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Vampire catfishes seek the aorta not the jugular: candirus of the genus *Vandellia* (Trichomycteridae) feed on major gill arteries of host fishes

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Abstract
Species of the trichomycterid catfish genus *Vandellia* (candirus) feed on blood from other fishes, usually entering the gill chamber of their hosts. However, exactly where these vampire fish attach themselves in the chamber to take blood remains unrecorded. Herein we present evidence that two candiru species, *Vandellia cirrhosa* and *V. sanguinea*, seek the major gill arteries. Both species bite mostly at the ventral or dorsal arteries, and the blood is presumably pumped into their gut by the hosts' blood pressure. We suggest that candirus do not need any special sucking or pumping mechanism become rapidly engorged themselves with blood but simply use their needle-like teeth to make an incision in an artery. This being the case, the notion of blood-sucking by the candiru is misleading.

Zusammenfassung
Die Arten der Schmerlenwels-Gattung *Vandellia* ernähren sich vom Blut anderer Fische, wobei sie gewöhnlich in die Kiemenhöhle ihrer Wirtstiere eindringen. Bisher wusste man jedoch nichts darüber, wo genau sich diese „Vampirfische“ in der Kiemenhöhle festsetzen, um Blut aufzunehmen. Bei unseren Untersuchungen konnten wir nachweisen, dass zwei der Arten – *Vandellia cirrhosa* und *V. sanguinea* – die Hauptschlagadern aufsuchen. Beide Arten beißen am häufigsten in die ventralen oder dorsalen Arterien und nutzen höchstwahrscheinlich den Blutdruck des Wirtsfisches, um das Blut in den eigenen Körper aufzunehmen. Nach unseren Ergebnissen benötigen die Schmerlenwelse keinen speziellen Saug- oder Pumpmechanismus, um sich das Blut des Wirtstiers möglichst rasch einzuverleiben, sie benutzen lediglich ihre nadelspitzen Zähne zu einem Einstich in eine Arterie. Die bisherige Beschreibung, es handle sich um „blutsaugende“ Fische, erweist sich damit als missverständlich.

Résumé
Les espèces de Trichomyctéridés du genre *Vandellia* (Candirus) se nourrissent du sang d'autres poissons, généralement en pénétrant dans la chambre branchiale de leurs hôtes. Cependant, l'endroit précis où ces poissons vampires se fixent dans la branchie pour sucer le sang restait ignoré. A ce sujet, nous avons relevé clairement que deux espèces de Candiru, *Vandellia cirrhosa* et *V. sanguinea* ciblent les artères principales des branchies. Les deux espèces mordent surtout les artères ventrales et dorsales et le sang leur parvient probablement par la pression sanguine de l'hôte. Nous pensons que les Candirus n'ont pas besoin de mécanisme particulier de succion ou de pompage, mais se servent de leurs dents en aiguilles pour inciser l'artère. Si c'est le cas, la notion de succion du sang par le Candiru est erronée.

Resumo
As espécies do gênero *Vandellia* (candirus) alimentam-se de sangue de outros peixes, habitualmente entrando na câmara branquial de seus hospedeiros. Entretanto, o local exato onde estes peixes-vampiros se agarram dentro da câmara para obter sangue é desconhecido. Apresentamos aqui evidências de que duas espécies de candirus, *Vandellia cirrhosa* e *V. sanguinea*, obtém sangue de artérias branquiais. Ambas as espécies mordem principalmente as artérias aorta ventral e dorsal, sendo o sangue presumivelmente bombeado no seu tubo digestivo pela pressão sanguínea do seu hospedeiro. Sugerimos que os candirus não precisam de nenhum mecanismo especial de sucção ou bombeamento para fartar-se de sangue, porém simplesmente usam seus dentes aguçados para fazer a incisão numa artéria. Sendo este o caso, a noção do candiru sugador de sangue é um conceito equivocado.

Sommario
Le specie di pesci gatto tricomicteridi del genere *Vandellia* (comunemente noti come candirus) si nutrono del sangue di altri pesci, di solito penetrando

nella camera branchiale dei loro ospiti. Tuttavia, il sito esatto su cui questi pesci si attaccano non è mai stato documentato. In questo articolo, viene illustrato come due specie di candiru, *Vandellia cirrhosa* e *V. sanguinea,* vadano alla ricerca dell'arteria branchiale principale. Entrambe addentano soprattutto le arterie dorsali e ventrali e il sangue viene così pompato nel loro corpo dalla pressione sanguigna del loro ospite. Si conclude che i candiru non necessitano di nessun apparato atto a succhiare o a pompare sangue per ingurgitarne la maggior quantità possibile, ma sono sufficienti i loro denti affilati per incidere la parete arteriosa. Ne consegue che la denominazione di succhiatori di sangue attribuita ai candiru non risulta corretta.

Introduction

The candirus, neotropical freshwater Vandelliinae catfishes, are known to feed on the blood of larger fishes, usually entering the gill chamber of the host to take the fluid there (Eigenmann, 1918; Kelley & Atz, 1964; de Pinna, 1998; Spotte *et al.,* 2001). Their feeding habits were recently summarised by Spotte (2002), and included stories of attacks on humans, as well as conjecture on the mechanism by which blood is taken from fish hosts. The common names of vandelliine candirus, "bloodsucking catfishes", and the presumptive descriptions of their feeding (Eigenmann, 1918; Kelley & Atz, 1964; de Pinna, 1998; Spotte, 2002) imply that the blood is sucked from the host. In their account on the feeding of the minute *Paravandellia oxyptera* (as *Branchioica bertonii),* Machado & Sazima (1983) suggest that this candiru takes blood from its host by biting the proximal and medial parts of the gill filaments, which would then bleed freely into the alimentary tract of the catfish. In their account of feeding experiments with the larger *Vandellia cirrhosa* (as *V.* cf. *plazaii),* Spotte *et al.* (2001) found no evidence of gill damage on the fishes offered to this candiru. Spotte (2002) describes a hypothetical blood-pumping mechanism to explain how a larger candiru might quickly ingest a large volume of blood.

Published photographs of the larger species of *Vandellia* feeding on captive goldfish show that this candiru is attached somewhere at the upper or lower gill corners, under the gill cover of the host fish (Kelley & Atz, 1964; Spotte *et al.,* 2001). Despite the fact that in these photos the candiru's head is hidden, its position in the gill chamber and the very short time needed for the fish to become engorged with blood strongly indicate that the catfish seizes one of the major blood vessels, most probably an artery. Recently de Pinna & Wosiacki (2003) suggested that the larger species of *Vandellia* use their specialised teeth to lacerate a major gill vessel of the host and feed on its blood, without damaging the gills. We recorded the feeding behaviour in captivity of two candiru species, *Vandellia cirrhosa* and *V. sanguinea*, and here present evidence that strengthens the suggestion of de Pinna & Wosiacki (2003) and weakens that of Spotte (2002) concerning the blood intake of the candirus of the genus *Vandellia*.

Methods

The candirus we studied were caught with seine nets in shallows with a muddy/sandy bottom in the Solimões and Amazonas Rivers, near the Ilha do Careiro (03°12'S, 59°60'W), Amazonas, northern Brazil. The net was dragged to the bank and its contents emptied into a large plastic bowl. Fishes other than candirus were released, and the candiru transferred with the water into plastic bags. In the laboratory, 95 candirus were placed in two large aquaria (70-90 l) with aerated water from their habitat, and kept unfed for 2-5 days. Mortality over one week was negligible (about 2%). Three laboratory-raised specimens of the tambaqui, *Colossoma macropomum* (Characidae: Serrasalminae), 187-222 mm standard length (SL) were used in staged encounters to record

Fig. 1. *Vandellia cirrhosa* taking blood in the gill chamber of a *Colossoma macropomum* host: positioned at the lower corner of the gill chamber (below), and somewhat higher (above). Note a little blood escaping from the gill chamber. Photos by I. Sazima.

the feeding behaviour of the candirus. The candiru attacking the tambaqui were observed directly, photographed, and video-taped. In a few photographs and video-records, the host fish was held in cotton-gloved hands. Occasionally, a submerged host fish was held belly up and its gill covers were gently lifted by hand to afford a better view of the candiru's position within the gill chamber. No tambaqui died from attacks by the candirus or as a result of handling. The host specimens were later anaesthetised and kept cool until death. A post-mortem inspection was carried out to discover wounds in the gill chamber and to verify which vessels had mostly been used by the candiru for taking blood.

The *V. cirrhosa* and *V. sanguinea* individuals observed measured 30.9-50.3 mm (n = 93) and 34.8-72.0 mm SL (n = 4) respectively. Focal animal and all occurrences samplings (Lehner, 1979) were used in observation sessions lasting 10-30 min. Special attention was paid to the site where the candiru gained access to the tambaqui gill chamber, and to its subsequent position on the gills. The length of stay in the gill chamber and the time needed for a candiru to become engorged itself were measured with a hand-held chronometer (the video-tapes were analysed and the results pooled with the direct observations). Avoidance behaviour of the host when attacked by the candiru was also recorded and video-taped. Voucher specimens of the candirus and tambaquis used in the observations are in the fish collections of the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Museu de História Natural da Universidade Estadual de Campinas (ZUEC). *Vandellia cirrhosa*: INPA 21449 (81); ZUEC 6202 (1); 6203 (3); *V. sanguinea*: INPA 21450 (2); 6204 (1); *Vandellia* sp.: INPA 15599 (27); 15600 (14); *Colossoma macropomum*: INPA 21451 (03). Digital images and the video-tape of feeding sequences are in the ZUEC fish photo and video files (tape #16).

Results

In about half of the netted candirus blood in the digestive tract was visible through the body tissues; some of them released blood from their cloacal opening on handling. The same behaviour was recorded under aquarium conditions, but no candiru was observed to regurgitate any trace of blood even if roughly handled. *Vandellia cirrhosa* and *V. sanguinea* displayed similar feeding behaviour. The feeding sequence began with the candiru approaching a host fish and swimming alongside it, aiming at the gill chamber. When close to the edge of the gill cover, the candiru attempted to penetrate the gill chamber by forcing itself underneath. The tambaqui displayed a repertoire of defensive actions aimed at avoiding or hampering the candiru attacks (see below). After some time the candiru generally succeeded in entering the gill chamber, usually through the lower angle (formed by the edge of the gill cover and the isthmus) (N = 23). It also entered through the upper angle

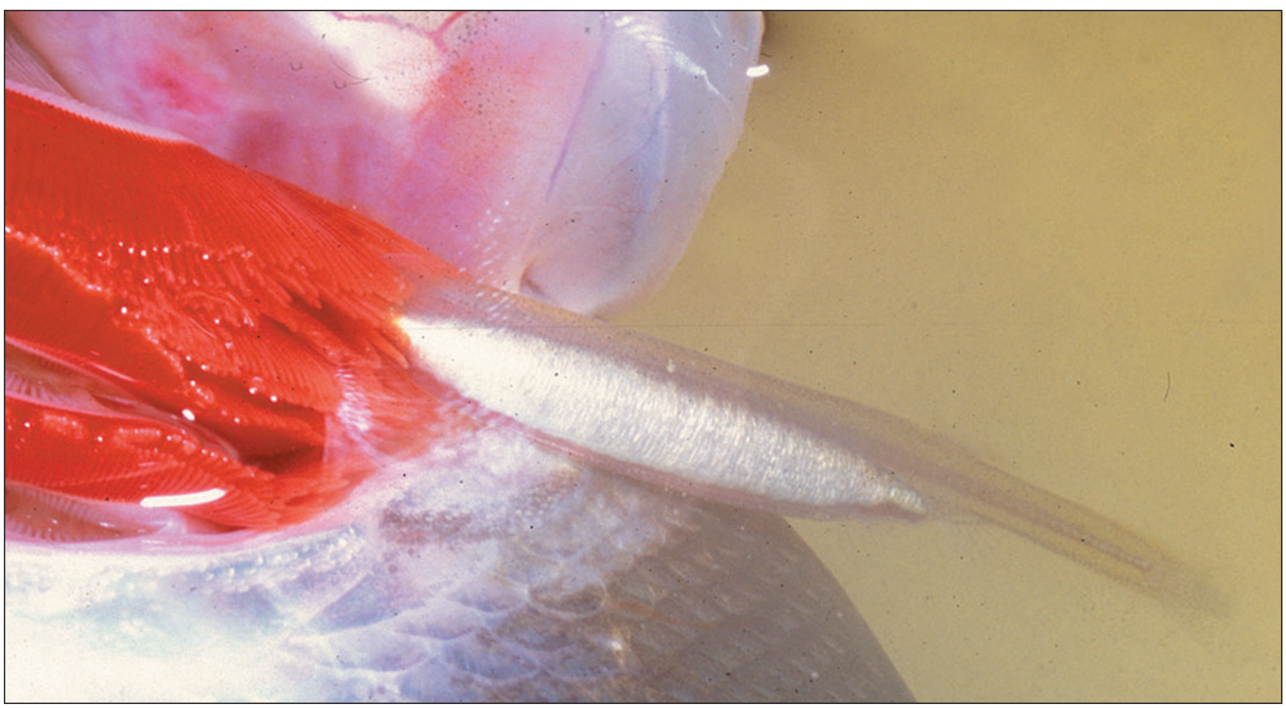

Fig. 2. *Vandellia cirrhosa* in the gill chamber of *Colossoma macropomum* (gill cover abducted) showing its positioning at the angle formed by the gill arch and the upper part of the gill cover. The candiru abdomen is beginning to swell with blood. Photo by I. Sazima.

(N= 7), very rarely under the middle portion of the gill cover (N = 3), and only once entered through the host's mouth (but see below). The host would often shudder or jerk a little as the candiru entered and moved within the gill chamber. Depending on the candiru's relative size, it either disappeared entirely into the gill chamber or remained partly exposed. When a part of the candiru body remained visible, sinuous movements seemingly related to its positioning within the chamber were clearly seen; shortly afterwards these movements ceased and the candiru hung limp (Fig. 1) rarely moving to reposition itself.

When the gill cover was spread so as to expose the tambaqui's gill chamber, the candiru could be seen positioned deep in the corner formed by the inner face of the gill cover and the base of the gill arches, or in a similar position in the upper corner (Fig. 2), presumably taking blood from the ventral or dorsal aorta (see below). The belly of the candiru was clearly seen to swell quickly and continuously as the host's blood was taken. After a while the candiru made a few, short forward movements, curved its body and left the gill chamber engorged with blood (Fig. 3). After the candiru attack, blood was sometimes observed to ooze or even pulse out of the gill chamber.

The lower corner of the gill chamber was preferred to the upper one (23 vs. 7; $X^2 = 8.533$; $P < 0.003$) irrespective of the host's position in the aquarium. When the candiru pushed itself under the middle portion of the gill cover and did not position itself in the lower or upper angle, it usually left the host without taking blood. However, it sometimes managed to attach itself to the gill arch and presumably took blood from an afferent or efferent gill artery (N = 2). In the last session on the fifth day of observation, a previously used tambaqui host resorted to an extreme defence strategy (see below): it closed all breathing openings and ceased ventilation. However, a candiru forced its way into the host's posterior nostril and succeeded in taking blood from there. After it left, two other individuals entered in the same way to feed on the host's blood. The time required by the candiru to become engorged with blood and leave the gill chamber varied between 30 and 145 sec (x=58.2; n= 6): it seemed to be related to the relative size of the catfish and to its success in attaching itself quickly to a large blood vessel.

The tambaqui was successful in circumventing or at least greatly hindering an attacking candiru by pressing it under the membranous gill cover flap, which caused the catfish to retreat, or by using its pectoral fin to press it against its own flank or to sweep it from the gill cover edge. Another method of defence was to slow down gill ventilation, making shallow breathing movements, or even stopping ventilation entirely during the attack. Additionally, the tambaqui was able to close the gill cover on the side under attack, and ventilate through the opposite side. The most extreme defence recorded was shutting both gill covers and mouth, completely closing off the gill chamber.

Post mortem inspection of the gill chamber of host fish under a stereomicroscope revealed no observable damage to the gill filaments. However, punctures and cuts were evident, mostly in the angle formed by the base of the first gill arch and the inner face of the gill cover and/or in a similar spot in the upper angle. The cuts were relatively deep, wide, crescent-shaped or elliptical wounds with coagulated blood inside (Fig. 4). Close to the opposing ends of the cut were conspicuous puncture marks. Occasionally a small but obvious cut was also seen on the median portion of the external face of the first gill arch.

Discussion

Our observations support the suggestion by de Pinna & Wosiacki (2003) that large candirus of the genus *Vandellia* take blood from their hosts through major gill vessels. The evidence obtained here supports the view that these vessels are the ventral and

Fig. 3. *Vandellia cirrhosa* swimming: it is engorged with blood after a feeding session. Actual size 37.2 mm SL (ZUEC 6202). Photo by I. Sazima.

dorsal aorta and/or the afferent and efferent gill arteries. This view is strengthened by the observation of the candiru's positioning, its quick engorging with blood, and the blood spurting from the gill chamber Blood pulses from a damaged artery, not from a vein. We favour the view that the preferred vessels are the ventral and dorsal aorta arteries, since these are larger in diameter and are situated in the angle where the candiru bites (see figures of a fish's main blood vessels in Helfman *et al.,* 1997). However, when the candiru is positioned under the middle of the gill cover, it is likely to take blood from the afferent or efferent gill arteries. This latter positioning was unusual and mostly occurred when experimentally exposing the gill arch by pulling back the host's gill cover, or when another candiru was already taking blood at the upper or lower corners (this is probably rare under natural conditions). Entry into the nostril is also rare and most probably due to the catfish having been starved for as long as five days. This may shed some light on the occasional reports of candirus entering body openings (e.g. cloaca) other than the gill chamber of their fish hosts, and may perhaps also relate to the highly unusual penetration of the human urethra or vagina by the candiru (see Spotte, 2002 for a few accounts).

We suggest that the blood pressure of the host fish is sufficient to pump blood steadily into the digestive tract of the candiru until it is gorged. That this parasitic catfish employs a pumping mechanism while feeding (e.g. Spotte, 2002) seems unlikely. Our view is supported by the fact that the blood pressure of several fish species varies between 30 and 70 mm Hg, with the highest values recorded at the ventral aorta artery (Randall, 1970). This latter fact may explain the candiru's preference for the anterior lower angle of the gill chamber. An alternative and not mutually exclusive explanation is that the ventral angle is slightly more accessible than the dorsal angle. The high blood pressure in the aorta would also explain the speed with which the catfish becomes engorged. As a reverse pressure is presumably exerted by the catfish's enormously swollen digestive tract, any further mechanism would probably involve some kind of valve or sphincter to prevent reflux of the ingested blood. The fact that under stress candirus only released blood via the cloacal opening lends support to this suggestion. Other trichomycterids under stress regurgitate recently ingested food, (pers. obs.). The idea that the candiru sucks blood is misleading, since the fish actually acts as a recipient for the blood entering its digestive tract under the pressure of the cardiovascular system of its host.

The view that the candiru does not suck blood is supported by an inspection of its oral structures: the oral chamber is of the generalised siluroid type (our pers. obs.), and the fish has no protrusible jaws or any other structure apparently suited for an efficient intake of fluids (e.g., the mandibular abductor muscles are weakly developed). Some species of the order Perciformes have protrusible jaws and several of them are able to suck water and prey into their oral chambers, but this behaviour is only intermittent (e.g., Lauder, 1982; Liem, 1991), whereas the intake of blood by the candiru is continuous. The gut of species of *Vandellia* is a straight tube, with loosely-spaced fibres within the connective tissue lining the walls (see figures in Spotte, 2002), features that most probably facilitate the quick and considerable swelling of the candiru's belly during the intake of blood.

The puncture-like wounds left by the candiru attack are probably due to the fish using the interopercular (and possibly opercular) spines to anchor itself in position. The crescent-shaped or elliptical cuts through which the blood is taken are probably made by the sharp, well-developed, teeth on the medial premaxilla (see illustrations in Spotte, 2002). The wounds are most probably widened by lateral movements of the candiru's head and front end whilst in the host's gill chamber.

Since the candiru may be vulnerable to predation and/or to mutilation of exposed parts while taking blood from its host, it may advantageous to keep the length of stay in the gill chamber to a minimum. Both the *Vandellia* species studied live in shallow water over a mud/sand bottom and have patchy distribution. Thus, if a host fish quickly moves into deeper water while the candiru is still in the gill chamber, when the latter leaves the chamber it would be remote from its usual territory and exposed to predators.

The avoidance mechanisms here recorded for *Colossoma macropomum* whilst under attack by the candiru (e.g., tightening its gill cover and using its pectoral fins) strongly indicate that this species is one of the potential hosts in the wild, and has therefore developed defensive measures. This view is strength-

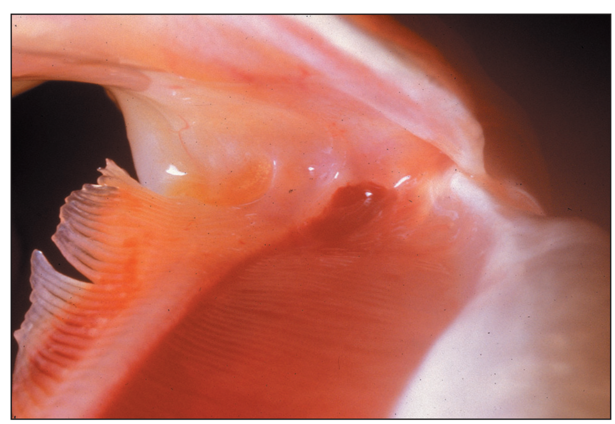

Fig. 4. The elliptical wound in the ventral aorta (centre, still bleeding) cut by *Vandellia cirrhosa* to feed on a *Colossoma macropomum* host. Note the position of the wound in the angle between the inner face of the gill cover and the base of the gill arches. Photo by I. Sazima.

ened by the fact that we only tested naïve, laboratory-raised tambaqui, which would not have learned defensive behaviour. No special avoidance mechanisms other than flight were recorded for the exotic goldfish *(Carassius auratus),* or for the relatively small native cichlid *(Cichlasoma amazonarum)* whilst under attack by the candiru (Spotte *et al.,* 2001). Fish hosts reported for vandelliine candirus under natural conditions include species of medium-sized to large characins, such as *Piaractus brachypomus*, *Pygocentrus nattereri*, *Salminus maxillosus*, *Brycon* sp., and large catfishes, such as *Brachyplatystoma vaillanti* and *Pseudoplatystoma* spp. (Eigenmann, 1918; Guimarães, 1935; Devicenzi & Vaz-Ferreira, 1939; Miles, 1943).

Machado & Sazima (1983) suggested that the minute *Paravandellia oxyptera* takes blood from its hosts by biting the proximal and medial parts of the gill filaments, which would then bleed freely into the alimentary tract of the candiru. This suggestion was supported by the presence of small scratches and further bleeding of the filaments seen after feeding by these candirus. However, this view remains untested, even if it may apply to small species which attack very large hosts, such as the catfishes *Pseudoplatystoma* spp. (Machado & Sazima, 1983). Minute candirus are unlikely to be able to cut through the relatively large, tough, major gill vessels of their large hosts; they most probably seek gill vessels of a diameter appropriate to their own size.

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