

Spawning in *Ancistrus* (Siluriformes: Loricariidae) with comments on the evolution of snout tentacles as a novel reproductive strategy: larval mimicry

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Most species of *Ancistrus* exhibit a striking sexual dimorphism, mature males having an elaborate complex of enlarged fleshy tentacles on the snouts. Snout tentacles appear to be modifications of the fleshy cutaneous sheath that surrounds the base of an odontode (integumentary tooth) and are best developed in breeding males. The tentacles are thought to serve as accessory sensory structures because they are covered with taste buds. We propose an additional function related to reproductive biology. Male *Ancistrus* guard eggs and larvae for up to 10 days after hatching in a cavity nest. In several cavity-nesting fishes with paternal care, females preferentially spawn with males guarding eggs over males in empty nests, and this preference has led to the evolution of deceptive mating strategies whereby males with empty nests can compete successfully with males guarding eggs. We hypothesize that female *Ancistrus* preferentially spawn with males guarding larvae, and that the male's snout tentacles stimulate this bias by mimicking the presence of larvae in an otherwise empty nest. We also provide information on our field observations of *Ancistrus* spawning in the río Aguaro, a tributary of the río Orinoco in central Venezuela.

Introduction

Loricariidae is a large family (about 600 species and 70 genera) of catfishes distributed from Costa Rica to northern Argentina and characterized by a body covering of bony plates and a ventral suckorial mouth (Isbrücker, 1980). Loricariids exhibit a variety of reproductive behaviors and strategies including cavity spawning (Moodie & Power, 1982), attachment of eggs to the under-surface of rocks (Page et al., 1993) and egg-carrying (Taylor, 1983). In many species, parental care

is well-developed and the male guards eggs and sometimes larvae. Considerable sexual dimorphism occurs in loricariids and is most pronounced during the breeding season (Isbrücker & Nijssen, 1992; Armbruster & Page, 1996). In *Loricariichthys*, for example, the male holds a clutch of eggs in a large membranous expansion of his lower lip (Taylor, 1983). In this example, the function of the sexually specific structure is evident; however, the significance of sexually dimorphic traits in most loricariids is unclear.

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Particularly intriguing is sexual dimorphism in *Ancistrus*, commonly known as bristle-nosed catfishes or plecós. *Ancistrus* is a large genus (ca. 57 species) in the subfamily Ancistrinae (Isbrücker, 1980), a group of loricariids with sharp evertible cheek spines (elongate odontodes or integumentary teeth). In *Ancistrus*, as in nearly all Ancistrinae, the cheek spines often are more developed in males (Regan, 1904; Isbrücker & Nijssen, 1992; pers. obs.) and are used in agonistic displays and combat (Burgess, 1989; Buck & Sazima, 1995). *Ancistrus* is distinguished by another sexually dimorphic feature unique among loricariids: mature males in most species have conspicuous fleshy tentacles on their snouts. Snout tentacles also occur in females and juveniles, but are generally much smaller, fewer, and more restricted in distribution.

Despite extensive documentation of their occurrence, there are very few published hypotheses about the function of snout tentacles. Breder & Rosen (1966) noted that "nothing is known of the significance of any of the [sexually dimorphic] structures" in *Ancistrus*, and Burgess (1989) commented that "the use of such tentacles is theorized by some to have to do with sensing the speed and direction of the currents and perhaps even with detecting odors". Ono (1980) found snout tentacles to be covered with taste buds and hypothesized that they evolved as additional sensory structures increasing surface area for the detection of gustatory stimuli; however, he also discovered in *Ancistrus* and other loricariids, that taste buds cover almost the entire surface of the body and fin spines. The use of snout tentacles as sensory structures does not adequately explain their tremendous sexual dimorphism and their putative role as secondary sexual traits needs to be explored.

We hypothesize that snout tentacles serve an additional function related to the reproductive biology of *Ancistrus*. In *Ancistrus*, the male guards a cavity in wood or rock where he spawns with one or more females and provides subsequent care for eggs and larvae (Burgess, 1989; pers. obs.). In a variety of fishes where the male cares for eggs in a nest, females show a strong preference for males whose nests already contain eggs (see Kraak & Weissing, 1996). In response, some species have evolved deceptive mating strategies whereby males with empty nests can compete successfully with males guarding eggs (Knapp & Sargent, 1989). We hypothesize that female *An-*

cistrus prefer to spawn with males whose nests already contain larvae, and that males have evolved snout tentacles as larval mimics in response to this preference.

The objectives of this paper are to provide a general description of snout tentacles and related structures, comment on their evolution, and summarize what is known on the reproductive biology of *Ancistrus*. We also review reproductive strategies in a variety of cavity-nesting species with paternal care and discuss our hypothesis for the use of snout tentacles in *Ancistrus* as a novel strategy: larval mimicry.

Materials and methods

Morphological descriptions are based on specimens of *Ancistrus* from Argentina, Bolivia, Panama, Peru, and Venezuela. Collection information is given for specimens cited. A list of additional loricariids examined can be found in Armbruster (1998). Specimens of *Ancistrus* were not identified to species because this large genus is in need of taxonomic revision. Unidentified species are referred to by number when appropriate (e.g., *Ancistrus* sp. 1). Measurements of standard length (SL) were made according to Boeseman (1968) using an ocular micrometer (larval specimens <20 mm SL) or dial calipers. Institutional abbreviations are as in Leviton et al. (1985).

Results

General morphology. Valenciennes (in Cuvier & Valenciennes, 1840: 513) reported d'Orbigny's observation that tentacles are less developed in juveniles. Valenciennes alternatively referred to these structures as tentacles, cirri, and filaments. All of these terms have been used interchangeably in subsequent species descriptions. Additional references to these structures include dendritic appendages (Breder & Rosen, 1966), rostral cutaneous processes (Ono, 1980), and fleshy protuberances (Schaefer, 1986). The term tentacles is most often applied and is used throughout this paper. We introduce a new term, tentacules, to refer specifically to tentacles that occur in direct association with odontodes.

Kner (1854) described the genus *Ancistrus* and was the first to recognize that snout tentacles are sexually dimorphic and best developed in ma-

ture males. A diagnostic character for *Ancistrus* is the lack of bony plates along the snout margin (Schaefer, 1986; Armbruster, 1997) which is covered with a thickened layer of epidermis (Ono, 1980). In males, the unplated area is expanded over much of the snout, and in some species, ends just anterior to the nares and orbits. Ono (1980) referred to this region as a "sensory shield" because it is covered with taste buds. In females and sometimes juvenile males, the unplated area is restricted to a narrow band encircling the entire snout margin.

Snout tentacles occur in the unplated areas in both males and females. In males, the pattern of tentacle distribution can be divided roughly into five regions (Fig. 1). Tentacles occur in one (sometimes two) rows on the snout margin. On each side of the head this marginal band can be separated into anterior and posterior regions where the groove between the snout and the dorsal surface of the lip ends anterodorsally (separation most distinct in mature males). At the evertible cheek plates, tentacles continue obliquely in an irregular row towards the anterior rim of the eye. On the dorsomedial surface of the snout, tentacles begin in a single row nearest the snout tip and finish posteriorly in two paired rows which diverge to form a Y-shaped pattern. Tentacles are generally absent from the unplated dorsolateral regions of the snout on either side of the medial row of tentacles. In these areas, the skin appears thickened, swollen, and extremely rugose. In females and juveniles, tentacles are largely confined to the snout margin; occasionally, one or two tentacles occur in the region just anterior to the evertible cheek plates.

In males, tentacles in the medial row on the dorsal surface of the snout are generally largest, most branched, and sometimes joined at their bases (Fig. 2a-b). The tentacles in the marginal band near the tip of the snout are also large and often branched. Tentacles are smaller and usually simple (unbranched) along the snout margin near the evertible cheek spines, becoming smallest in the oblique row extending towards the eye. The tentacles are pigmented much the same as the rest of the body and, in some species, have large yellow or white spots. Tentacles are much smaller, less numerous and usually simple or weakly branched in females (Fig. 2c) and juveniles.

Snout tentacles generally become larger, more branched and more numerous in larger speci-

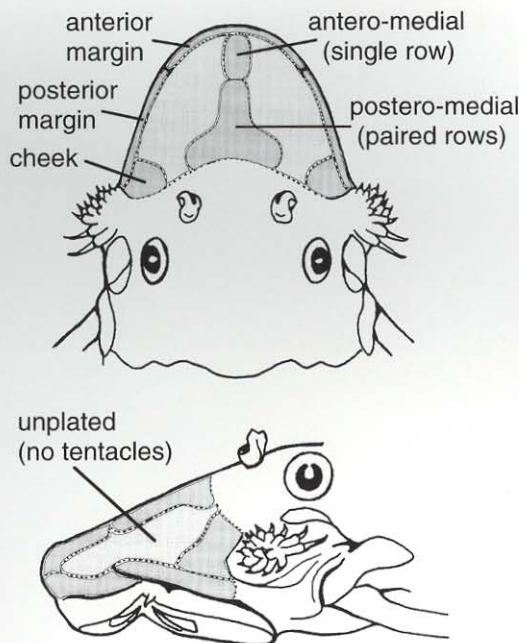


Fig. 1. Head of male *Ancistrus* showing unplated area of snout (stippled) and regions where snout tentacles generally occur (darker stippling; tentacles not shown). a, dorsal view; b, lateral view.

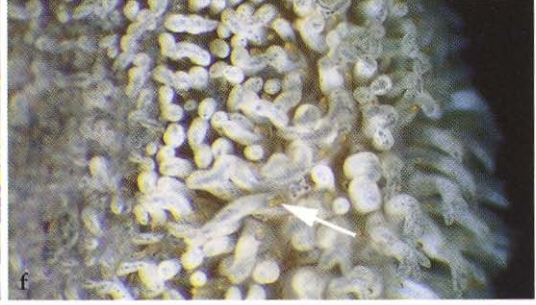
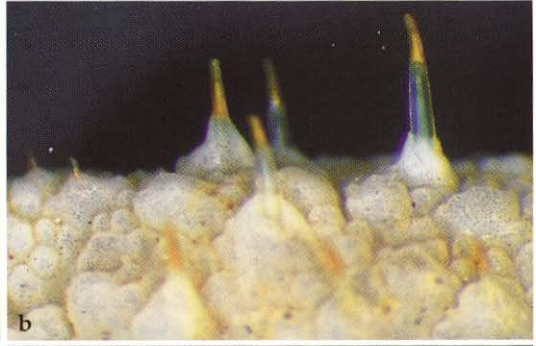
mens and are especially well-developed in breeding males. The size of mature males ranges considerably among species of *Ancistrus*. The largest male examined (*Ancistrus* sp. 1, INHS 39771; Fig. 2e) measured 159.1 mm SL. The smallest mature male (*Ancistrus* sp. 2, INHS 35367) measured only 47.8 mm SL, but had well-developed testes and tentacles. Two larger conspecific males (48.1, 61.7 mm SL) from the same collection (INHS 35367) had very small, weakly developed tentacles and undifferentiated testes, suggesting a relationship between reproductive condition (i.e., gonadal size) and tentacle development. Burgess (1989) commented that the tentacles may grow larger during the spawning season and decrease in size after the season is over, but he did not cite specific evidence.

In at least one species, *Ancistrus* sp. 3, the snout tentacles are not conspicuously developed even among large males in breeding condition (Fig. 2d). Specimens from the río Apure basin of Venezuela (INHS 27764, 31858) include large males (up to 104.0 mm SL) with well-developed testes that were collected with females bearing



Fig. 2. Variation in snout tentacles in species of *Ancistrus*. **a**, dorsal view of head of breeding male *Ancistrus* sp. 4 removed from cavity nest with eggs, INHS 36334, 78.1 mm SL; **b**, male *Ancistrus* sp. 5 with well developed tentacles, INHS 39005, 110.6 mm SL; **c**, female, *Ancistrus* sp. 1, INHS 39004, 108.7 mm SL, same collection as b; **d**, male *Ancistrus* sp. 3 with poorly developed tentacles, INHS 27764, 104.0 mm SL; **e**, lateral view of large male *Ancistrus* sp. 1, INHS 39771, 159.1 mm SL. (Photographs K. S. Cummings).

Fig. 3. **a**, Juvenile *Ancistrus* sp. 4, INHS 34357, 18.81 mm SL, showing cutaneous sheaths (arrow) in which \triangleright hypertrophied cheek odontodes develop; **b**, snout odontodes in *Isbrueckerichthys duseni*, UMMZ 215262, 88.8 mm SL; **c**, cheek spines in male *Ancistrus* sp. 5, INHS 39005, 127.7 mm SL; **d**, pectoral-fin spine odontodes in *Cochliodon plecostomoides*, INHS 34067, 226.0 mm SL; **e**, snout odontodes in *Dekeyseria scaphirhyncha*, INHS 61500, 133.9 mm SL, with free distal portion of cutaneous sheath appearing as small tentacule (arrow); **f**, snout odontodes (arrow) dwarfed by associated tentacles in male *Lasiancistrus* sp. 1, INHS 28650, 110.4 mm SL; **g**, dorsal view of head of *Lasiancistrus* sp. 1 (same specimen as f). (Photographs M. H. Sabaj [a-f], K. S. Cummings [g]).



ripe eggs. The unplated area of the snout is expanded posteriorly in mature males of *Ancistrus* sp. 3, and tentacles occur in each of the five regions as in other *Ancistrus*. However, the tentacles are very small and relatively inconspicuous.

Tentacles (i.e., small tentacles directly associated with odontodes) occur on the pectoral-fin spines in some *Ancistrus* species. The fin tentacles are best developed in males on the dorsal surface just before the fin tip where the epidermis is especially thickened. Pectoral-fin tentacles measure up to 4.5 mm long (*Ancistrus* sp. 1, INHS 39004, 138.7 mm SL) and are fairly conspicuous in some large specimens. The tentacles arise along the sides and in the axil of the odontodes which are angled towards the fin tip. When a single large tentacle arises in the axil, its base often engulfs that of the odontode which appears to erupt from the side of the tentacle. Odontodes on the dorsodistal portions of the pectoral-fin spines become inconspicuous among the larger and more crowded tentacles. Tentacles have not been observed on the pelvic-fin spines; however the epidermis does appear thickened and small papillae occur among the odontodes. Fin tentacles also occur in females and juveniles but are much smaller and less numerous.

Snout tentacles and fin tentacles appear to be modifications of the fleshy cutaneous sheath that surrounds the base of an odontode and presumably facilitates its formation. In loricariids, odontodes can develop almost anywhere on the external surface of the body (e.g., plates, exposed bones, fin spines and rays) and first appear soon after hatching (present in yolk sac larvae in *Ancistrus* and *Rineloricaria* Bleeker, pers. obs.). Like snout tentacles, odontodes occur in a tremendous variety of shapes and sizes, and are often sexually dimorphic, becoming larger in nuptial males as breeding odontodes (Isbrücker & Nijssen, 1992; Armbruster & Page, 1996). In *Ancistrus*, Ono (1980) found taste buds associated with the cutaneous sheath that surrounds cheek spines (elongate odontodes) and odontodes on all fin spines. He hypothesized that the hard odontodes provided protection for the nearby sensory receptors which, in *Ancistrus* and other loricariids, cover almost the entire surface of the body and fin spines.

The cutaneous sheath that surrounds an incipient odontode (Fig. 3a) may be homologous to an enamel organ, the epidermal structure which forms the enamel crown of vertebrate teeth and

the exposed surfaces (i.e., spines) of placoid scales in elasmobranchs (Barghusen & Hopson, 1979; Krejsa, 1979). During an odontode's formation, its sharp tip eventually pierces the cutaneous sheath. In some instances, the odontode erupts through the tip of the fleshy sheath which then persists either as a short basal collar (e.g., snout odontodes in *Isbrueckerichthys* Derijst; Fig. 3b) or a longer sleeve around the shaft of the odontode. Examples of the latter condition are the cheek spines in *Ancistrus* (Fig. 3c), and odontodes on the pectoral-fin spines in *Cochliodon* Heckel (Fig. 3d). Alternatively, the odontode may erupt subterminally leaving the terminal portion of the sheath intact as a small tentacle. This tentacle may persist free from or adhered to the odontode shaft; however, in either case, the odontode is generally much longer than the sheath and remains the dominant feature (e.g., snout odontodes in *Dekeyseria* Rapp Py-Daniel; Fig. 3e). The elongate snout and pectoral-fin odontodes in *Lasiancistrus* Regan exhibit yet another condition: the odontodes erupt from the base of the cutaneous sheath leaving the associated tentacle almost entirely intact (Fig. 3f). In mature male *Lasiancistrus*, the enlarged tentacles often dwarf their associated odontodes and many are branched. Based in part on the presence of enlarged snout tentacles in *Lasiancistrus* (Fig. 3f-g) and snout tentacles in *Ancistrus* (Fig. 2a-b, e), Armbruster (1997) suggested that *Lasiancistrus* and *Ancistrus* are related as sister taxa.

The evolution of snout tentacles in loricariids (Fig. 4) is hypothesized to be as follows: first, the distal portion of the fleshy cutaneous sheath became separated from its supporting odontode (as in *Dekeyseria*). Eventually, the free portion of the sheath became longer and branched as the odontode began to erupt near its base (*Lasiancistrus*). Next, the odontodes and plates along the snout margin were lost (female *Ancistrus*). The cutaneous sheaths persisted as small fleshy tentacles disassociated from odontode formation, and possibly were retained as accessory sensory structures as proposed by Ono (1980). Finally, the unplated area expanded posteriorly over the snout in male *Ancistrus* and facilitated the development of the medial rows of tentacles. The more salient development of snout tentacles in mature males during the breeding season suggests that these structures have adopted a novel function whose evolution is influenced by sexual selection.

This mode of evolution for snout tentacles is

supported by the occasional presence on evertible cheek plates of tentacle-like structures that are as long as the surrounding hypertrophied odontodes. A particularly compelling example is a paratype of *Scobinancistrus aureatus* Burgess (AMNH 217762, 209.9 mm SL) which lacks odontodes on the evertible plates, but retains tentacles similar in size and number to the cheek odontodes in other specimens of *Scobinancistrus* Isbrücker & Nijssen.

Reproductive biology. The earliest record of spawning in *Ancistrus* appears in the description of *A. cirrhosus* by Valenciennes (in Cuvier & Valenciennes, 1840: 514) who reported d'Orbigny's field observations that this species attaches its eggs under rocks with a "gluten". *Ancistrus* readily spawns in captivity and much of the following information on their reproduction is derived from published aquarium observations (e.g., Burgess, 1989; Schopf, 1991; Cerny, 1996; Neal, 1996; Teague, 1996).

Ancistrus is a cavity-nester. The male typically selects a dark cavity in wood or rock as a nest site. In aquaria, a male will nest in clay flowerpots and bamboo tubes or excavate a cavity beneath a flat stone or driftwood placed over sand or fine gravel. The nesting male is territorial and guards the site against all intruders, especially conspecific males. The male may clean the cavity with his mouth and, eventually, allows females to approach and inspect the nest. Courtship consists largely of displays of raised dorsal and caudal fins, and leading behaviors whereby the male attempts to escort the female back to his nest.

At times during courtship the female may remain in the nest cavity to inspect the nest site and clean it with her mouth. While she is in the cavity, there is a great deal of contact between the pair as the male arches his body over hers. If the female leaves the nest, the male may follow and resume leading behaviors. If she chooses to spawn, the male fertilizes the eggs as they are released, while constantly prodding her with his snout. The female deposits a clump of 20-200 eggs usually on the ceiling but also on the sides and floor of the cavity. The eggs are about 2-3.2 mm in diameter, adhesive, and yellowish orange. The spawning act may be repeated until the female releases all of her eggs. After oviposition, the female either leaves the nest or is forcibly evicted, and takes no more interest in eggs or fry.

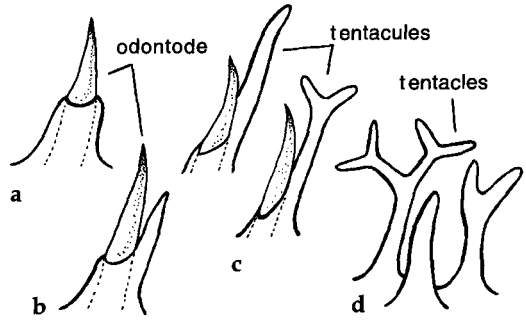


Fig. 4. Hypothesized evolution of snout tentacles. **a**, odontode with fleshy basal collar (e.g., snout odontodes in *Isbrueckerichthys*); **b**, odontode with small distal tentacle (e.g., snout odontodes in *Dekeyseria*); **c**, odontodes with large basal tentacles which sometimes are branched (e.g., snout odontodes in *Lasiancistrus*); **d**, odontode lost, large fleshy tentacles persist (e.g., snout tentacles in *Ancistrus*).

Male *Ancistrus* care for eggs and fry in the nest cavity. A male uses his fins and mouth to clean the eggs and clear the cavity of detritus. He aerates the clutch by fanning it with his pectoral fins, and may inspect it to remove infertile or diseased eggs. According to several accounts (Burgess, 1989; Schopf, 1991; Neal, 1996), parental males seldom leave their brood and either do not feed or only occasionally take food and quickly return to the nest. The eggs hatch in 4-10 days, over a 2-6 hour period, depending on incubation temperature and possibly species. The yolk sac larvae remain clustered and attached by their mouths to the ceiling and sides of the cavity. The yolk sacs are absorbed 2-4 days after hatching, and the fry become free swimming. The fry remain grouped together in the nest cavity where they are guarded by the male for 7-10 days after hatching (Fig. 5).

Nesting males are extremely territorial and aggressively defend the nest cavity from rival males and potential predators. A nesting male and an intruder may engage in agonistic displays during which the two fish remain parallel, head to tail, with their dorsal and caudal fins raised and cheek spines everted. If escalated to combat, the two males may circle each other while directing attacks at their opponent's head. If a non-nesting male successfully evicts a parental male from his nest, the usurping male may cannibalize eggs guarded by the parental male (Teague, 1996).

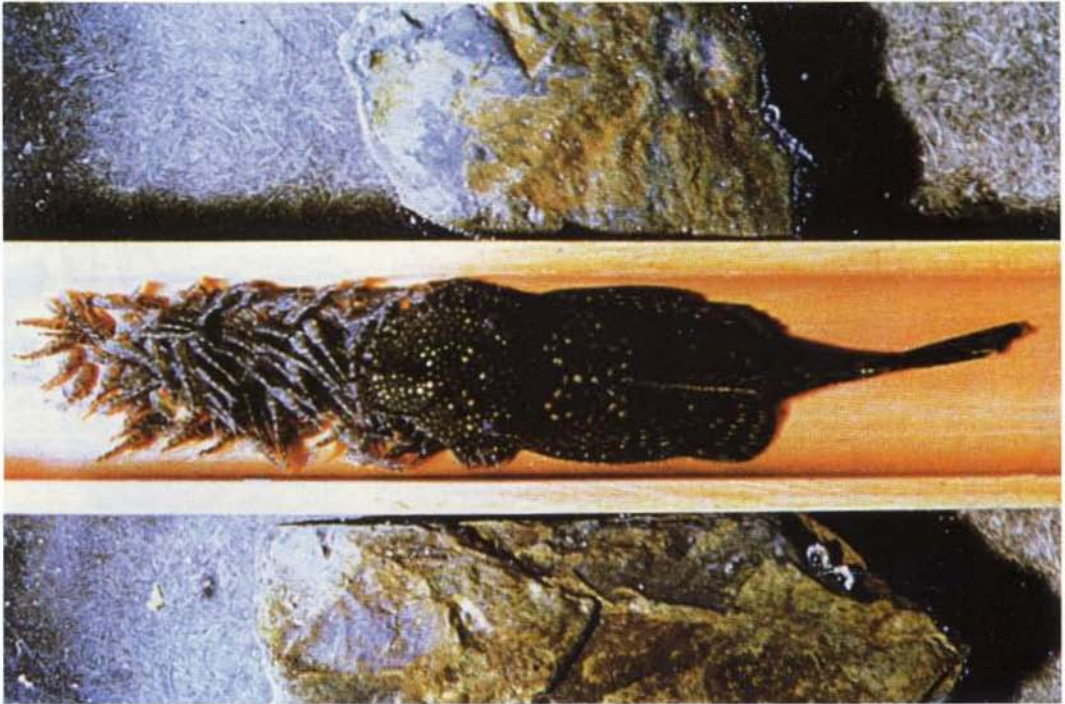


Fig. 5. Male *Ancistrus* sp. indet. guarding school of larvae clustered together in a cavity nest formed by a section of tubing (photograph H. J. Franke).

In an aquarium, a male will spawn repeatedly with multiple females and care for clutches of eggs and fry simultaneously; however, there are no detailed accounts of *Ancistrus* spawning in nature. We collected nesting males of *Ancistrus* sp. 4 on 10 January 1995 (middle dry season) in the río Aguaro, a tributary of the río Orinoco in the savannas of central Venezuela. The río Aguaro, where sampled, was a small (about 8 m wide) clear stream. The site consisted of a large upstream pool followed by a long riffle with substrates dominated by large lateritic boulders. The swiftest flowing areas were highly vegetated with submerged macrophytes. Below the riffle was a long pool with a bottom of sand and mud. While collecting, we removed several lateritic boulders to search for catfishes that might be hiding in holes in the rock. Lateritic material is remarkably porous because during its formation in wet tropical climates, the soluble components of the parent rock are dissolved away creating numerous cavities and crevices (Strahler, 1975).

In a large boulder removed from a slowly flowing riffle, two males of *Ancistrus* sp. 4 were

found guarding the entrances of separate cavities. The nest cavity of the larger male (INHS 36334, 78.1 mm SL) contained a number of yolk sac larvae (7.0-7.4 mm SL, 9.2-9.6 mm TL, n=3 preserved). Their yolk sacs were moderately large (ca. 37% SL), and all fins were well developed (Fig. 6a). Dentary teeth were absent and premaxillary teeth were barely noticeable as 2-5 thin sharp structures per ramus. Minute particles of red laterite were found in the buccal cavity, on the upper oral disk, and on the snout suggesting that the yolk sac larvae were securely attached to the cavity walls when captured. Several larvae were kept alive for up to a week after collection. After 3 days, the larvae (9.7-9.8 mm SL, 13.5-13.6 mm TL, n=2) had absorbed their yolk sacs and were almost uniformly brown except for a thin tan saddle at the base of the dorsal-fin spine. Fins were clear with brown markings. Small sharp odontodes occurred on the head, caudal region, and fin spines and their teeth (11-14 per ramus) had developed the bicuspid mitten-shape characteristic of many loricariids (Muller & Weber, 1992). After 7 days, the opercle was well defined,



Fig. 6. Larvae of *Ancistrus* sp. 4. a, lateral view of yolk sac larva, INHS 36334, 7.4 mm SL, removed from cavity nest of male shown in Fig. 2a; b-c, lateral and dorsal view of older larva, ca. 7 days, INHS 36333, 10.6 mm SL, removed from second nest.

but there was little evidence of cheek spines (10.6-10.8 mm SL, 13.8-14.9 mm TL, n=2).

The nest cavity of the smaller male (INHS 36333, 63.7 mm SL) contained larvae and a clump of adhesive eggs. Growth rates observed in the

first nest's larvae suggest that the second nest contained larvae of two age classes. One larva from the second nest measured 9.2 mm SL (~2-3 days old), and a second measured 10.6 mm SL (~7 days old, Fig. 6b, c). Both larvae had ab-

sorbed their yolk sacs and were apparently free swimming (no laterite dust on mouth and snout). The eggs were 2.9-3.2 mm in diameter ($n=4$) and the embryos had developed eyes and pectoral-fin buds. Our field observations corroborate aquarium observations that show larvae remain associated with the nest cavity and parental male for at least a week after hatching.

Discussion

Few hypotheses have been published on the potential function or significance of snout tentacles in *Ancistrus*. Ono (1980) found snout tentacles to be covered with taste buds and hypothesized that they evolved as additional sensory structures increasing surface area for the detection of gustatory stimuli; however, he also noted that taste buds cover almost the entire external body surface of *Ancistrus*. Burgess (1989) similarly speculated that tentacles may be used to detect odors or water currents. Additional hypotheses are that the tentacles serve as accessory respiratory organs (Taphorn, pers. comm.) or as a reverse gill provisioning oxygen to eggs and larvae; however, *Ancistrus* breathes air under hypoxic conditions (Gee, 1976) and presumably uses pectoral-fin fanning to aerate its eggs. The tentacles may be used to keep the attached eggs free of silt and detritus; however, based on aquarium observations, males accomplish this using their mouth and fins. These hypotheses and that of larval mimicry are not mutually exclusive.

We hypothesize that snout tentacles in *Ancistrus* evolved as sexually selected structures related to the reproductive strategies of cavity-nesting and paternal care. In several fishes where the male defends a cavity-nest, females show a strong preference for males whose nests already contain eggs (see Kraak & Weissing, 1996). Examples are the fathead minnow, *Pimephales promelas* (Unger & Sargent, 1988), threespine stickleback, *Gasterosteus aculeatus* (Ridley & Rechten, 1981), river bullhead, *Cottus gobio* (Marconato & Bisazza, 1986), and fantail darter, *Etheostoma flabellare* (Knapp & Sargent, 1989). The benefits to females exhibiting a preference for nests with eggs are thought to include greater paternal investment in care for a larger brood (Coleman et al., 1985; Sargent, 1988; Sikkel, 1989), and the dilution effect whereby the risk per egg of being eaten is reduced (DeMartini, 1987; Kraak & Weissing,

1996). Furthermore, the presence of eggs in a male's nest suggests that he is of 'good parental quality' (Ridley, 1978), and is likely to produce offspring of good genetic quality (Williams, 1966) or sons who inherit his secondary sexual traits (Houde, 1992). Kraak & Weissing (1996) noted that these potential benefits are not mutually exclusive and may act in concert to varying degrees.

Female preference for nests with eggs presumably selects for mating tactics whereby males with empty nests can compete successfully with males guarding eggs (Knapp & Sargent, 1989). Male reproductive strategies which may exploit female preference for nests with eggs include egg-mimicry (Page & Swofford, 1984; Knapp & Sargent, 1989; Page & Bart, 1989) and two forms of allopaternal care (egg-raiding and nest take-over) whereby one male acquires and cares for another male's eggs (Unger & Sargent, 1988). In egg-raiding, the male steals eggs from another male's nest and places them in his own nest (van den Assem, 1967; Rohwer, 1978). In nest take-over, the male usurps a nest by forcibly evicting the resident male and cares for all or a portion of the adopted eggs (Constantz, 1985; Bisazza & Marconato, 1988; Unger & Sargent, 1988; Bisazza et al., 1989).

Whereas egg-raiding and nest take-over are primarily behavioral tactics, egg-mimicry is a strategy with a large morphological component. Egg-mimicry is hypothesized for several species of cavity-nesting darters (Percidae) in two subgenera (*Boleosoma* and *Catonotus*) of *Etheostoma* (Page & Swofford, 1984; Knapp & Sargent, 1989; Page & Bart, 1989). During the breeding season, large males develop fleshy knobs on the distal ends of either the first dorsal-fin spines (*Catonotus*), the second dorsal-fin rays (*Catonotus*), or the pectoral and pelvic-fin rays (*Boleosoma*). These morphological specializations resemble eggs in size, shape, and pigmentation and are thought to attract females by mimicking eggs in an otherwise empty nest. Female *Etheostoma* (*Catonotus*) *flabellare* prefer males with eggs over males without (Knapp & Sargent, 1989), and there is some evidence that female *Etheostoma* (*Boleosoma*) *olmstedii* also prefer to spawn with males guarding eggs (Constantz, 1985). Therefore, egg-mimicry presumably allows males with empty nests to exploit a female preference for nests with eggs. The subgenera *Boleosoma* and *Catonotus* are considered to be unrelated (Page, 1981; Bailey &

Etnier, 1988; Wood & Mayden, 1997) suggesting that selection for egg-mimicry is particularly strong in cavity-nesting darters.

In *Ancistrus*, we hypothesize that females prefer to spawn with males guarding larvae as well as eggs, and that in breeding males, the complex of snout tentacles mimics a school of larvae to seduce females to spawn in an otherwise empty nest. As previously described, the larvae remain clustered together in the nest with the parental male for 7-10 days after hatching (Fig. 5). A single tentacle with its wide base and flexible, tapered end may mimic a larva resting on the male's head or attached to the walls of the cavity by its mouth and freely waving its tail. The male's snout tentacles presumably mimic the appearance and perhaps the tactile sensation of a school of larvae to a female investigating the nest cavity. Larval mimicry may enable a male to signal his attractiveness to an approaching female without his leaving the nest and possibly alerting rivals or predators to its location. In aquaria, a pair of male *Ancistrus* in breeding condition will compete for a single available nest site (Teague, 1996). A nesting male may reduce his risk of eviction by attracting females while displaying from within his cavity. The use of nest take-over and larval mimicry as reproductive strategies in *Ancistrus* requires experimental investigation.

The evolution of the putatively larval-mimicking tentacles in *Ancistrus* is presumably similar to that of egg-mimicking fin knobs in darters, particularly those that exhibit knobs on their dorsal-fin spines. Page & Swofford (1984) hypothesized that knobs originated as fleshy masses on the tips of the dorsal spines to reduce the likelihood of rupturing eggs during nest-guarding. The original knobs, vaguely resembling eggs in color and shape, may have exploited a preexisting female bias (Ryan & Keddy-Hector, 1992) for nests containing eggs, or for the eggs themselves as a source of food (Knapp & Sargent, 1989). Ryan (1990) proposed the term sensory exploitation to explain the evolution of such signals (e.g., fin knobs) which take advantage of preexisting receiver traits. In a related sense, Christy (1995) proposed the sensory trap hypothesis as a particular mode of signal evolution wherein male courtship signals mimic a stimulus to which females respond in other contexts.

Snout tentacles initially may have served an adaptive role as accessory sensory structures

(Ono, 1980), or by reducing the risk of egg rupture by the sharp snout odontodes (present in *Lasiancistrus*, genus sister to *Ancistrus*). The snout tentacles' superficial resemblance to larvae may have exploited a preexisting female bias for males guarding larvae (or for the larvae themselves), which in turn selected for the tentacles' elaborate development in breeding males. Females may prefer males guarding larvae for the same reasons proposed for species where females prefer males guarding eggs. A key difference is that in all other cavity nesting fishes studied, the larvae leave the nest immediately after hatching and receive no further parental care. In contrast, a male *Ancistrus* guards his larvae in the cavity nest and has the opportunity to prove himself of better parental quality than a male guarding eggs. There is evidence that in the bicolor damselfish, *Stegastes partitus*, females assess the parental quality of mates (or the quality of their territories) based on the survival of previous broods against predation, and avoid nests that have a low probability of offspring survival (Knapp, 1993). If female *Ancistrus* assess the quality of a male or his territory based on the presence of larvae in his cavity nest, female choice may select for larval mimicry as a reproductive strategy.

Material examined

List includes only specimens cited in text. *Ancistrus* sp. 1: INHS 39004, 13, 80.2-138.7 mm SL; Peru: Loreto: caño Sacarito (río Orosa Drainage), 108 km ENE Iquitos at bearing 266°; M. H. Sabaj et al., 13 Aug 1996. – INHS 39771, 1, 159.1 mm SL; Peru: Loreto: lago Pabellon (río Orosa Drainage), 91.9 km E Iquitos at bearing 273°; J. W. Armbruster et al., 15 Aug 1996. *Ancistrus* sp. 2: INHS 35367, 19, 13.5-71.8 mm SL; Venezuela: Zulia: caño Taguara (L. Maracaibo drainage), 18 km N Puerto Catatumbo; D. C. Taphorn et al., 2 Feb 1995. *Ancistrus* sp. 3: INHS 27764, 7, 48.5-104.0 mm SL; Venezuela: Barinas: caño Curito (río Apure Drainage), 14 km NE Santa Bárbara; L. M. Page et al., 7 Jan 1992. – INHS 31858, 8, 39.4-107.4 mm SL; Venezuela: Barinas: río La Yuca (río Apure Drainage), 17 km N Barinas; D. C. Taphorn et al., 31 Dec 1993. *Ancistrus* sp. 4: INHS 34357, 12, 10.6-75.9 mm SL; INHS 36333, male 63.7 mm SL, 2 larvae 9.2-10.6 mm SL; INHS 36334, male 78.1 mm SL, 7 larvae 7.0-10.8 mm SL; Venezuela: Guarico: río Aguaro (río Orinoco Drainage), Parque Na-

cional Aguaro-Guariquito, ca. 15 km S Paso Cachimbo; D. C. Taphorn et al., 10 Jan 1995. *Ancistrus* sp. 5: 39005, 7, 43.4-127.7 mm SL; Peru: Loreto: caño Sacarito (río Orosa Drainage), 108 km ENE Iquitos at bearing 266°; M. H. Sabaj et al., 13 Aug 1996. *Cochliodon plecostomoides*: INHS 34067, 2, 214.1-226.0 mm SL; Venezuela: Guarico: río San Bartolo (río Orinoco Drainage), Parque Nacional Aguaro-Guariquito; D. C. Taphorn et al., 8 Jan 1995. *Dekeyseria scaphirhyncha*: INHS 61500, 3, 53.5-133.9 mm SL; Venezuela: Apure: caño San Miguel (río Cinaruco Drainage), ca. 40 km N Puerto Pérez; L. M. Page et al., 20 Jan 1992. *Isbrueckerichthys duseni*: UMMZ 215262, 20, 25-90 mm SL; Brazil: Parana: Ribeirao Pulador (trib. río Ponta Grossa, río Ribeira Drainage), 3 km S Campinhos; P. A. Buckup et al., 8 Feb 1988. *Lasiancistrus* sp. 1: INHS 28650, 1, 110.4 mm SL; Venezuela: Portuguesa: río Portuguesa (río Apure Drainage), Mata Larga; D. C. Taphorn et al., 1 Jan 1993. *Scobinancistrus aureatus*: AMNH 217762, 1, 209.9 mm SL; Brazil: Para: Ilha da Fazenda, Río Xingu; A. Schwartz et al., Jan 1994.

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Literature cited

- Armbruster, J. W. 1997. Phylogenetic relationships of the sucker-mouth armored catfishes (Loricariidae) with particular emphasis on the Ancistrinae, Hypostominae, and Neoplecostominae. Unpubl. Ph. D. dissertation, Univ. Illinois, 409 pp.
- 1998. Phylogenetic relationships of the suckermouth armored catfishes of the *Rhinelepis* group (Loricariidae: Hypostominae). *Copeia*, 1998: 620-636.
- Armbruster, J. W. & L. M. Page. 1996. Redescription of *Aphanotorulus* (Teleostei: Loricariidae) with description of one new species, *A. annophilus*, from the Río Orinoco basin. *Copeia*, 1996: 379-389.
- Assem, J. van den. 1967. Territory in the three-spined stickleback, *Gasterosteus aculeatus* L., an experimental study in intra-specific aggression. *Behavior*, 16: s1-s164.
- Bailey, R. M. & D. A. Etnier. 1988. Comments on the subgenera of darters (Percidae) with descriptions of two new species from the southcentral United States. *Misc. Publ. Univ. Mich. Mus. Zool.*, 175: 1-48.
- Barghuser, H. R. & J. A. Hopson. 1979. The endoskeleton: the comparative anatomy of the skull and the visceral skeleton. Pp. 265-326 in M. H. Wake (ed.), *Hyman's comparative vertebrate anatomy*, 3rd ed. University of Chicago Press, Chicago.
- Bisazza, A. & A. Marconato. 1988. Female mate choice, male-male competition and parental care in the river bullhead, *Cottus gobio* L. (Pisces, Cottidae). *Anim. Behav.*, 36: 1352-1360.
- Bisazza, A., A. Marconato & G. Marin. 1989. Male competition and female choice in *Padogobius martensi* (Pisces, Gobiidae). *Anim. Behav.*, 38: 406-413.
- Boeseman, M. 1968. The genus *Hypostomus* Lacépède, 1803, and its Surinam representatives (Siluriformes, Loricariidae). *Zool. Verhand.*, 99: 1-89.
- Breder, C. M., Jr. & D. E. Rosen. 1966. Modes of reproduction in fishes. Natural History Press, Garden City, NY, 941 pp.
- Buck, S. & I. Sazima. 1995. An assemblage of mailed catfishes (Loricariidae) in southeastern Brazil: distribution, activity, and feeding. *Ichthyol. Explor. Freshwaters*, 6: 325-332.
- Burgess, W. E. 1989. An atlas of freshwater and marine catfishes. T.F.H. Publications, Neptune City, NJ, 784 pp.
- Cerny, J. 1996. Breeding the albino *Ancistrus*. *Trop. Fish Hobbyist*, 45: 130-132.
- Christy, J. H. 1995. Mimicry, mate choice, and the sensory trap hypothesis. *Amer. Nat.*, 146: 171-181.
- Coleman, R. M., M. R. Gross & R. C. Sargent. 1985. Parental investment decision rules: a test in bluegill sunfish. *Behav. Ecol. Sociobiol.*, 18: 59-66.
- Constantz, G. D. 1985. Allopaternal care in the tessellated darter, *Etheostoma olmstedii* (Pisces: Percidae). *Environ. Biol. Fishes*, 14: 175-183.
- Cuvier, G. & A. Valenciennes. 1840. *Histoire naturelle des poissons*, vol. 15. Pitois, Paris, 540 pp.
- DeMartini, E. E. 1987. Paternal defence, cannibalism and polygamy: factors influencing the reproductive success of painted greenling (Pisces, Hexagrammidae). *Anim. Behav.*, 35: 1145-1158.
- Gee, J. H. 1976. Buoyancy and aerial respiration: factors influencing the evolution of reduced swim-bladder volume of some Central American catfishes (Trichomycteridae, Callichthyidae, Loricariidae, Astroblepidae). *Can. J. Zool.*, 54: 1030-1037.
- Houde, A. E. 1992. Sex-linked heritability of a sexually selected character in a natural population of *Poecilia reticulata* (Pisces: Poeciliidae) (guppies). *Heredity*, 69: 229-235.

- Isbrücker, I. J. H. 1980. Classification and catalogue of the mailed Loricariidae (Pisces, Siluriformes). Versl. Techn. Gegevens, Univ. Amsterdam, 22: 1-181.
- Isbrücker, I. J. H. & H. Nijssen. 1992. Sexualdimorphism bei Harnischwelsen (Loricariidae). DATZ, Sonderheft Harnischwelse, 19-33.
- Knapp, R. A. 1993. The influence of egg survivorship on the subsequent nest fidelity of female bicolor damselfish, *Stegastes partitus*. Anim. Behav., 46: 111-121.
- Knapp, R. A. & R. C. Sargent. 1989. Egg-mimicry as a mating strategy in the fantail darter, *Etheostoma flabellare*: females prefer males with eggs. Behav. Ecol. Sociobiol., 25: 321-326.
- Kner, R. 1854. Die Hypostomiden. Zweite Hauptgruppe der Familie der Panzerfische (Loricata vel Goniodontes). Denkschr. Akad. Wiss. Wien, Math.-naturwiss. Cl., 7: 251-286.
- Kraack, S. B. M. & F. J. Weissing. 1996. Female preference for nests with many eggs: a cost-benefit analysis of female choice in fish with paternal care. Behav. Ecol., 7: 353-361.
- Krejsa, R. J. 1979. The comparative anatomy of the integumental skeleton. Pp. 112-191 in M. H. Wake (ed), Hyman's comparative vertebrate anatomy, 3rd ed. University of Chicago Press, Chicago.
- Leviton, A. E., R. H. Gibbs, E. Heal & C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia, 1985: 802-832.
- Marconato, A. & A. Bisazza. 1986. Males whose nests contain eggs are preferred by female *Cottus gobio* L. (Pisces, Cottidae). Anim. Behav., 34: 1580-1582.
- Moodie, G. E. E. & M. Power. 1982. The reproductive biology of an armoured catfish, *Loricaria uracantha*, from Central America. Environ. Biol. Fishes, 7: 143-148.
- Muller, S. & C. Weber. 1992. Les dents des sous-familles Hypostominae et Ancistrinae (Pisces, Siluriformes, Loricariidae) et leur valeur taxonomique. Rev. Suisse Zool., 99: 747-754.
- Neal, T. 1996. Breeding the dwarf bristlenose pleco. Trop. Fish Hobbyist, 44: 102-108.
- Ono, D. 1980. Fine structure and distribution of epidermal projections associated with taste buds on the oral papillae in some loricariid catfishes (Siluroidei: Loricariidae). J. Morph., 164: 139-159.
- Page, L. M. 1981. The genera and subgenera of darters (Percidae, Etheostomatini). Occas. Pap. Mus. Nat. Hist. Univ. Kans., 90: 1-69.
- Page, L. M. & H. L. Bart. 1989. Egg mimics in darters (Pisces: Percidae). Copeia, 1989: 514-518.
- Page, L. M., G. B. Mottesi, M. E. Retzer, P. A. Ceas & D. C. Taphorn. 1993. Spawning habitat and larval development of *Chaetostoma stannii* (Loricariidae) from río Crucito, Venezuela. Ichthyol. Explor. Freshwaters, 4: 93-95.
- Page, L. M. & D. L. Swofford. 1984. Morphological correlates of ecological specialization in darters. Environ. Biol. Fishes, 11: 139-159.
- Regan, C. T. 1904. A monograph of the fishes of the family Loricariidae. Trans. Zool. Soc. Lond., 17: 191-324.
- Ridley, M. 1978. Paternal care. Anim. Behav., 26: 904-932.
- Ridley, M. & C. Rechten. 1981. Female sticklebacks prefer to spawn with males whose nests contain eggs. Behavior, 76: 152-161.
- Rohwer, S. 1978. Parent cannibalism of offspring and egg raiding as a courtship strategy. Amer. Nat., 112: 429-440.
- Ryan, M. J. 1990. Sexual selection, sensory systems and sensory exploitation. Oxford Surv. Evol. Biol., 7: 157-195.
- Ryan, M. J. & A. Keddy-Hector. 1992. Directional patterns of female mate choice and the role of sensory biases. Amer. Nat., 139: s4-s35.
- Sargent, R. C. 1988. Paternal care and egg survival both increase with clutch size in the fathead minnow, *Pimephales promelas*. Behav. Ecol. Sociobiol., 23: 33-37.
- Schaefer, S. A. 1986. Historical biology of the loricariid catfishes: phylogenetics and functional morphology. Unpubl. Ph.D. dissertation, Univ. Chicago, 290 pp.
- Schopf, H. 1991. Keeping bristlenose plecos. Trop. Fish Hobbyist, 39: 106-112.
- Sikkel, P. C. 1989. Egg presence and developmental stage influence spawning-site choice by female garibaldi. Anim. Behav., 38: 447-456.
- Strahler, A. N. 1975. Physical geography, fourth edition. Wiley, New York, 643 pp.
- Taylor, J. N. 1983. Field observations on the reproductive ecology of three species of armored catfishes (Loricariidae: Loricariinae) in Paraguay. Copeia, 1983: 257-259.
- Teague, C. 1996. Spawning the bushy-nosed pleco. N. Amer. Catfish Soc. Mag., 1: 13-15.
- Unger, L. M. & R. C. Sargent. 1988. Allopaternal care in the fathead minnow, *Pimephales promelas*: females prefer males with eggs. Behav. Ecol. Sociobiol., 23: 27-32.
- Williams, G. C. 1966. Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton, NJ, 307 pp.
- Wood, R. M. & R. L. Mayden. 1997. Phylogenetic relationships among selected darter subgenera (Teleostei: Percidae). Copeia, 1997: 265-274.

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