Comparative morphology of scales of four teleost fishes from Sudan and Yemen

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Abstract

The scale morphology of four teleost fishes, Barbus arabicus, B. exolatus, Labeo niloticus (Cyprinidae), and Lates niloticus (Centropomidae), was studied using both light and scanning electron microscopy. The considerable variation in scale shape on different parts of the body makes it difficult to nominate a typical scale for particular species to be used in taxonomic studies. However, some character states of the inter-radial denticles, cteni, and the focus area appear to be good taxonomic criteria.

Keywords: Barbus, cteni, Labeo, Lates, morphology, scales, SEM, Sudan, Yemen

Introduction

The use of scale morphology and squamation (lepidology) in fish classification can be traced back to the time of Agassiz (1834), who apparently was the first to use fish scales for taxonomy and divided fishes into four groups according to the structure of their scales: Placoidei, Ganoidei, Ctenoidei, and Cycloidei.

The importance of scale morphology in systematic studies increased dramatically during the late 19th century and the first half of the 20th century, with great advancements in the field of light microscopy (Williamson 1851; Baudelot 1873; Timms 1905; Cockerell 1910, 1913, 1914, 1915; Chu 1935; Lagler 1947; Kobayasi 1951, 1952, 1953, 1955; McCully 1961; and others). The value of scale morphology used in classification was enhanced with the introduction and development of scanning electron microscopy (SEM) (DeLamater and Courtenay 1973, 1974; Hughes 1981; Roberts 1993; Lippitsch 1990, 1992, 1993). However, some problems in the use of scale morphology due to environmental factors, and variation in shape, size and structures according to age and position on the body have been reported (Lippitsch 1990; Pou and Gallego 1990).

A comparative morphological study of the scales of four freshwater fishes from the Nile River at Dongola, Sudan and stream water at Eib province, Republic of Yemen was...
undertaken with the aim of establishing the degree of differentiation of the scales between species, and between different regions of the body.

Materials and methods

*Barbus arabicus* Trewavas, 1941 and *B. exulatus* Banister and Clarke, 1977 are the most common freshwater fish species in Yemen (Al-Safadi 1992), and are widely distributed in southern Arabia (Krupp 1983), reaching up to 305 and 295 mm SL, respectively (El-Etreby 1993). On the other hand, *Labeo niloticus* (Forsskal, 1775) and *Lates niloticus* (Linnaeus, 1758) dominate the basins of the major rivers in Africa. *Labeo niloticus* is found in north-east Africa with the drainage system of the Nile (Blue and White), and attains 470 mm SL. *Lates niloticus*, the Nile perch, is a demersal species widespread throughout Africa and occurring commonly in all major river systems. It attains 1900 mm SL (Froese and Pauly 2004).

Twenty-five adult specimens each of *Barbus arabicus*, *B. exulatus*, *Labeo niloticus* (Cyprinidae), and *Lates niloticus* (Centropomidae) collected from Sudan and Yemen were analysed. Specimens of *B. arabicus* 120–210 mm in total length and *B. exulatus* 140–227 mm in total length were collected in May 1993 from a small stream near Eib province, south-east of Sana’a, Republic of Yemen. Specimens of *Labeo niloticus* (Cyprinidae) 160–280 mm in total length and *Lates niloticus* (Centropomidae) 350–980 mm in total length were collected in August 1993 from Dongola, north of Khartoum, Sudan.

Lepidological observations using light microscopy were performed following the methods of Takagi (1953), Roberts (1993), Lippitsch (1993), and Kuusipalo (1998). For the purposes of this study, the fish body was divided into eight regions (Figure 1) to facilitate the study of variation in the shape and size of the scales. Four fields were recognized in the scale of species of both families studied: anterior, two laterals, and

Figure 1. Areas where scales were removed from left side of fish.
posterior (Figure 2). Scales were removed from each region of the left side of the fish with forceps and cleared with 1% potassium hydroxide solution. Remaining adhering tissue was removed under a dissecting microscope. Scales were stained with alizarine Red-S stain for 2–3 days, flattened between glass slides.

The squamation pattern was recorded following Lippitsch (1990, 1992). SEM was used to investigate scale ultrastructure following Lanzing and Higginbotham (1974), Lippitsch (1992), Roberts (1993), and Kuusipalo (1998). Scales to be used for SEM were air dried and mounted on an aluminium stub using double-sided carbon tape. Stubs were sputter coated with gold to a thickness of 28–30 mm in a vacuum of about $40 \times 10^{-3}$ torr. Scales were viewed in a Philips XL45 FEG at 5.0 kV.

Figure 2. Principal scale fields. (A) Body scale (Lates niloticus); (B) body scale (Barbus exolatus); (C) lateral line scale (Lates niloticus); (D) lateral line scale (Barbus exolatus). AF, anterior field; LF, lateral field; PF, posterior field.
Results

*Barbus arabicus* (Figure 3)

The head, operculum, nape, base of pectoral fin, belly, and ventral side of the caudal peduncle are naked. Scale size and shape vary over body: large scales in regions 1, 4, and 6; pentagonal scales in regions 1–4, elongate pentagonal scales in regions 5–7. The scales in region 8 show inconsistent shapes and those around the anal region are mainly elongate. There are eight scales anterior to the dorsal fin, four between the anterior tip of the dorsal fin and lateral line, five between the posterior tip of the dorsal fin and lateral line, and 10 around the caudal peduncle.

Body covered with pentagonal cycloid scales. Both sides of anterior field rounded with two notches near antero-lateral angles. Middle portion of anterior end produced into a broad convex process with a single terminal spine. The edges are slightly undulated and rounded, maximum breadth of scale at about the middle, apex wavy. Focus at about anterior third, surrounded by a circulus on anterior side only. There are five to six radii in the anterior field, many incomplete. There are three radii in the lateral field and 14–15 prominent radii in the posterior field. No denuded area in the anterior field.

Delimitation between lateral and anterior fields clear by the inflection in curvature of circuli, the lateral and posterior fields not separated by change in curvature of circuli but rather by the clear separation of the radii in the lateral fields from those in the posterior field.

Circuli perfectly defined in anterior and lateral fields, but they are further apart and less well defined in posterior field, and arranged parallel to the edges of all fields. Annuli clearly marked in anterior and lateral fields by alternate wide light and dark, narrow spaces, that correspond to summer and winter growth (Miranda and Escola 2000).

Lateral fields are extensive, triangular, their radii crossing diagonally from anterior field, curving away from focus. The radii of the posterior field are near the longitudinal axis of the scale, aligned in a zigzag pattern, reaching the posterior free margin and producing a wavy effect. The anterior field is rhomboidal to triangular with numerous radii. The posterior field is bell-shaped and forms the widest part of the scale. The anterior part of the posterior field with a series of structures in an irregular network (poorly developed, resulting from disorganization of the circuli during growth (Miranda and Escola 2000), occupying a more or less triangular area (Rubin 1981).

The lateral line scales (Figure 3L) are generally similar to body scales except for the absence of protuberances and the presence of a long straight, longitudinal canal traversing over two-thirds of the length of the scale, with the anterior end reaching focus; anterior and posterior ends c-shaped, no constriction, and with large tubercles in the inter-radial areas of the canal.

The inter-radial denticles are 0.84–1.35 μm long, broad, irregular in shape, and crowded (Figure 7A). The area inside the focus is covered with granules. The radii extend to centre of focus (Figure 7B).

The scales from different body regions of *Barbus arabicus* show several variations from each other. The scales are elongate-pentagonal on body regions 5–7 (Figure 3E–G), and are irregular at the base of the caudal fin. Positions of the main apex and the focus seem to be diverted from the centre in scales from region 8, and on some scales from the area around the anus. The shape of the posterior field is narrow and elongate in scales from regions 2, 5–8 and scales from around the anus are irregular. Deformed circuli (protuberances) are well defined on scales from regions 1 and 3–7.
Figure 3. Scales from different body regions of *Barbus arabicus*. (A–G) Regions 1–7; (H, I) region 8; (J, K) area around anus; (L) lateral line scale. Scale bars: 1 mm.
It is possible to separate body scales into four main shape groups. Group (1) consists of scales with a pentagonal shape, occurring on regions 1–4. Group (2) scales have an elongate-pentagonal shape, occurring on regions 5–7. Group (3) scales are oblong and occur on region 8. Group (4) scales are variable in shape and are limited to the area around the anus.

The shapes of the anterior field and the left and right upper corners, the position of the focus, and the shape of radii in the anterior, posterior, and lateral fields are consistent on scales from seven of the eight regions studied in this species. These characters were also clear in the lateral line scales. Other characters such as shape of the posterior field and presence of tubercles were shown to be inconsistent, and only found in scales from certain body regions (Figure 3).

**Barbus exulatus** (Figure 4)

The morphology of the scales of B. exulatus differs from that of B. arabicus in the following combination of characters: base of dorsal, anal, and caudal fins and belly are all scaly. Large scales are in regions 1–5. Nine scales are in front of dorsal fin, five between posterior end of dorsal fin and lateral line, and 9–10 scales around caudal peduncle. The edges of the scales are slightly rounded and the apex is slightly wavy. There are 8–11 radii in the anterior field, and few are incomplete. There are two to three radii in the lateral field and some lateral and posterior radii integrating in such a way as to make it difficult to distinguish true radii.

Lateral and posterior fields are not separated by changes in curvature but rather by the closeness of radii in the posterior field.

Circuli are well defined in the posterior field.

Lateral fields are triangular to rounded in shape, some of the radii are short and not reaching the focus. The radii of the posterior field have an undulating shape and reach the posterior free margin of the scale. The anterior field has a triangular shape, although it is rhomboidal in scales from other body regions.

Lateral line scales (Figure 4K) are mainly hexagonal, straight-sided, undulating posterior end, and with indented frontal apex. Lateral line canal is slightly curved. There are two main lines of tubercle-like structures in the posterior field distributed between radii, but they are concentric with the focus (Figure 7C, D).

The inter-radial denticles are short, blunt, widely spaced, and with broad base ranging from 0.72 to 1.75 μm in length (Figure 7E, F).

Several morphological variations were traced in scales from different body regions in Barbus exulatus. Narrow scales occur in regions 3 and 7, and there are oblong scales in regions 5, 8, and in the area around the anus. The main apex is low or absent in scales from the area around the anus and in region 8. The posterior field progressively narrows in scales from region 3 and in the area around the anus. Bony structures are less obvious on scales from regions 3–5 and 8, and in the area around the anus. There is more pigmentation in scales from regions 1, 4, 6, and 7, than in scales from other regions.

The shape of scales from different body regions falls in three main groups. Group (1) scales with broad pentagonal shape, from regions 1, 2, 4, and 6. Group (2) scales with an elongated posterior field, from body regions 3, 5, and 7, and the area around the anus. Group (3) scales are variable in shape, and occur in region 8 and in the area around the anus. The general broad shape of the scale, the shape and pattern of divergence of radii in the anterior, posterior, and lateral fields, and the position of the focus, are consistent in scales from all body regions studied except for those from region 8 and some from the area...
Figure 4. Scales from different body regions of *Barbus exolatus*. (A–G) Regions 1–7; (H) region 8; (I, J) area around anus; (K) lateral line scale. Scale bars: 1 mm.
around the anus. The shape of the anterior and posterior fields is inconsistent in scales from different body regions studied.

**Labeo niloticus (Figure 5)**

The morphology of the scales of *L. niloticus* differs from that of *B. arabicus* in the following combination of characters: belly scaly. Six to seven scales between the anterior tip of dorsal fin and lateral line. Five to six scales between posterior tip of dorsal fin and lateral line and 18–20 scales around caudal peduncle.

- Body covered with cycloid scales of broad pentagonal shape. No variation in shape and size of scales from different body regions. Both sides of the anterior field are without notches. Apex rounded. Focus just in front of the middle of the scale. Four to six radii in both anterior and posterior fields.
- Delimitation between the lateral, anterior, and posterior fields is not clear; a gradual disappearance of inflection in curvature of circuli. However, scales from some body regions showed differentiated lateral and posterior fields by clear separation of the radii in both fields.
- Circuli in the posterior field appeared to lose their circular form and are not well recognized.
- Lateral fields are rounded but not extensive. Radii crossing surface diagonally from anterior field to reach focus. The radii of the posterior field are almost straight. Anterior field with few radii and scales from different body regions have a slightly raised apex.
- Lateral line scales (Figure 5J) are squarish-oblong in shape with straight sides, rounded anterior end and an indented posterior end. Lateral line canal with v-shaped anterior and c-shaped posterior openings. No intra-radial denticles (Figure 7G). The focus is rounded (Figure 7H).

In *Labeo niloticus*, scales from different body regions differ from each other in several morphological characters. Narrow scales occur in regions 3–8 and around the anus; there is a slightly raised apex on the anterior field of scales from regions 4–8. The posterior field is slightly constricted in scales from regions 1 and 3, and the area around the anus. The number of radii ranges from zero to two in scales from regions 1 and 2.

- Body scale shape falls into two main groups. Group (1) scales broad and short, occurring in regions 1 and 2. Group (2) scales long and narrow, occurring in regions 3–8 and the area around the anus. The lateral line scales have a completely different shape from those of the body. The anterior and lateral fields are each characterized by a hump and raised corners, respectively.

**Lates niloticus (Figure 6)**

Head and pre-operculum covered with embedded ctenoid scales; operculum naked except for posterior edge, which is scaly; bases of the pectoral, dorsal, anal, caudal, pelvic fins, ventral side of caudal peduncle, and belly scaly; 12–13 scales between the anterior tip of dorsal fin and lateral line; 10–11 between the anterior tip of soft part of dorsal fin and lateral line; 18–20 around the caudal peduncle.

- Body covered with ctenoid scales, those from body regions varying in shape and size; anterior field straight sided; anterior end wavy; posterior end rounded; focus a short distance behind centre of scale; circuli thick, widely spaced; four to seven radii extending toward anterior end. Lateral and anterior fields clearly separated by change in curvature of
circuli. Circuli clearly defined in anterior and lateral fields, replaced by cteni in posterior field. Several rows of cteni on body scales, those in front row slightly shorter than others. Lateral fields not extensive, straight. Radii present in anterior field only. Anterior field typically triangular in shape, although some scales from different body regions have a slightly undulating anterior end, with several radii reaching focus.

Figure 5. Scales from different body regions of *Labeo niloticus*. (A–H) Regions 1–8; (I) area around anus; (J) lateral line scale. Scale bars: 300 μm.
Figure 6. Scales from different body regions of *Lates niloticus*. (A–H) Regions 1–8; (I) area around anus; (J) lateral line scale. Scale bars: 1 mm.
Lateral line scales (Figure 6J) squarish, sides slightly rounded; anterior end wavy, a notch at posterior end; several radii and several secondary radii in anterior field; long, broad lateral line canal traverses two-thirds of scale surface, slightly displaced at anterior end.
toward ventral side, anterior and posterior ends c-shaped, posterior end opening to a notch; cteni in two series of several rows separated by posterior notch.

Inter-radial circuli with long, slender, curved, widely spaced, minute denticles. Focus irregular, with broken and wavy circulus, focal area with bumps of varying size (Figure 8A, B). Four regions are distinguished on posterior part of scales (from margin towards the focus; Figure 8C): (1) a region immediately along scale margin, composed of rows of recently formed, long, tapered ctenial spines, most of which are straight, but some curved and orientated backwards; (2) a region anterior to the ctenial spines composed of eroded ctenial spines that are less upright than younger ones; (3) an intermediate region in which short ctenial spines are distributed irregularly; (4) a more central region composed of concentric network ornament.

Toward the focus region from the posterior margin, ctenial spines show clear, gradual ontogenetic change. They are regularly arranged into longitudinal lines towards the posterior edge of the scale in areas 2 and 3, but in area 1 these lines become distorted due to presence of an extra cteni inserted between others. Cteni 45–68, 53–71, and 42–52 μm apart in regions 1, 2, and 3 respectively. Cteni in area 1 perpendicular to rounded posterior margin (Figures 2, 6). Marginal ctenial spines tapered, cone-shaped, 105.2–138.6 μm long and 2.5–2.7 μm wide at anterior and posterior ends. Some spines with a medial gutter at base. Others with deep or shallow bifurcation (Figure 8C). Surface of bifurcated ends of most spines smooth or with fine tubercles (Figure 8D). Marginal ctenial spines smooth, remaining ctenial spines with a depression on both sides of longitudinal axis (Figure 8D, E). Signs of abrasion at distal region of some eroded ctenial spines (Figure 8F), and a number of lacunae at site of abrasion, which range from 4.03 × 6.61 μm to 6.93 × 10.36 μm in size, are similar to Howship’s lacunae (Sire and Arnulf 2000) and may be due to osteoclastic activity. The tip of each ctenial spine is inserted into the medial gutter of the next one in the same line, a pattern that is repeated along individual lines from the scale margin towards the focus (Figure 8C, G), thus interlocking adjacent cteni. The length of the eroded ctenial spines varies from ~130 μm in the cteni immediately in front of the marginal ones, to ~106 μm at a distance of three cteni in front of them; anteriorly, the remnant ctenial spines are 93 μm long. A few randomly distributed tubercles of different sizes and shapes anterior to last row of the eroded ctenial spines. Concentric circuli and no ctenial spine in central region. All sculptural elements of the posterior region of the scale are clearly different from the regularly arranged circuli in the anterior, which have a dorsal row of slender, curved, pointed, and regularly spaced denticles 0.17 μm high (Figure 8H).

Some morphological variations were evident in scales from different body regions of Lates niloticus. Rectangular-shaped scales occur in region 3, oblong scales in the area around the anus, and squarish scales elsewhere on the body scales in region 3 have asymmetric left–right anterior corners; scales from regions 3, 5, and 6 have a markedly wavy anterior end. Radii are longer in scales from regions 3 and 8, and around the anus. The area with granulations in scales from regions 6 and 8 is triangular with flat apices.

Four groups of shapes can be identified in the scales from different body regions. Group (1): rounded, occurring in region 1. Group (2): roundly hexagonal, occurring in regions 2
and 4–8. Group (3): rectangular, occurring in regions 3 and 4. Group (4) scales are oblong and occur around the anus. Lateral line scales are hexagonal.

With the exception of scales from around the anus, the following characters appeared to be consistent in scales from other body regions: position of the focus, position of the radii in anterior field, the shape of anterior margin of scale, and the rounded-hexagonal shape of the scale. On the other hand, characters such as shape of the sides and the upper corners of the lateral fields, and the shape and width of the posterior field were inconsistent in scales from different body regions.

Discussion

The shape of the scales from different body regions is inter- and intraspecifically variable in the four species studied. At this stage it is important to (1) identify consistency in the presence of characters in scales from different body parts and (2) to identify scales of which body region will be the typical representative of the species for taxonomical studies. The results of the present study showed that the character of body scale shape cannot be considered as a basis to identify the fish species in question and hence, no single representative scale can be chosen for these species. Accordingly, when using scales as a taxonomic tool to separate species, it is advisable to use the consistent characters found in body scales of each species (see above).

In spite of the inconsistency present in the scale characters of the cyprinids under investigation, the scales of the two *Barbus* species showed a consistency in focus position and pattern of divergence of radii in anterior, lateral, and posterior fields. The consistency in the characters mentioned above in the two *Barbus* may be taken as supporting evidence that they are congeneric. Similarly, the consistency in characters between the *Barbus* and *Laboeo* species suggests that they are perhaps congeneric.

The scales of *B. arabicus* are clearly different from those of *B. exulatus*. This is consistent with the systematic work of Krupp (1983) on these species in which he suggested that they are two different species, separated on the basis of the number of anal fin rays.

There are several characters that the scales of the two *Barbus* species studied here share with congeners from India (Haque 1955) and Spain (Miranda and Escola 2000), specifically the position of the focus, the angle of divergence of radii in the anterior, lateral, and posterior fields, and the shape of the upper corners of the lateral fields. From the image and description of the scale of *Barbus (Puntius) chrysopterus* (McClelland, 1830) provided by Haque (1955), it is clear that this species differs in focus position, the general structure of the scale, and the divergence of radii from the other *Barbus* species studied by Haque (1955) and those studied here. Menon (1999) referred *B. chrysopterus* to *Puntius* McClelland, with which I concur on the basis of similarities of scale morphology. The shape of the body and the lateral line scales of the spanish barb species reported by Miranda et al. (1996) and Miranda and Escola (2000) are consistent with those given for the barb species studied here. Similarly, the scales of *L. niloticus* differ markedly from those of *L. chariensis* Pellegrin, 1904 and *L. parvus* Boulenger, 1902 (Tshibwabwa and Teugels 1996) and from the three Indian *Laboeo* species (*L. rohita* (Hamilton, 1822), *L. calbosu* (Hamilton, 1822), and *L. gonius* (Hamilton, 1822)) (Haque 1955), which might support the specific status of the three cyprinid species (*B. arabicus*, *B. exulatus*, and *L. niloticus*) in question.

Since only one species of the genus *Lates* has been available for study, it is currently very difficult to ascertain whether or not scale characters are good taxonomic criteria for
separation of the species from the other members of the genus. In general, there are not many differences in the shape of the scale from the general percoid scale reported by other workers (DeLamater and Courtenay 1974; Coburn and Gaglione 1992).

The ultrastructure of the scales showed some fine structures and features. Scale denticles are among the fine structures seen on the inter-radial area of the anterior field. Scale denticles have been described in elasmoid scales by DeLamater et al. (1972), DeLamater and Courtenay (1974), Lanzing and Higginbotham (1974), Yoshida et al. (1974), Fouda (1979), and Yamada and Watabe (1979). The possibility that denticles might ensure the anchorage of the scales in the dermis was suggested by Lanzing and Higginbotham (1974) and Fouda (1979). In the three cyprinid fish studied at present, which are considered as a lower group of teleosts (Greenwood et al. 1966), scale denticles were observed only in *B. arabicus* and *B. exolatus*. Yet the denticles of those two species are confined to the anterior part of the scale and are not as well developed as those of the *Tilapia mossambica* (Peters, 1852), *Pomatoschistus microps* (Kroyer, 1838), and *Fundulus heteroclitus* (Linnaeus, 1880) described by Lanzing and Higginbotham (1974), Fouda (1979), and Yamada and Watabe (1979). According to these authors, the fully developed denticles of *Tilapia* or *Fundulus* species are 2–4 μm in length while in *B. arabicus* and *B. exolatus* they reach only 0.72–1.73 μm. These small-sized processes located on the crest or on the surface of the circuli cannot anchor the scale in the dermis as securely as can the well-developed denticles previously described by other investigators. In their work on the cyprinid species *Carassius auratus* (Linnaeus, 1758) and *C. carpio* (Linnaeus, 1758), Zylberberg and Meunier (1981) suggested that the scale is anchored in the surrounding tissue by the bundles of collagen fibres connecting the upper part of the scale to the overlying dermis. Since no transmission electron microscopy has been carried out in the present work, it is impossible to predict at this stage the presence of such bundles in the two cyprinid species studied. This is also true for the scale denticles of *Lates niloticus*, which has small thin denticles.

Among the fine features of scales studied by SEM is the focus area sculpture. This area is shown to be either smooth or to have a granulate sculpture. The latter structure varies in shape and size between teleosts and is believed to be formed by disintegration of circuli (Lippitsch 1992). In both barb species studied, the focus area is sculptured with fine bumps. A reticulate pattern is found in *B. arabicus*, while a partially granulate area is present in *B. exolatus*. In *Labeo niloticus*, the focus area is smooth apart from a few small tubercles. On the contrary, other *Labeo* species, *L. chariensis* and *L. parvus*, showed a variable pattern of granulation on the focus area (Tshibwabwa and Teugels 1996). The smooth focus area and absence of denticles on the inter-radial circuli are considered the characteristic features to distinguish *Labeo niloticus* from at least two *Labeo* species mentioned above.

In *Lates niloticus*, the focus area is distinctively sculptured with coarse granules. In the absence of comparative material, it is difficult to decide whether or not this pattern is peculiar for this species. Further studies in this field taking into consideration more *Lates* species are needed to show the taxonomic importance of this character.

The most distinctive character of the ctenoid scales seen by SEM in this study is the ctenial spine. According to Roberts (1993), the ctenial spines of *Lates niloticus* should fall into the ctenoid type and more precisely into the ctenoid subtype “transforming cteni”, which occurs in many perciforms (Roberts 1993; Sire and Arnulf 2000) and specifically in the Percomorpha (Roberts 1993). In *Lates niloticus*, the length of the marginal ctenial spines at the posterior border showed a two-fold increase (from 52.6 μm in 25 cm SL juveniles, to 105.2 μm in 87 cm SL adults) while the fish standard length increases nearly four-fold. The
ctenial spines are relatively larger in juveniles than in adults, the ratio of spine length to SL being 2.1 in juveniles versus 1.2 in adults. This difference between juveniles and adults could be explained by the hydrodynamical function of this element (Sire and Arnulf 2000). Burdak (1986) found that ctenial spines have a hydrodynamic function by controlling water flow in the boundary layer, promoting the lowering of frictional drag. Burdak (1986) has demonstrated that the ctenial spine efficiency is higher in small specimens because the reduction of drag is more important. Similar results were obtained for different teleost fishes (Sire and Arnulf 2000).

The present SEM observations of ctenial spine replacement (or resorption process as others refer to it; Sire and Arnulf 2000) confirm McCully’s suggestions (McCully 1961) that older spines tend to lie flatter than younger ones, and that their tips are amputated. Hughes (1981) and Roberts (1993) also interpreted the mechanism of spine loss as a progressive resorption rather than a sudden shedding. The reduction in length of the spines in *Lates niloticus* is not severe and stops after approximately the tip of the spine length has been resorbed (Figure 8C). A severe resorption condition reported for some other teleost fishes leads to the complete disappearance of the spine (Roberts 1993). The resorption of ctenial spines, as a character, seems to be a characteristic of broader taxonomic groups such as genera and families rather than isolated species within these groups (C. D. Roberts, personal communication). Unless comprehensive study takes into consideration further species of the family Centropomidae, it is impossible to judge whether the slight resorption is a species-specific character or is characteristic of a wider taxonomic group. In *Lates niloticus*, truncation of ctenial spines is caused by resorption of their distal parts. These non-functional spines are characterized by the presence of Howship’s lacunae, which in this case have a squarish shape, suggesting that osteoclasts are responsible for this resorption. Bone, scales, and dermal plates of several teleost species appeared to be resorbed through the osteoclast process (Sire et al. 1990).

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