be some indication that it, if any, is the "primitive" site. Moreover, within a family (Cyprinidae for instance) as well as in holostean fishes, the squamation can develop from sites located in different regions of the body. Consequently, the development of squamation may be used with caution to establish phylogenetic relationships. However, Potthoff (1974) found a possible use of squamation development in systematics to discriminate scombrid species.

Proposed factors involved in scale induction. From the previous part of the discussion, it appears that there are probably no relationships between the site of the first scale appearance and phylogeny, systematics, or the scale type. Until now, only one hypothesis has been proposed to explain the localization of the first scales formed: the lateral-line

induction. Some investigators proposed that the development of the lateral-line neuromasts could induce the formation of the first scale (Neave, 1936; Wallin, 1957; McCrimmon and Swee, 1966). This speculation is based on the observation that the first scales appear in the vicinity of the lateral line. Indeed, in numerous teleost species (for instance in cichlids), the first scales to be formed are commonly those constituting the lateral-line scales later. The neuromasts have been experimentally demonstrated as inducing the formation of the canal characterizing the lateral-line scales (Mori, 1931; Parker and Paine, 1934), or the dermal bones of the skull (Devillers, 1947) but there is not any demonstration of their possible role on the position of the body scale rudiments and, concerning the scales appearing on the cranial vault (site 6), further studies are needed to check the relationships between scale localization and the neuromasts of the head sensory system. However, 1) in closely related species scales can be formed either on the anterior part of the lateral line or on its posterior part; 2) in a single species there are sometimes several sites of scale formation, some of which are not close to the lateral-line system, as for instance on the pectoral peduncle or on the belly; and 3) several species show no relationship between the first site of scale appearance and the localization of the lateral line (*Brevoortia patronus*, *Pomoxis nigromaculatus*, *Xiphias gladius*).

These observations let us propose another hypothesis as a tentative to explain the induction and formation of scales in other sites than those related with the lateral line. This hypothesis is that scale induction could be related to mechanical constraints imposed to the fish skin during swimming. This induction could be related to the shape of the fry before scale formation (elongated or not, flat or high) and to its behavior (continuous swimming or intermittent swimming, pelagic or benthic, etc.). During swimming, the repeated movements of the muscles in a definite region of the body (as for instance in the caudal peduncle or pectoral peduncle), transmitted as tension forces to the skin, could induce a previously genetically programmed cell population to enter a differentiation process leading to the scale formation. Unpublished personal observations on the swimming behavior of cichlid fry in aquaria have shown that the caudal peduncle (on which scales appear first) is very active. This epigenetic induction by mechanical constraints would explain the main different pattern of squamation

development in fishes when the lateral line is not concerned. This hypothesis is now being investigated by new observations on the swimming of fry of different shapes before the scales are formed and by histological studies of the skin and muscles in the regions where the scales will develop first.

In *Poecilia reticulata*, the first scales develop on the caudal peduncle (site 1) when the fry are still in the belly of the female parent. Consequently, the initiation of the scale development cannot be related to an external factor. The first scales appear in the caudal peduncle, in the lateral-line region, favoring the hypothesis of a lateral-line induction; but this region of the fry is mobile, as seen in fry freshly removed from the female parent, and that could also be explained by the hypothesis of movement induction. In the case of *P. reticulata* also, the hypotheses of nervous, or mechanical, inductions may not be rejected, and further results on the behavior of the fry in the mother's belly are needed for better understanding.

Thus, in the actual state of our knowledge of the squamation development in fishes, we can only note that the induction by the lateral line, if it exists, is not the only factor influencing the first scale formation.

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真骨類 4 種における鱗の生じ方

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真骨類 4 種, *Cichlasoma octofasciatum* (カワスズメ科), グッピー *Poecilia reticulata* (カダヤシ科), *Barbus barbus* (コイ科), *Corydoras arcuatus* (Callichthyidae) における鱗の生じ方を記載し, これまで知られていた他種 (主として真骨類) の場合と比較した。真骨類の体表では最初に鱗が出現しうる場所は 7 箇所ある。種によってはただ 1 箇所 (通常尾柄上) に出現するが, 2 箇所以上に出現する種もある。これらの場所が体表に複数局在することを, 後生的な要因により説明できるかを議論した。