CHAPTER

8

Feeding Mechanisms

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The highly diverse group catfishes exhibits an extremely wide range of body forms and habitat niches. The body varies in shape from truncated and robust (as in Malapteruridae) to anguilliform (as in some Clariidae). It may be laterally depressed (as in Schilbeidae) or extremely dorsoventrally flattened (as in Chacidae) (Nelson, 1994). This wide variety of body shapes is also reflected in the range of feeding mechanisms evident in the order Siluriformes. Many catfishes can be considered generalised carnivorous, benthic and nocturnal feeders on small invertebrates, for which prey detection is assisted by their several barbels, ampullary organs and the highly developed Weberian apparatus (Alexander, 1965). Although some catfishes show highly specialised trophic specialisations, little is known about the functioning of the feeding mechanisms. The only paper, to my knowledge, dealing with biomechanical aspects of feeding, is that of Alexander (1970). This reflects the lack of current knowledge on feeding mechanisms and thus the evolution of strategies for survival in catfishes. Several papers have dealt with the general cranial morphology and numerous trophic adaptations

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formulated on this basis. A complete overview of feeding mechanisms in all catfish lineages is thus not possible in this short article, nor consideration of them in a phylogenetic-evolutionary context. Hence this chapter offers only some reflections on the most important structural implications of trophic specialisations in some catfish lineages, starting from the plesiomorphic condition. Some considerations regarding possible evolutionary adaptations as well as ontogenetic adaptations are also presented.

BASIC PATTERN OF FEEDING MECHANISMS IN CATFISHES

Before looking at the ontogeny of the feeding apparatus, as well as specialisations in feeding mechanisms in some catfish lineages, an overview of what could be considered the basic, plesiomorphic feeding apparatus is necessary. Several traits which characterise the basic configuration of the catfish feeding apparatus can be related to some structural transformations typical of catfishes, for example the dorsoventral flattening of the skull and formation of a palatine-maxillary mechanism. In addition to these specialisations of the feeding apparatus per se, modifications of the neuronal control (both sensory and motor control) of the apparatus have occurred as well (Finger, 1997).

Consequences of a Dorsoventrally Flattened Skull

Several morphological traits of siluriforms have been linked to the dorsoventral flattening of the skull. Tightly linked to this flattening is reduction in eye size; in general, the ratio of the eye diameter and the interorbital distance in catfishes is markedly smaller than in other ostariophysans (Adriaens and Verraes, 1997e). Other consequences of the dorsoventral flattening, in combination with eye reduction are: shortening of the eye muscles and consequently the myodomes, reduction of post-temporal fossa, a platybasic skull (instead of a tropibasic type), formation of a precerebral lamina (instead of an internasal septum), and the absence of a post-orbital sphenotic spine (Alexander, 1965; Adriaens and Verraes, 1997e).

In generalised, non-dorsoventrally flattened fishes, suction feeding is a widespread and dominant aspect of food capture (Lauder, 1983). It can thus be expected that some of the aforesaid transformations might have

strong implications on the functioning of feeding mechanisms, and especially suction feeding. Firstly, dorsoventral flattening of the skull implies its broadening and reduction in height. Each factor has a consequence of its own. Broad skulls imply that without the presence of a platybasic skull, the force components of the m. adductor arcus palatini would be strongly disadvantageous for suspensorial adduction (Alexander, 1965; Adriaens and Verraes, 1997e). Additionally, a broad skull means a broad mouth floor, which means a larger volume increase for a certain amount of hyoid depression (Adriaens and Verraes, 1997e). Reduction in skull height has implications for the contribution of suspensorial abduction in orobranchial expansion, needed for suction feeding: for a specific outward rotation of the suspensoria, the resultant volume expansion will be less, as well as the lateral displacement of the caudal tip of the hyoid bars in low suspensoria will be reduced.

For bottom-dwelling fishes, which generally have a dorsoventrally flattened head, it has been suggested that for respiratory purposes, the suction pump system (through expansion of the opercular cavity) would be far more important than the pressure pump system (through constriction of the buccal cavity). The opposite is true for laterally depressed fishes (Hughes, 1970). As suction feeding is an extensive respiratory movement, the importance of the suction pump system in catfishes can thus be suggested. Morphological evidence towards an improved opercular abduction has been observed in *Clarias* (Adriaens and Verraes, 1997d). An extensive abduction of the opercular bone, and thus also the branchiostegal membrane, is particularly noticeable during suction feeding in *Clarias* (Fig. 8.1) (Van Wassenbergh, pers. comm.). It has been suggested that as a result of flattened skulls, an extensive depression of the hyoid would be disadvantageous, and that as a result of the reduced mobility of the hyoid bars, the interhyal becomes reduced in many catfishes (Adriaens and Verraes, 1994). Feeding *Clarias*, however, appear to exert a rather substantial hyoid depression during suction feeding, but in a way that benthic stability is not completely overruled (Fig. 8.1).

Consequences of the Palatine-maxillary Mechanism

Many modifications of the feeding apparatus are unique to catfishes, as they are related to the formation of the control mechanism for movements of the maxillary barbels, i.e., the palatine-maxillary mechanism. The most

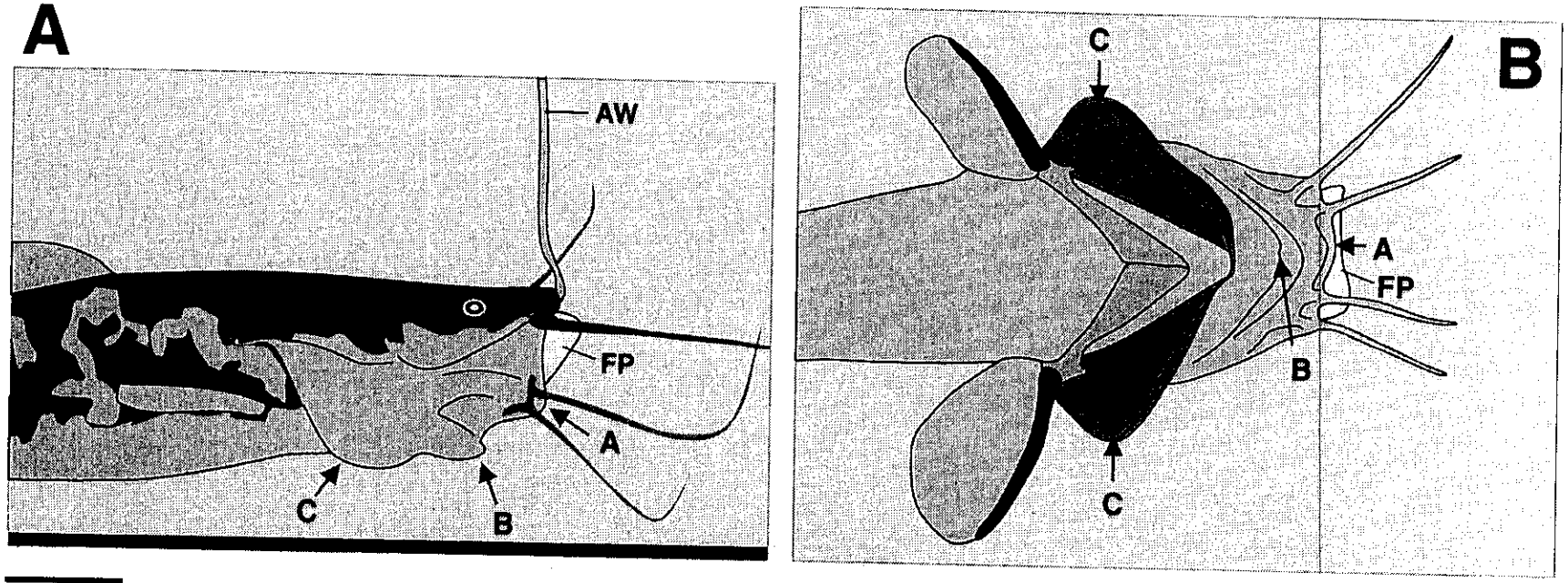

Fig. 8.1 Buccal cavity expansion during suction feeding *Clarias gariepinus:* **A.** Lateral view; **B.** Ventral view (Abbreviations: A: rostral tip of the lower jaw; AW: attachment wire; B, rostral tip of the hyoid bar; C, caudal margin of the branchiostegal membrane; FP, food particle).

important transformations, involving a vast impact on the feeding mechanism, are: (1) isolation of the palatine, (2) isolation of the anterior part of the adductor arcus palatini muscle, (3) shift in insertion of the medial part of the m. adductor mandibulae complex, (4) decoupling of the maxillary bone from the jaw apparatus and (5) absence of a protrusible premaxillary bone (Fig. 8.2).

As a synapomorphic feature of Siluriformes, the palatine has become isolated from the rest of the suspensorium (Gosline, 1975; Fink and Fink, 1981). This has two important implications for the feeding apparatus: (1) the rostral articulation of the suspensorium is lost and (2) the palatine no longer forms a solid base for a rotating maxillary bone (and thus upper jaw). The former is partially solved by increasing the rigidity of the hyomandibular articulation with the neurocranium, thus preventing the hyomandibula from being dislocated during feeding. In catfishes, this involves the formation of a hyomandibular articulatory ridge, instead of two separate condyles, as observed in most other teleosts (Fink and Fink, 1981; Arratia, 1992; Adriaens and Verraes, 1997d). In some catfishes, forward sliding of the hyomandibular joint is prevented by the formation of a sphenotic spine locking the anterior margin of the hyomandibula (Adriaens and Verraes, 1998: fig. 21E). In some clariids, which show a hypertrophied adductor mandibulae complex, the suspensorium is prevented even more from dislocation by means of interdigitations between the hyomandibula and the neurocranium (Cabuy et al., 1999; Devaere et al., 2001). Modelling of the force components provides supporting arguments for the hypothesis of rotational forces being exerted on the hyomandibula-neurocranium articulation during biting (Herrel et al., 2002).

The problem of the rotating upper jaw, in the form of a maxillary bone, is solved as well, since the latter bone no longer functions as the upper jaw (with the exception of *Diplomystes*). In catfishes, the maxillary bone retains its articulation with the palatine, but functions as a supporting socket for the mandibular barbel, as well as in most cases an insertion site for the tentacular retractor muscle (Regan, 1911; Alexander, 1965; Gosline, 1975). As a consequence, rotations of the maxillary bone (for barbel movements) have been decoupled from premaxillary protrusion (for feeding movements) in catfishes. As protrusion of the premaxillaries requires an articulation with a forward swinging maxillary, this is no longer possible in catfishes (Motta, 1984). Lack of an ascending process and firm attachment with the mesethmoid support this impossibility. These traits

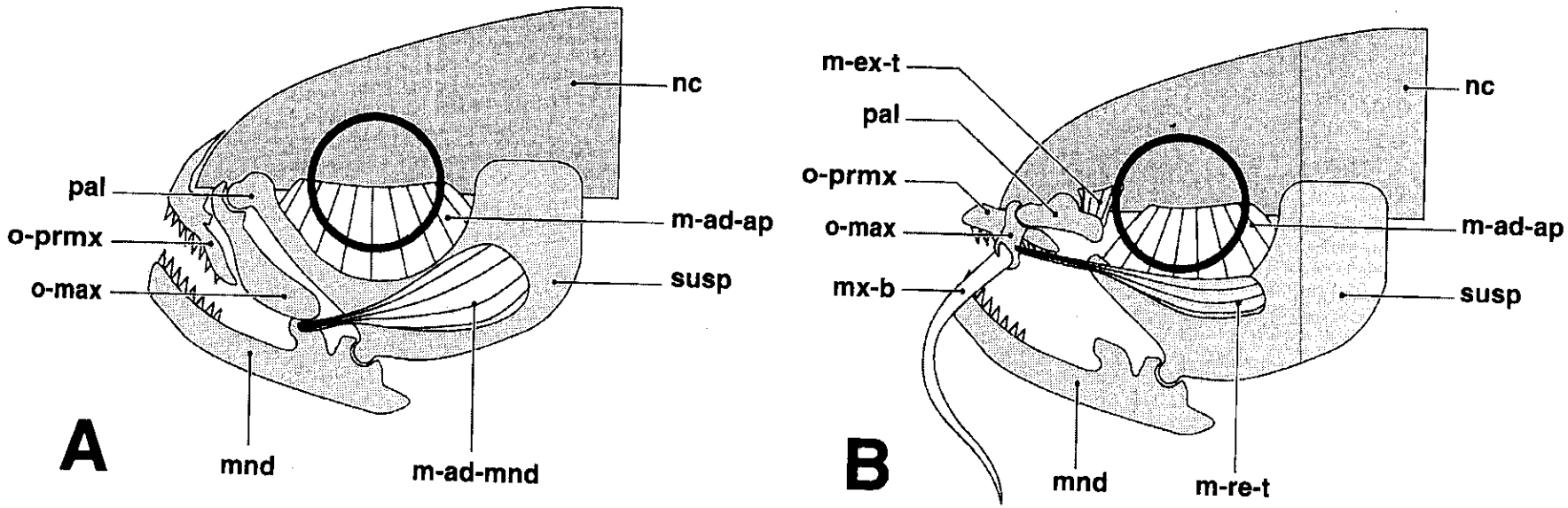

Fig. 8.2 Structural transformations of the feeding apparatus in catfishes, related to the formation of the palatine-maxillary mechanism: **A.** Scheme of the related structures in a basic configuration of the teleostean feeding apparatus; **B.** Scheme of the transformed structures in siluriforms. Abbreviations: m-ad-ap, m. adductor arcus palatini; m-ad-mnd, m. adductor mandibulae complex; m-ex-t, m. extensor tentaculi; mnd, mandibula; mx-b, maxillary barbel; m-re-t, m. retractor tentaculi; nc, neurocranium; o-mx, os maxillare; o-prmx, os praemaxillare; pal, palatine; susp, suspensorium. (From Adriaens and Verraes, 1997e).

are also observed in Diplomystidae, suggesting that, although toothed, the maxillary bone is no longer primarily involved in feeding (Arratia, 1987).

Muscular modifications are related to muscular control of the palatine-maxillary mechanism. Isolation of the palatine implies separation of that part of the m. adductor arcus palatini inserting on it. This decoupling enables separate muscular control of the palatine, in most cases resulting in retraction of the palatine, and thus extension of the maxillary barbel (Gosline, 1975; Adriaens and Verraes, 1997c). As an antagonist of this extensor tentaculi muscle, a medial subdivision of the m. adductor mandibulae complex presumably shifted its insertion dorsally along a primordial ligament, thus attaching to the maxillary bone (Howes, 1983b; Diogo and Chardon, 2000). This muscle directly pulls onto the distal part of the maxillary bone, thus retracting the maxillary barbel. Although this is the most common mechanism, other strategies exist (Alexander, 1965; Singh, 1967; Gosline, 1975; Ghiot et al., 1984).

Even though consequent loss of structures related to the feeding mechanism, as a result of differentiation of the palatine-maxillary mechanism, both mechanisms remain, however, functionally coupled in many catfishes. Firstly, detection of prey is not only facilitated by the presence of many taste-buds and superficial neuromasts on the elongated barbels (Arratia and Huaquín, 1995) (Fig. 8.3), but secondly, coupling of the mouth opening to the barbel extension is assumed to play an important role in prey detection and prey guidance to the mouth opening (Alexander, 1965; Gosline, 1973).

Basic Feeding Apparatus in Catfishes

So, based on the above-mentioned facts, what can be considered as the basic feeding apparatus and mechanism in catfishes? It has been suggested that in Diplomystidae, in general considered to be the most primitive siluriform, the feeding apparatus can be considered a plesiomorphic configuration (Howes, 1983b; Gosline, 1989; Diogo and Chardon, 2000). The adductor mandibulae complex is well developed in catfishes. In the plesiomorphic situation, the complex consists of a superficial part, a middle part and a deeper part (Fig. 8.4). Although similar to the typical acanthopterygian configuration, a different strategy in differentiation has been suggested in ostariophysans (Gosline, 1989; Diogo and Chardon, 2000). According to the nomenclature used by the latter authors, the plesiomorphic configuration in catfishes consists of a superficial A1-OST,

Fig. 8.3 SEM image of the distal tip of the nasal barbel in a larval *Clarias gariepinus*, showing the presence of sensory buds (scale bar = 100 μm).

which inserts on the dorsolateral side of the lower jaw. Medial to it lies the A2 (homologous to the A2 of acanthopterygians), which inserts onto the coronomeckelium and the tendon of the A_{ω}. The deeper part, the A3 (subdivided into a ventral and a dorsal part), inserts on the coronomeckelium and the medial side of the lower jaw. In many catfish groups, further subdivisions of these parts have occurred (e.g., up to nine different bundles in *Amphilius*) (Diogo et al., 2000; Diogo and Chardon, 2000).

Jaws are short, bearing a high coronoid process. Low and longer mandibulae are considered derived, and are frequently accompanied by loss of the A_{ω} (Diogo and Chardon, 2000). The oral jaws bear conical teeth, spread on the dentary (lower jaw), premaxillary and vomer (upper jaw). In contrast to all other catfishes, Diplomystidae and †Hypsidoridae

Fig. 8.4 Basic pattern of the jaw apparatus in catfishes (*Diplomystes chilensis*: right lateral view): A. Superficial parts of the m. adductor mandibulae complex; B. Deeper parts (Abbreviations: A1-OST, superficial A1-part of the m. adductor mandibulae of Ostariophysi; A2, A2-part of the m. adductor mandibulae complex; A3-d, dorsal part of the A3-subdivision of the m. adductor mandibulae complex; A3-v, ventral part of the A3-subdivision of the m. adductor mandibulae complex; IO, interopercular bone; LAP, m. levator arcus palatini; LO, m. levator operculi; Mnd, mandibula; Mx, maxillary bone; O, opercular bone; P, palatine; PMx, premaxillary bone; PO, preopercular bone; RT, m. retractor tentaculi) (Redrawn and terminology of the m. adductor mandibulae complex from Diogo and Chardon, 2000).

still bear teeth on the maxillary bone (Grande, 1987; Arratia, 1987). In some lineages, additional autogenous toothed bony plates may form against the palatine, the pterygoid bones (such a tooth-plate can also be observed in the diplomystid genus *Olivaichthys*) and the fourth ceratobranchial (Grande, 1987; Arratia, 1987; 1992; Blaber et al., 1994; de Pinna, 1996; Cabuy et al., 1999). A differential fusion between tooth-plates characterises different groups of catfishes as well (e.g., Pangasiidae and Ariidae) (Roberts and Vidthayanon, 1991; Blaber et al., 1994).

The hyoid bars are well developed and attached to the parurohyal bone through ligaments (Adriaens and Verraes, 1997b; 1998; Diogo et al., 2000). The sternohyoideus muscle, originating on the pectoral girdle inserts on this parurohyal. The ligamentous connection between the hyoid bar and the lower jaw, as well as the muscular connection (i.e., the m. protractor hyoidei), couple the hyoid depression (during m. sternohyoideus contraction) to the mouth opening (see below). Hyoid depression, in combination with contraction of the hyohyoid abductor muscles, is also coupled to the expansion of the branchiostegal membrane, which is supported by eight to ten branchiostegal rays (Arratia, 1987). Constriction of this membrane is enabled through contraction of the hyohyoid adductor muscles and presumably, the inferior hyohyoid and intermandibular muscles contribute to constriction of the buccal cavity.

The pharyngeal jaw apparatus in catfishes is generally little specialised. The upper pharyngeal jaws are formed by a tooth-plate, supported by the third and fourth infrapharyngobranchials (Arratia, 1987; Adriaens and Verraes, 1998). The fifth ceratobranchials bear a dorsal, elongated tooth-plate, thus forming the lower pharyngeal jaws. In contrast to some acanthopterygians, the left and right fifth ceratobranchials remain separated from each other.

CHANGES IN FEEDING MECHANISMS DURING ONTOGENY

Importance of Changes in Feeding Mechanisms

Ontogenesis has a vast impact on feeding mechanisms in fishes and certainly in catfishes with a specialised feeding mechanism (see below). Not only do nutritional demands change during ontogeny, the feeding apparatus itself has to be formed and become functional. These factors, as well as allometries, physical constraints (such as mouth gape) or

environmental factors (e.g., seasonal floodings), lie at the base of the frequently observed ontogenetic shifts in feeding behaviour in fishes (Thomas, 1966; Mol, 1995; Cook, 1996; Mérigoux and Ponton, 1998). Although exceptions do exist, many catfishes undergo an ontogenetic shift in diet and feeding behaviour, which consequently implies a shift in feeding mechanisms. Changes in feeding mechanisms generally involve changes in ram- and suction-feeding capacities, which arise due to allometric growth and species-specific differentiations of the elements of the feeding apparatus. Ontogenetic convergence towards one of these feeding strategies is also linked to ontogenetic differentiation of body shape (Osse and van den Boogaart, 1995; Osse et al., 1997; Mérigoux and Ponton, 1998).

The different strategies of feeding mechanisms that arise during ontogeny are initially linked to the prehatching period and the yolk-sac phase. The presence of a well-developed yolk sac (with or without a prolonged prehatching stage) enables the larvae to feed endogenously, thus allowing the formation of a functional feeding apparatus. In some Clariidae, hatchlings (i.e., age 24 hours post-fertilisation) have a yolk-sac phase of three days, whereas some Ariidae remain within the egg envelope for up to 75 days (see Adriaens and Vandewalle, this volume, Chapter 21). In the former, a very primordial feeding apparatus has formed at hatching, whereas the most important structures are present at the moment the yolk sac is absorbed (Adriaens and Verraes, 1997a, 1998; Adriaens et al., 2001). In ariids, on the other hand, prolonged incubation allows formation of a fully ossified cranial skeleton at the moment of hatching (Tilney and Hecht, 1993). It is clear that the latter ontogenetic strategy is much safer in terms of avoiding critical periods during which feeding might not be possible. However, the costs for allowing this are substantial: males have to incubate the egg in the oral cavity for quite a long period. For clariids, which inhabit swamps and seasonally flooded regions and migrate overland, this parental care behaviour would be difficult. Conversely, in some other catfishes, in which parental care is restricted to guarding the eggs, hatchlings look very similar to adults, although the yolk-sac stage is also restricted to 3-5 days (Riehl and Patzner, 1991).

Ontogenetic Shift in Mouth Opening in a Catfish

Very little is known about the ontogeny of feeding mechanisms in fishes (Otten, 1982; Hunt von Herbing et al., 1996). For catfishes, some

evidence is provided for one part of the mechanism in a clariid catfish, i.e., the mouth-opening mechanism (Adriaens et al., 2001). In *Clarias gariepinus*, some facts from ontogenesis (morphology, ethology, physiology), related to nutritional and respiratory demands, enable distinguishing five important phases during the early life history. The occurrence of important steps in this life history appears to be related to a possible ontogenetic shift in mouth-opening mechanisms.

At hatching (*phase 1*), mouth opening is still lacking. Respiration presumably occurs through cutaneous diffusion, assisted by a hyoid vascular network (Greenwood, 1955). A well-developed yolk sac makes a mouth-opening mechanism for feeding requirements superfluous at this moment. The onset of mandibular movements (*phase 2*) starts at about 5.0 mm standard length. Mouth closure is enabled, as a rudimentary adductor mandibulae complex is present and functional (Surlemont et al., 1989; Adriaens and Verraes, 1996). The initial, passive mouth-opening mechanism may allow restricted opening, relying on the release of stored (during mouth closure) strain energy in the cartilaginous connection between the lower jaw and suspensorium (Fig. 8.5A).

Additionally, and especially shortly after during ontogeny (once the latter cartilaginous connection between the lower jaw and suspensorium is lost), a second mechanism may become functional. This mechanism enables the first muscular depression of the lower jaw (Fig. 8.5B). The absence of a functional m. sternohyoideus at this stage would prevent fixation of the hyoid bars. However, differences in resistive forces in the connections with the suspensorium (for the lower jaw and the hyoid bar), as well as differences in the moment of rotation, suggest mouth opening. While improving mouth opening during this phase, the yolk-sac period also allows a learning process, in order to improve mouth opening and prey-capturing efficiency (Coughlin, 1994).

Transition to exogenous feeding (*phase 3*) implies increasing importance of a well-functioning mouth-opening mechanism. At a certain moment (i.e., 6.2 mm standard length), two such mechanisms may be present: the ligamentous and muscular hyoid mouth-opening mechanisms. In both these mechanisms, the m. sternohyoideus (now functional) may retract or fix the hyoid bars. In the former mechanism, a ligament couples the depression/retraction of the hyoid bar to the depression of the mandibula (Fig. 8.5C). In the latter, the mandibula would be depressed through contraction of the protractor hyoid muscle, pulling on to it (Fig. 8.5D). Teeth form shortly prior to the moment of

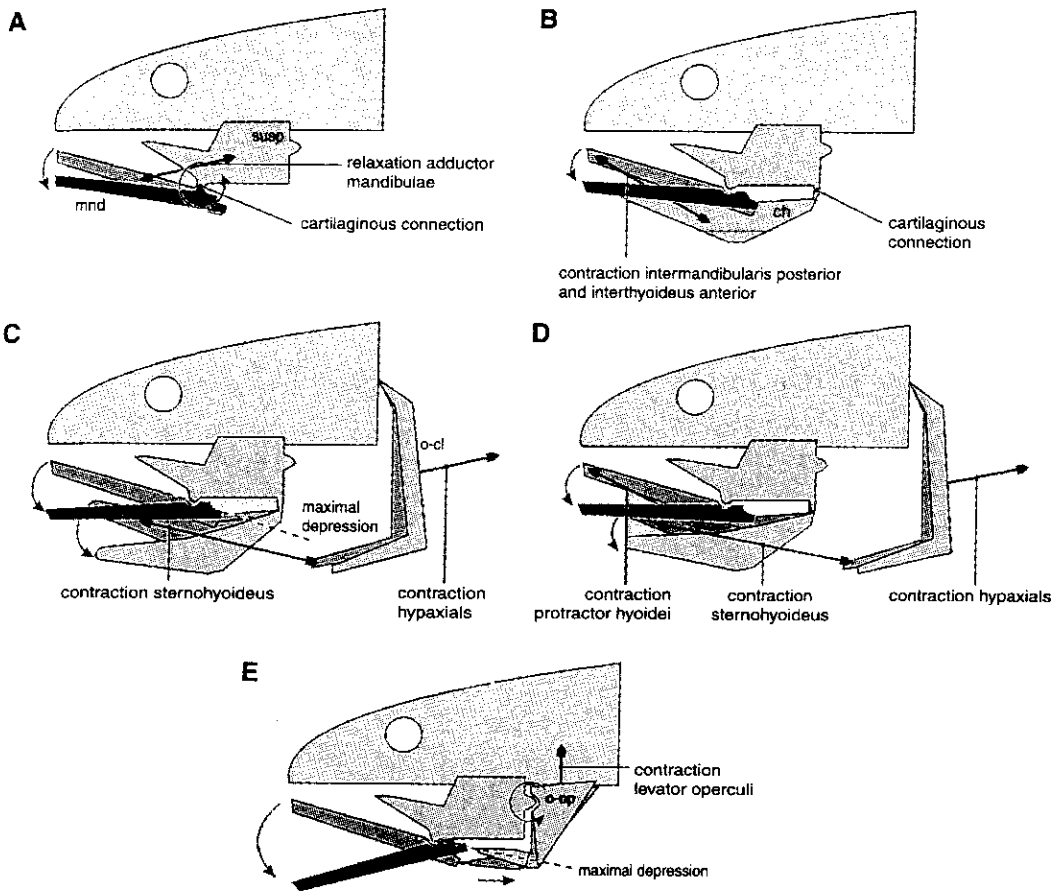

Fig. 8.5 Ontogeny of mouth opening mechanisms in *Clarias gariepinus:* **A.** Passive mouth opening mechanism; **B.** Passive-active mouth opening mechanism; **C.** Ligamentous hyoid mouth opening mechanism; **D.** Muscular hyoid mouth opening mechanism; **E.** Opercular mouth opening mechanism. Abbreviations: ch: ceratohyale; mnd; mandibula; o-cl: os cleithrum; o-op: os operculare; susp: suspensorium. (From Adriaens et al., 2001).

complete yolk-sac depletion. Although initially feeding on small invertebrates, the larvae quickly shift to piscivorous feeding, in the form of cannibalism (at 8 mm total length in several clariids): in *Clarias gariepinus* this is at three-and-a-half days after the onset of exogenous feeding, whereas in *Heterobranchus longifilis* this already starts one day after yolk sac resorption (Hecht and Appelbaum, 1988; Baras, 1999).

Finally, the feeding apparatus, including the digestive system, becomes completely functional (*phase 4*). Mouth opening is now assisted by the opercular mouth-opening system (Fig. 8.5E) which presumably plays a protagonistic role with the hyoid mechanisms. The start of this phase is also characterised by differentiation of the stomach, involving formation of a distinct pylorus, functional glandular cells and a pH that

has dropped below 5 (Stroband and Kroon, 1981). As both mouth opening and the digestive system are completely functional (as well as the other structures involved in feeding), the piscivorous behaviour of *Clarias* can be fully exploited at this stage.

An additional phase (*phase 5*) can be distinguished, which does not involve feeding, but is characterised by a shift in respiratory mechanisms. At 20 mm, the suprabranchial organ is formed, which allows aerial respiration (Greenwood, 1961; Haylor and Oyegunwa, 1993). This differentiation implies that a mechanism, different from the one for aquatic respiration is needed (Hellin and Chardon, 1983; Vandewalle and Chardon, 1991). As no new structures are formed at this stage, it appears that those apparatuses (both respiratory and feeding) present are sufficiently functional to allow aerial respiration, but presumably rely on a different mottor pattern.

Specialised Feeding Strategies in Catfishes

One of the striking features of catfish diversity, is the wide range of trophic niches that have become occupied. Some opportunistic feeders even show adaptations to different types of feeding mechanisms (Thomas, 1966). The plesiomorphic type can be considered a benthic, invertebrate larva feeder (confirmed by the feeding regime of Diplomystidae) (Arratia, 1987). As mentioned in the introduction, giving a complete overview of the phylogenetic pattern in feeding strategies is impossible at the present. Instead, some highly specialised feeding mechanisms (and related structures), especially the adaptations in algae scrapers are discussed. To provide some idea of the wide range of trophic specialisations, a brief overview of dentition morphology is given as an example.

Dentition

Specialised teeth can be found in many catfish lineages. The plesiomorphic condition in Siluriformes is to have simple, conical teeth, as observed in Diplomystidae (Alexander, 1965; Arratia, 1987; de Pinna, 1996). Both in Neotropical and African lineages, specialised teeth morphology can be observed, in relation to a presumed specialised feeding behaviour. Conical teeth may be simple or bear a broadened tip (Fig. 8.6A). In some sisorids, teeth are incisiviform with a concave upper margin (Fig. 8.6B). Jaws can be heterodont, bearing differently sized molariform teeth, as in some Bagridae (Jayaram, 1970). The most diverse tooth

morphology can be observed in algae-scraping species, where teeth are generally elongated. Teeth of Mochokidae are claw-like, the shape of the teeth being species-specific (Fig. 8.6C-D). In Loricariidae, teeth are generally Z-shaped, consisting of an attachment plate, a shaft and a crown. A wide range of variation can be observed in the size of the shaft and crown. The crown itself is generally bicuspid, with the two cusps iso- or heteromorphic, but may also be unicuspid in some species (Fig. 8.6E-K).

Cusp polymorphism has been found to involve certain jaw teeth, but not all (Schaefer and Stewart, 1993). In *Cochliodon* and *Panaque*, the teeth are spoon-shaped (Muller and Weber, 1992; Schaefer and Stewart, 1993). In loricariids, not only does the shape differ, but also the number of teeth shows a wide range. Within genus *Hypostomus*, the number may range from 6 to 125, and increase with increase in body size (Muller and Weber, 1992). An increase in tooth number is observed in catfishes that have additional tooth-plates (see above). The number, arrangement and especially degree of fusion between these plates, has been correlated to trophic guilds in some catfishes (Blaber et al., 1994).

Differences in tooth morphology and number may expectedly be related to small differences in algae-scraping kinematics, as adaptations to their way of feeding is rather convergent, i.e., by means of a rasp or a gouge (even compared with invertebrate scrapers) (Arens, 1994). Gouge-like teeth can also be observed in algae-scraping cichlids (Wautier-et al., 2002). For example, although largely similar to other loricariids, the spoon-like teeth of *Panaque* may be advantageous for their wood-eating behaviour, which can be regarded as a specialised form of scraping (Schaefer and Stewart, 1993).

In several lineages, the secondary loss of teeth has occurred independently. A lack of dentition on the oral jaws can be observed in some ictalurids (Lundberg, 1982), callichthyids (Huysseune and Sire, 1997; Reis, 1998), aspredinids (Friel and Lundberg, 1996; de Pinna, 1996), amphiliids (He et al., 1999) and auchenipterids (Vari et al., 1984). However, in all those species lacking oral teeth, the pharyngeal tooth battery is generally present.

Algae Scrapers

The South American Loricarioidea comprises a group of catfishes exhibiting a wide range of feeding behaviour: Astroblepidae and Trichomycteridae are presumed to be omnivorous, whereas Callichthyidae feed on benthic invertebrates. Nematogenyidae are carnivorous, feeding

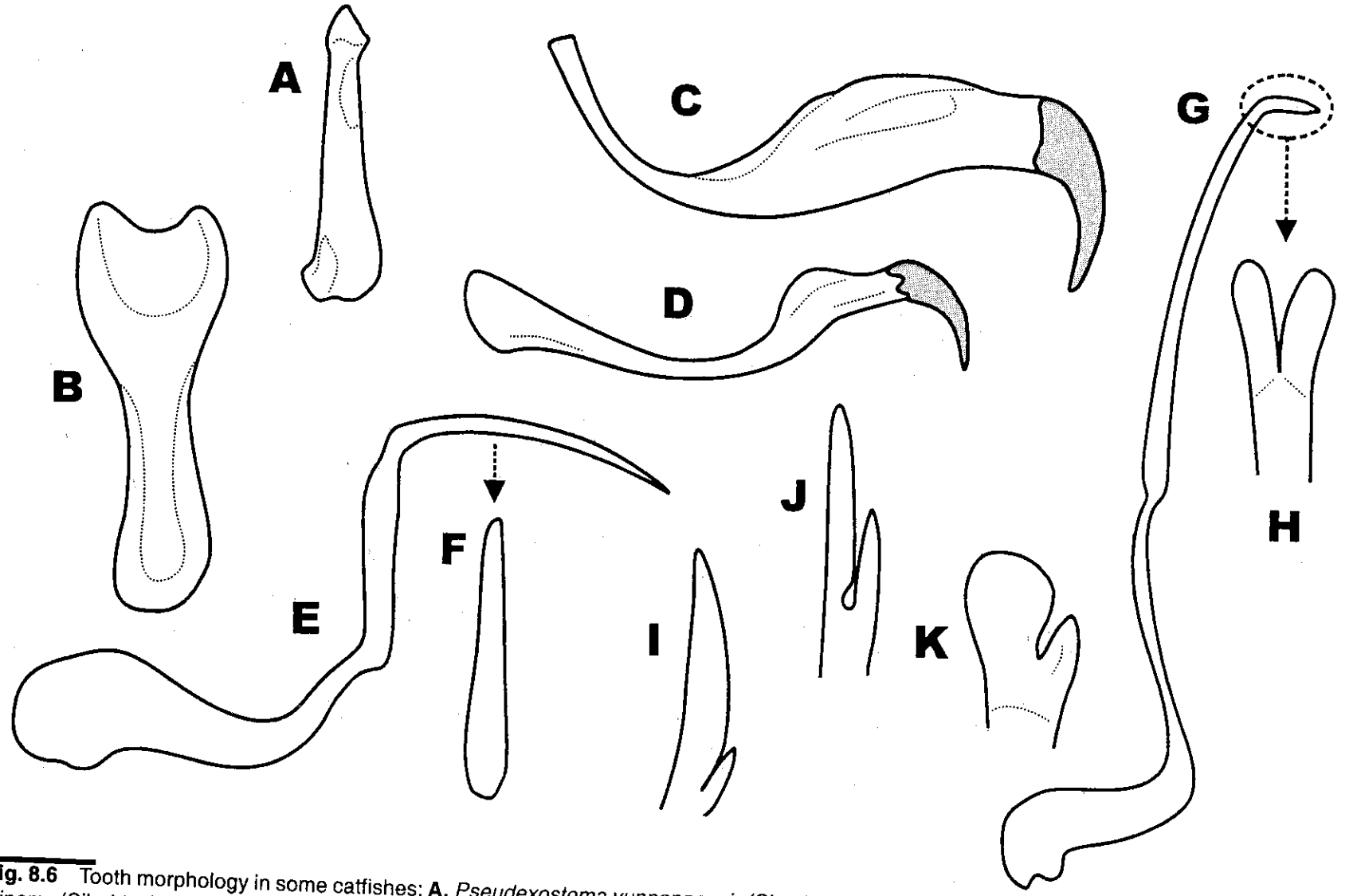

Fig. 8.6 Tooth morphology in some catfishes: **A.** *Pseudexostoma yunnannensis* (Sisoridae) (Redrawn from de Pinna, 1996); **B.** *Belodontichthys dinema* (Siluridae) (Redrawn from Howes and Fumihito, 1991); **C.** *Synodontis frontosus* (Mochokidae); **D.** *S. centralis* (Redrawn from Poll, 1971); **E-F.** *Ancistrus* sp. (Loricariidae); **G-H.** *A.* sp.; **I.** *Ancistrus bufonius*; **J.** *Chaetostoma lineopunctatum*; **K.** *A.* aff. *derbyi* (Redrawn from Muller and Weber, 1992).

on insects and crustaceans (Schaefer and Lauder, 1986; Arratia and Huaquín, 1995; Trajano, 1997; Aranha et al., 1998; Mérigoux and Ponton, 1998). For a phylogenetic relationship between these families, see de Pinna (1998). Loricariidae, in general, are known to be highly specialised benthic algae scrapers, which requires a substantial differentiation of the generalised feeding apparatus. Scraping behaviour may not only be for algae, but for the substrate itself as well (e.g., wood-eating *Panaque*) (Schaefer and Stewart, 1993). On the other hand, even though most are scrapers, Loricariidae show a wide range in teeth morphology and feeding-apparatus diversity. Other food types, including detritus, insect larvae, nematodes, molluscs and even fish, have been detected in the stomachs of some loricariids (Fugi et al., 1996; Aranha et al., 1998). As noted by Schaefer and Lauder (1986), it remains uncertain whether the typical transformations are a direct adaptation to a scraping behaviour, or are related to the ability of the fish to attach to the substrate by means of their sucker mouth.

The structural transformations of the feeding apparatus in loricarioids are believed to have occurred in several stages (Schaefer and Lauder, 1986; Schaefer, 1990). The plesiomorphic condition comprises a system wherein the adductor mandibulae complex is poorly differentiated and the premaxillary is firmly attached to the mesethmoid. Mouth opening occurs both through the hyoid linkage system (i.e., by means of the mandibulo-hyoid ligament) and the opercular four-bar system (i.e., by means of the interoperculo-mandibular ligament), and the protractor hyoidei muscle is undivided. The first stage in trophic specialisations involves decoupling of the premaxillary, which becomes highly mobile. Initial muscular control of this premaxillary becomes possible as a result of a dorsal extension of the lateral part of the adductor mandibulae complex and the shift in insertion of the retractor tentaculi, now both inserting on the ligamentous sheet between the lower jaw and maxillary bones (i.e., the primordial ligament). This configuration can be observed in Callichthyidae (Fig. 8.7) and represents the synapomorphic situation for Callichthyidae, Scoloplacidae, Astroblepidae and Loricariidae.

In the latter three groups, which represent one monophyletic lineage, decoupling of the maxillary bones is more pronounced: the retractor tentaculi inserts on the maxillary bone only, whereas the latter bone is no longer connected to the lower jaw through the primordial ligament. This increases the individual mobility of the premaxillaries, which can be moved independently due to the attachment of a separate m. adductor

dinema (Siluridae) (Redrawn from Howes and Fumihito, 1991); **C.** *Synodontis frontosus* (Mochokidae); **D.** *S. centralis* (Redrawn from Poll, 1971); **E-F.** *Ancistrus* sp. (Loricariidae); **G-H.** *A.* sp.; **I.** *Ancistrus bufonius*; **J.** *Chaetostoma lineopunctatum*; **K.** *A.* aff. *derbyi* (Redrawn from Muller and Weber, 1992).

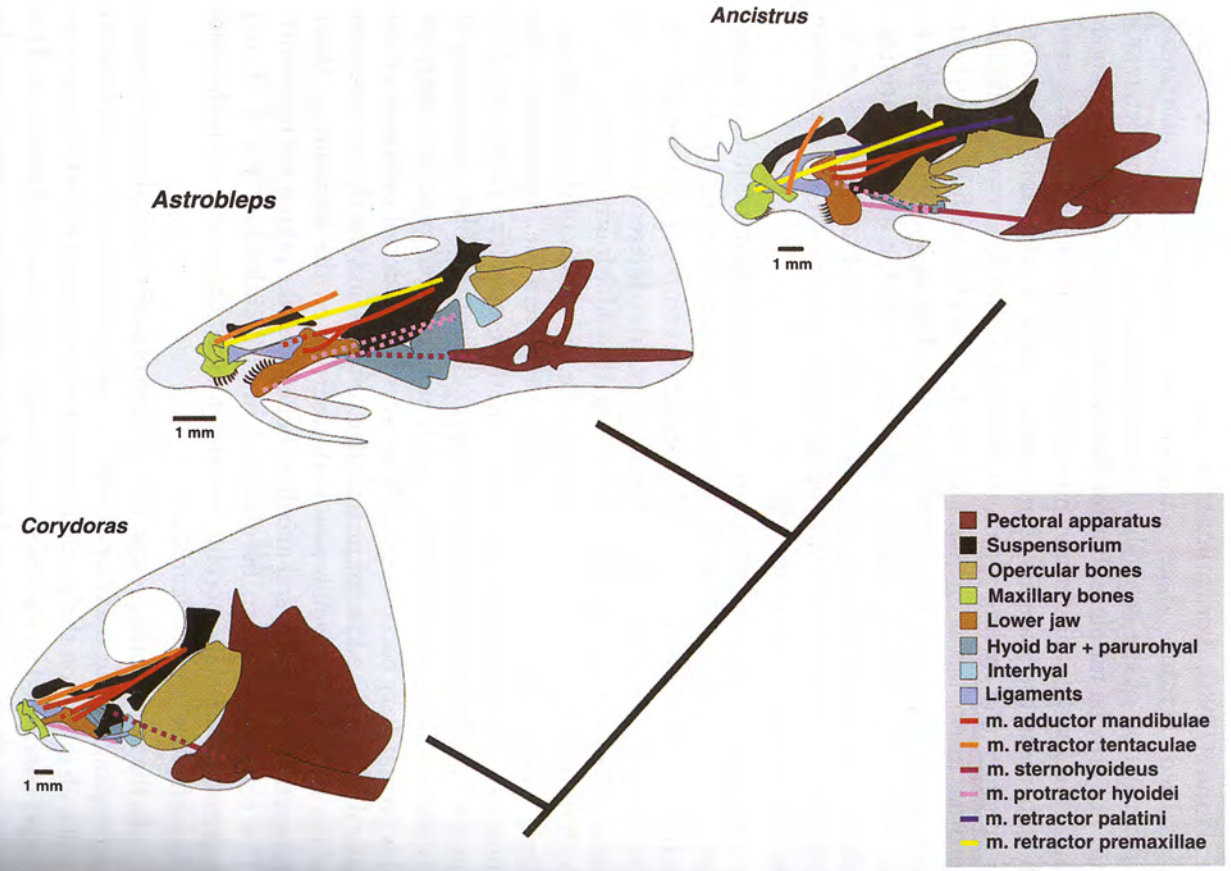

Fig. 8.7 Transformations in the feeding apparatus in Loricarioidea: **A.** *Corydoras* (Callichthyidae); **B.** *Astroblepus* (Astroblepidae), **C.** *Ancistrus* (Loricariidae) (Redrawn from Schaefer and Lauder, 1986; phylogeny based on de Pinna, 1998).

mandibulae subdivision directly onto the highly mobile premaxillary (i.e., retractor premaxillae or muscle c of Howes, 1983a) (Fig. 8.7). This set of specialisations characterises the Scoloplacidae and the Astroblepidae, whereas the Loricariidae even go one step further. Here, a separate muscle (derived from a subdivision of the adductor mandibulae complex) inserts onto the primordial ligament (i.e., the retractor palatini or muscle d of Howes, 1983a). This ligament thus interconnects the lower jaw, premaxillary bone and palantine. Another important transformation at this stage involves the loss of the interoperculo-mandibular ligament, thus annulling any possible action of the opercular mouth-opening system (Lauder, 1982). This is believed to improve the independent bilateral movements of the lower jaws, where in Astroblepidae and Loricariidae the two jaws are no longer firmly attached to each other through a symphysis but an intermandibular cartilaginous plug (Schaefer and Lauder, 1996). Formation of this plug is related to the subdivision of the protractor hyoidei muscle: the dorsal bundle attaches to the lower jaw, whereas the ventral bundle inserts on the cartilaginous plug, as well as on the lower jaw. In contrast to Astroblepidae, the intermandibular cartilaginous plug in Loricariidae is directly attached to the hyoid bar, thus establishing a unique coupling system between hyoid depression and mouth opening. This implies the presence of a double coupling system between the last two functions since a mandibulo-hyoid ligament is present as well (Schaefer and Lauder, 1986).

Scraping feeding behaviour has had implications for the respiratory mechanism as well, since apposition of the mouth against the substrate, while maintaining a suction force, disables expansive actions of the buccal cavity. However, as a result of decoupling of the mandibular rami, they can be moved independent of each other, thus allowing lateral displacement (Vandewalle et al., 1986). This lateral displacement creates a small furrow at the corner of the mouth gape, through which inhalation water can enter. In these fishes, mouth closure is established by an enlarged valve (small valves are present in most teleosts), which prevents water (containing food) escaping from the buccal cavity. All these factors presumably decrease the water influx rate during respiration, compared to other catfishes (see below).

Parasitic Behaviour

Blood parasitism is found in at least two subfamilies of the Trichomycteridae (Stegophilinae and Vandellinae) (Kelley, 1964; Burgess,

Fig. 8.7 Transformations in the feeding apparatus in Loricarioidea: **A.** *Corydoras* (Callichthyidae); **B.** *Astroblepus* (Astroblepidae), **C.** *Ancistrus* (Loricariidae) (Redrawn from Schaefer and Lauder, 1986; phylogeny based on de Pinna, 1998).

1989). Some Cetopsidae are sometimes considered parasitic; however, they are merely scavengers (de Pinna and Vari, 1995). Field observations suggested a feeding mechanism quite similar to that of agnathans: the mouth is used as a sucking apparatus while the long teeth in the middle part of the upper jaw rasp away tissue (Kelley, 1964). Enlarged teeth can also be observed in the middle of the lower jaw in some cetopsids, where they are attached to a process protruding into the mouth cavity (Fig. 8.8A) (Ferraris, 1996). In trichomycterids and cetopsids in general, the mouth is inferior and wide, thus allowing formation of a sucker mouth. *Vandellia* or "candiru" is the only vertebrate parasite of humans. This species is notorious for its parasitic behaviour, as it enters all kinds of orifices of wading mammals (including humans). It has been known to swim up to the urethra of urinating people, possibly mistaking the urine for exhalation water of fish gills. Having entered, it attaches inside the organ by means of erectable opercular and interopercular spines (a mechanism responsible for spine erection during display in loricariids and other trichomycterids). In general, these fish enter the ventilating gill cavity of fishes through the gill slit, where they attach themselves to the gills while feeding on them (Fig. 8.8B) (Kelley, 1964). As expected, the whole habitus of this species is adapted to such a behaviour, as it is comparable to that of lampreys.

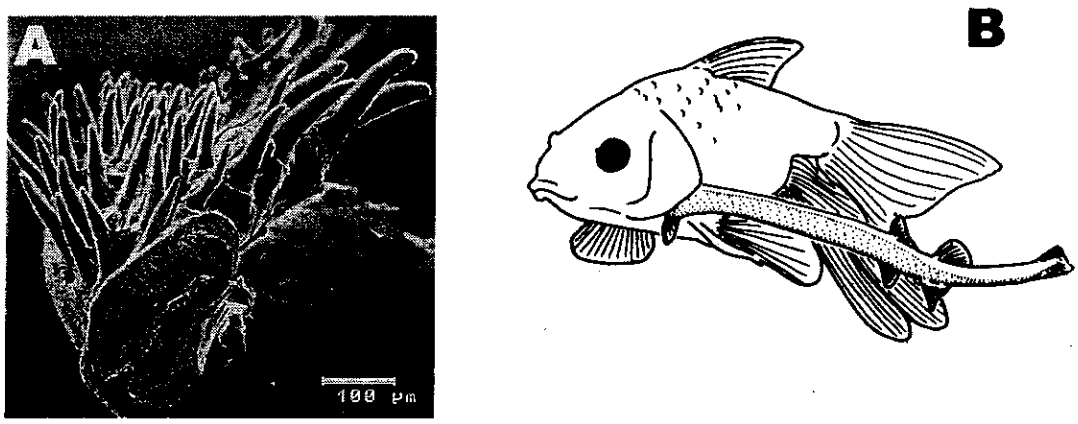

Fig. 8.8 Parasitic feeding behaviour in catfishes: **A.** SEM of enlarged mandibular teeth in *Denticetopsis sauli* (Modified with permission of author and the Californian Academy of Sciences, from Ferraris, 1996); **B.** *Vandellia* sp. feeding on the gills in a goldfish (Redrawn from Kelley, 1964).

LIFE HISTORY AND ECOLOGICAL CONSTRAINTS

As expected, the life history of catfishes, and especially the trophic niches they occupy, is driven by many specific ecological constraints, for example

food availability (both in biomass as well as food type). Adaptations related to occupancy of these specific trophic niches will undoubtedly have an impact on non-trophic aspects, just as non-trophic related constraints will have an impact on the evolution of the feeding apparatus. Some examples are given.

The size range in catfishes, which has an overall impact on the catfish "Bauplan", will have a constraining influence on the kind of trophic niche that can be occupied and therefore, on the feeding mechanisms as well. This is not only the case during ontogeny, but also in the adult stage. Miniature catfishes, for example some Aspredinidae (e.g., max. standard length of 16 mm in mature *Micromyzon*) will have a much more constrained feeding regime than most moderately sized catfishes, whereas the spectrum in large species like some clariids, claroteids, pangasiids and 'pimelodids' will be even larger (Burgess, 1989; Ng, 1992; Friel, 1995; Friel and Lundberg, 1996; Barthem and Goulding, 1997). Size increase, however, does not always imply a shift to larger prey. The large size of *Clarias gariepinus*, has allowed a very opportunistic feeding regime, including filter feeding (by means of large and numerous gill rakers) (Teugels, 1986), phytophagic feeding, benthic feeding, and also piscivorous feeding (Groenewald, 1964; Thomas, 1966). An ontogenetic shift in body size and shape has also been coupled to changes in diet (Mérigoux and Ponton, 1998).

Although many catfishes can be classified as generalised carnivores, feeding on aquatic insects, many trophic specialisations have arisen independently in several lineages. This is demonstrated for example, by the occurrence of resource partitioning of different catfishes (and other fishes) in the same river (Aranha et al., 1998). The life history of these groups suggests that trophic specialisations not only have large implications on other functional systems, but are frequently strongly linked. A good example are the Neotropical Loricariidae. One can consider the driving force to the selection for a sucker mouth in these fishes to be an adaptation to living in strong currents. These transformations would have allowed a feeding mechanism, by which algae could be scraped from a substrate. This niche of algae scraping appears to be nutritionally valuable and could thus explain why the largest diversity in catfishes exists in the Loricariidae (Isbrücker, 1980; Power, 1984). Convergent structural adaptations, linking a sucker mouth to both living in torrential rivers and having a scraping feeding behaviour, have also been observed in some African Amphiliidae and Mochokidae (Diogo et

al., 2000). A similar selection for an adhesive function of the pectoral girdle has been found in some sisorid catfishes inhabiting similar rivers (Saxena and Chandy, 1966). A plausible scenario, of course, is that algae scraping occurred first, thereby enabling colonisation of strong currents. An argument against this hypothesis is that such a suction mouth is not necessary to live in torrential streams, since for example loricarioid and non-loricaroid catfishes can be found in the same river (Fernández and Aquino, 1993). Further research is needed to understand the evolution of the sucker mouth.

As mentioned above, scraping feeding behaviour may impose some constraints on the respiratory mechanism, which could have resulted in the formation of accessory respiratory organs in loricariids (i.e., stomach respiration). However, since accessory respiratory organs have evolved independently in other lineages (e.g., suprabranchial organ in clariids, modifications of different parts of the digestive tract in callichthyids and scoloplacids, or the swim bladder in pangasiids), which do not exhibit scraping feeding behaviour, other factors are involved as well (Datta Munshi, 1961; Browman and Kramer, 1985; Graham, 1997; Armbruster, 1998). The presence of accessory respiratory organs may also have evolved as an adaptation to living in aquatic environments, which experience seasonal deoxygenation (Helfman et al., 1997). Such fluctuations, whether seasonal or even diel, have a tremendous impact on the feeding ecology of many catfishes. Feeding activity is known to be synchronised with circadian alternation of light and dark regimes (and not oxygen levels), reflected in the nocturnal activity of most catfishes (Boujard et al., 1990; Fugi et al., 1996). In that way, predator avoidance behaviour plays a crucial role in feeding behaviour (Power, 1984). Seasonal fluctuations are known to influence the food supply available for several catfishes (Power, 1984; Fugi et al., 1996; Trajano, 1997). As a response to these fluctuations, the migratory behaviour of some catfishes (including 'pimelodids') presumably eliminates the necessity for a highly specialised feeding mechanism and behaviour, as opposed to, for example, non-migrating Loricariidae.

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