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Twenty years "sperm drinking" by female catfishes – and still nothing new? An essay about the different perception of amateurs and professionals

Zwanzig Jahre „Spermatrinken" weiblicher Welse – und immer noch nichts Neues? Ein Essay über die unterschiedliche Wahrnehmung von Amateuren und Profis

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Summary: In 1995 Khoda et al. published a study, in which they described a "unique reproductive behaviour and a new mode of egg insemination" (p. 1) of the armoured catfish *Corydoras aeneus*. From their observations and experiments the authors claimed to have demonstrated that the females swallow the sperm of males during spawning ("sperm drinking") and that after the passage through the gut these sperm inseminate and fertilize the eggs in the fin pocket formed by the female pelvic fins. Since then sperm drinking seems to be a commonly accepted fact in the primary and secondary scientific literature and was never seriously questioned herein. However, the way ejaculated sperm take to inseminate and fertilize egg was vigourously discussed already at the beginning and middle of the 20th century in the so-called "gray" literature by German and later North American aquarists on the basis of numerous observations, hypotheses and even experiments. For example, Schubert (1907) suggested the oral uptake of sperm by the female and Liebig (1912) considered the possibility of „sperm drinking" and the intestinal passage of sperm, but also other fertilization scenarios were taken into consideration. Especially the aquaristic literature from USA favoured the view that eggs are inseminated and fertilized during egg deposition. Later Knaack (1955 ff.), who intensively studied the reproductive behaviour of several *Corydoras* spp., confirmed not only the earliest, but largely forgotten observations made by Carbonnier (1881), but also plausibly rejected the intestinal passage of sperm performing similar experiments as Khoda et al. We give a brief overview of the lively debate on this subject in the first half of the last century, acknowledge the experiments performed by Knaack as well as by Khoda et al., and discuss some problems that arise from these studies. Generally, our essay tells about an interesting episode of aquaristics and illustrates how much useful information and ideas are hidden in the so-called "gray" literature.

Keywords: *Corydoras* spp., reproductive behaviour, T-position, „sperm drinking", insemination and fertilization, fin pocket, aquaristics, gray literature.

Zusammenfassung: Khoda et al. veröffentlichten im Jahr 1995 eine Studie, in der sie ein „unique reproductive behaviour and a new mode of egg insemination" (p. 1) bei dem Panzerwels *Corydoras aeneus* beschreiben. Die Autoren glaubten aufgrund von Beobachtungen und einer Reihe von Experimenten nachgewiesen zu haben, dass die Weibchen während des Laichaktes die Spermien der Männchen verschlucken („sperm drinking") und die Spermien die Eier in einer Flossentasche, die von den Bauchflossen des Weibchens gebildet wird, erst nach einer Passage durch den Darm besamen und befruchten. Dieses „Spermatrinken" wird seitdem bis heute in der wissenschaftlichen Primär- und Sekundärliteratur als Fakt angesehen und ist dort unseres Wissens auch niemals ernsthaft in Frage gestellt worden. Demgegenüber stehen zahlreiche Veröffentlichungen in der sogenannten „grauen" Literatur, vor allem Anfang bis Mitte des 20. Jahrhunderts, in denen aufgrund von Beobachtungen, Hypothesen und sogar Versuchen zunächst deutscher, dann aber

auch nordamerikanischer Aquarianer heftig diskutiert wurde, wie die Spermien zu den Eiern gelangen und diese befruchten. So vermutete beispielsweise Schubert (1907) bereits ein Aufsaugen der Spermien durch das Weibchen und Liebig (1912) erwog die Möglichkeit des „Spermatrinkens" und der Darmpassage der Spermien, doch wurden darüber hinaus noch andere Befruchtungsszenarien vermutet, unter anderem, vor allem in der insgesamt relativ spärlichen nordamerikanischen aquaristischen Literatur, dass die Eier während der Eiablage befruchtet würden. Knaack (1955 ff.) hat dann nach intensivem Studium des Ablaichverhaltens mehrerer *Corydoras*-Arten nicht nur die ersten diesbezüglichen, aber zum Teil in Vergessenheit geratenen Beobachtungen von Carbonnier (1881) bestätigt, sondern bereits 1955 mit Versuchen, die im Wesentlichen denen von Khoda et al. entsprachen, eine Darmpassage der Spermien plausibel zurückgewiesen. Wir geben einen kurzen Überblick über die lebhaften Diskussionen zu diesem Thema aus der ersten Hälfte des vorigen Jahrhunderts, würdigen die Experimente von Knaack und von Khoda et al. und erörtern einige sich daraus ergebende Probleme. Generell behandelt unser Essay eine interessante Episode der Aquaristik und zeigt auf, wie viele Anregungen und Informationen in der so genannten grauen Literatur verborgen sind.

Schlüsselwörter: *Corydoras* spp. Fortpflanzungsverhalten, T-Stellung, „Spermatrinken", Besamung und Befruchtung, Bauchflossentasche, Aquaristik, „graue" Literatur.

1. Introduction

About 20 years ago the journal „Environmental Biology" published a study entitled „Sperm drinking by female cat fishes: a novel mode of insemination" (Khoda et al. 1995). The authors of this study claimed to have (indirectly) found evidence that during mating females of *Corydoras aeneus* (and probably also females of other *Corydoras* species) take up sperm with the mouth, which then pass through the intestine within seconds reaching a "pocket" formed by the female's pelvic fins, in which the just deposited eggs were fertilized.

Understandably, this „novel mode of insemination" has attracted considerable attention in the subsequent literature. However, it is remarkable that immediately after publication of this phenomenon critical discussions were primarily initiated by aquarium enthusiasts. The majority of aquarists was not convinced either according to the saying "nothing can happen that isn't allowed to happen", referring to own observations and ideas or to reports in the so-called "gray" literature, which the Japanese authors and many professional scientists apparently were not aware of, or more or less carefully weigh the differing views down to the present time (e.g. Finley 1995; Pinter 1996; Steinle 1996; Ander 1997; Schmid 2004; van der Jeught 2013). According to the various notes published in the "gray" literature, this issue appeared to be settled at the latest since 1955 by Knaack (1955) – but not in the sense of Khoda et al. (1995) – , and Knaack's interpretation was accepted by several authors of manuals and encyclopedias (see Frey 1957, 1974; Sterba 1963; Currier & Smith 1969; Vogt 1970; Klee 1970; Franke 1983, 1985).

Professional scientists, however, seemed and seem to take "sperm drinking" for granted in both original articles (e.g. Huysentruyt & Adriaens 2005; Mazzoldi et al. 2007; Franceschini-Vicentini et al. 2007) as well as in text books of ichthyology and reviews (e.g. Helfman et al. 2007; Nelson & Dehn 2011; Armbruster 2011; Mol 2012; Pandian 2012; Wotton & Smith 2014).

The idea behind our present essay, in which we reopen the debate on whether sperm drinking in catfishes is likely or not, was

- to summarize the most important data on reproduction, in particular on insemination and fertilization of the eggs in callichthyid catfishes published since 1891 and not or insufficiently considered by scientific studies;
- to acknowledge the "gray" literature, which clearly shows that the hypothesis of sperm drinking in catfishes has been formulated as early as 1912 by Liebig, but was rejected later due to reliable experiments and their plausible interpretations, and last but not least
- to call attention to an interesting and obviously still acute episode of ichthyology and to acknowledge the informational content of

some so called "gray" literature.

We are aware of the problems of our essay, because the "gray" literature is hardly to be mastered, i.e. in the present case the numerous observations published in magazines for aquarium enthusiasts. However, the early phase in the discussion of this phenomenon seems to have been largely a German matter. Therefore, our selection, especially of non-German articles, remains subjective. Contrary to convention, we add an appendix with detailed textual passages mainly of the concerned "historic" authors (both original and in an English translation).

2. Observations on the reproductive behavior of *Corydoras* spp. (1881-1955)

2.1. The early work of nature-lovers and pioneers of aquaristics

Already since the end of the 19th century and especially in the first half of the 20th century armoured catfishes were bred successfully and their reproductive behaviour was observed carefully by many aquarists. At that time, however, only *Corydoras paleatus* and somewhat later *Corydoras aeneus* were available, but were described under different names (tab. 1). However, the interpretation of what the authors had seen during courtship and mating differed considerably. Certainly, this was due (among others) to their different background, such as experience in breeding exotic fishes, talent for observation, imagination and general scientific training. The problematic fields heavily discussed were (1) the sex-specific activity of the mates, (2) the significance of the so-called T-position, namely at what site and how the female adheres to the male, and (3) how and where sperm fertilize the eggs (see tab. 2).

The French ichthyologist Pierre Carbonnier (1828–1883) was the first to describe the reproductive behaviour of the peppered catfish *Corydoras paleatus* (Carbonnier 1880, 1881). Especially his observations published in the "Bulletin de la Société d'Acclimatation", a former journal of the French "Société nationale de protection de la nature (SNPN)" are pretty good and the interpretation of what he has seen is essentially correct (Carbonnier 1881). Carbonnier (l. c.) considered the male as the active partner during courtship, mentions an attachment of the male in transverse position ("se posa en travers", p. 106), later called T-position. Further, he recognized that the male blocks the female by clasping her barbels with the first spine of his pectoral fin and suspected that the eggs become fertilized in a pocket formed by the ventral fins of the female.[1] The data concerning courtship and mating were translated into German and published twelve years later (1893) in the "Blätter

Tab. 1: List of the species names used for *Corydoras paleatus* and *Corydoras aeneus* by the various authors cited in this essay. Note that in some articles the same species was mentioned with different names.
Tab. 1: Liste der Artnamen, unter denen *Corydoras paleatus* und *Corydoras aeneus* von den in diesem Essay zitierten Autoren erwähnt wurden. Man beachte, dass in einigen Artikeln ein und dieselbe Art unter verschiedenen Namen erwähnt wurde.

***Corydoras paleatus* (Jenyns, 1842)**	
Callichthys fasciatus	Carbonnier (1880, 1881, 1893), Köhler (1904), Boeker (1909), Bade (1931), Breder & Rosen (1966).
Callichthys punctatus	Jürgens (1900, 1906, 1909), Liebscher (1904), Schäme (1907), Thumm (1909), Reitz (1905, 1910), Haefner (1910), Liebig (1912).
Corydoras punctatus	Steche (1914).
Corydoras marmoratus	Gill (1905), Liebig (1912), Wittig (1913), Breder & Rosen (1966).
Corydoras paleatus	Rachow (1912), Mertens (1917), Jürgens (1923), Liebig (1924 a–e), Kolbe (1926), Bade (1931), Breder & Rosen (1966).
***Corydoras aeneus* (Gill, 1858)**	
Corydoras aeneus	Adams (1939), Hart (1947), Card (1949), Breder & Rosen (1966).
Corydoras schultzei	Bogenschütz (1961), Breder & Rosen (1966), Zukal (1968, 1973 a).

Tab. 2: Key elements of the reproductive behaviour of *Corydoras* spp. and ways of interpreting events suggested by aquarists until 1955.
Tab. 2: Elemente des Fortpflanzungsverhaltens von *Corydoras* spp. und verschiedene Interpretationsvorschläge von Aquarianern bis 1955.

Activity	
Female	JÜRGENS (1900, 1906, 1909), REITZ (1910 a), MÜLLER (1932)
Male	CARBONNIER (1981), LIEBSCHER (1904), SCHUBERT (1907), BOECKER (1909), RÖBEN (1909), THUMM (1909), LIEBIG (1912, 1924 a), WITTIG (1913), STECHE (1914), DÖRSCHEL (1925), MICHAILOVITS (1932), KNAACK (1955)
Contact in T-position	
Female adheres to the genital or anal region of the male (mainly by suction)	SCHUBERT (1907), SCHÄME (1907), BOECKER (1909), THUMM (1909), LIEBIG (1912), SACHS (1923), STOYE (1934), ROELICKE (1933), ROHRBACH (1939) SIMANOWSKI (1954)
Female adheres to other regions of the body, e.g. near the base of the pelvic fin (by suction)	JÜRGENS (1900, 1906, 1909, 1923, 1939) REITZ (1905, 1910 a), RÖBEN (1909), WITTIG (1913), STECHE (1914), MERTENS (1917), DÖRSCHEL (1925), MICHAILOVITS (1932), SELEUTHNER (1938, 1950), ROHRBACH (1939), BRETTLING (1940), SPRENGER (1954), PINTER (1955)
Male blocks the female (by clasping her barbels)	CARBONNIER (1880, 1881), LATHAM (1935), STOYE (1952), KNAACK (1955)
The way of sperm and insemination	
Ejaculation in the environment	
Fertilization in the fin pocket	JÜRGENS (1900, 1906, 1909, 1923, 1939), REITZ (1905, 1910 a, b), RÖBEN (1909), MERTENS (1917), DÖRSCHEL (1925), SEELEUTHNER (1938), STETTLER (1950), KNAACK (1955)
Release the sperm onto the female's ventral fin and insemination immediately during final deposition	CARD (1949)
Female swims to an area, where males have ejaculated sperm	SHAW (1935), CARD (1949)
Oral uptake by the female	
Discharge through the gill openings and fertilization in fin pocket	ROHRBACH (1939), BRETTLING (1940), FEIGS (1954), NIEUWENHUIZEN (1955)
Transfer through the gut and fertilization in the fin pocket	LIEBIG (1912), ROELICKE (1933), ROHRBACH (1939), SELEUTHNER (1950)
Insalivation and deposition of sperm before or after final deposition of eggs	SCHUBERT (1907), BOEKER (1909), THUMM (1909), FRIEBE (1924), WITTIG (1913), MÜLLER (1932), KELLY (1938), ADAMS (1939), HART (1947), SPRENGER (1954), CARD (1949), PINTER (1955)

für Aquarien- und Terrarienkunde", a popular magazine for aquarists and herpers founded 1890. GILL included CARBONNIER's description in his review of "Parental care among freshwater fishes" (GILL 1906).

In spite of these careful descriptions, in the following period, especially in the first half of the 20th century, the above mentioned issues were discussed intensively and controversially, especially in magazines. The literature primarily intended for scientists remained reserved (if this issue was concerned at all) considering the question of insemination and fertilisation unsolved (e.g. KOSSWIG 1936).

In German magazines, reports on this matter were published in rapid succession, sometimes even simultaneously. However, respecting the interests of the principal target group of those magazines, reports were often confirmatory, redundant mostly without any debate on information available from previous reports of other aquarists, much less the scientific literature. A

"culture of citation" did not exist, although it was urged by Willy Wolterstorff (1910), at that time editor of the "Blätter für Aquarien- und Terrarienkunde". Therefore, it is often difficult to distinguish between independent observations and foreign influences, e.g. from previous publications. We have selected only those articles that illustrate in our opinion the "struggle for truth" most impressively.

From these early observations five rather self-confident notes on *Callichthys punctatus* (now *Corydoras paleatus,* see tab. 1) by Jürgens (1900, 1906, 1909, 1923, 1939) are noticeable, from which those from 1900 and 1939 are the most important. In 1900 Jürgens considers the female as the more active partner, clearly describes the T-position, says that the female firmly adheres to the male by suction, while the male moves convulsively, and hears growling sounds of the latter (studied 1998 in detail by Pruzsinszky & Ladich 1998). He assumes, as Carbonnier did, that eggs become inseminated and fertilized in the pocket the female forms with her ventral fins.

Jürgens does not explicitly mention discharge of sperm into the water, but obviously assumes that this has happened during the convulsive movements of the male.[2] The note of 1906 confirms earlier statements[3], but Jürgens thinks that the bending of the male's body guides spermatozoa towards the belly of the female, which then were captured by folding of the ventral fins, and shows for the first time a drawing of the T-position (fig. 1). By the way, he quotes (for the first time in his articles) Carbonnier (1881), but obviously expects his readers to know French, because he cites a paragraph from the original without a translation, and Reitz (1905 b), who assumed that the male merely presses against the female to discharge his sperm in the fin pocket. In 1909 Jürgens criticized the article from Boeker (1909), who wrote that the females suck off sperm from the male's genital pore, spits them on the site of final egg deposition and then glues eggs to this site.

In 1923 and 1939 Jürgens defends his opinion against other views, which he believes to be wrong. Especially in the article published in 1939,

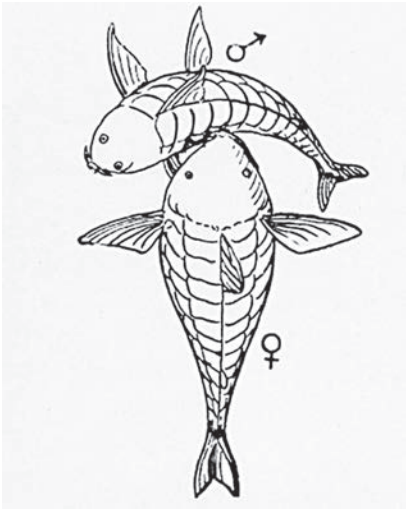


Fig. 1: The first drawing of the T-position in *Callichthys punctatus* (today *Corydoras paleatus*) (from Jürgens 1906).
Abb. 1: Erste zeichnerische Darstellung der T-Stellung bei *Callichthys punctatus* (heute *Corydoras paleatus*) (aus Jürgens 1906).

a kind of review, he rejects the views of Schubert (1907), Reitz (1910 a, b), Mertens (1917), Roelicke (1933), and Rohrbach (1939) – which are briefly described below – ending with the note „all has been resolved, there is only the need to answer the question how sperm come from the male's genital pore in the fin pocket, but the story of sucking in the sperm and in salivating the eggs must be henceforth dismissed in the "boundless area of fantasy" and must disappear from our aquarium literature („alles ist geklärt, nur die Frage, wie gelangen die Spermatozoen vom Geschlechtsporus des Männchens in die Flossentasche, muß noch gelöst werden, aber das Märchen von dem Absaugen des Spermas und der „Einspeichelung" der Eier muß von jetzt ab in das „uferlose Phanatasie Gebiet der Dichtung" verwiesen werden und aus unserer Aquarienliteratur verschwinden." (Jürgens 1939, p. 356)).

However, it may be of interest to take some notice of the observations and their interpretation in the articles published between 1900 and 1939 in particular, because some of them contained some new aspects and some others were totally ignored by Jürgens.

Schubert (1907) doubts fertilization of the eggs in the fin pocket. Rather he thinks that the female sucks the sperm with her mouth, insalivates them and spit them onto the substrate before deposition of the eggs.[4] Curiously, in an article of Thumm (1909) there is a bit of everything. The author describes that the male grasps the female as described by Jürgens, but after that she grasps his anus to suck there. Reitz (1910) emphasizes that the female attaches to the centre of the males' body and not to his genital opening and thinks that sperm move along the belly of the female to reach the fin pocket, that she heavily breathes after separation from the male, and – the new result – he verifies that eggs become inseminated already in the fin pocket by raising larvae from eggs that were removed from this pocket.[5]

An author, who really enriched the debate on the way sperm may take after ejaculation, was Liebig (1912, 1924 a-e). Strikingly, he was totally ignored by other aquarists, namely by Jürgens. In his notes – in reality two longer articles published in serial form – Liebig confirmed the known facts (T-position, female adheres to the male near the anus, male slightly tilts on his side and shivers, etc.), but considered for the first time a passage of sperm through the intestine (Liebig 1912 a), stressing, however, that this is only a wild guess.[6] In 1924 some notes followed with own ideas and speculations providing altogether a good and precise analysis of the hitherto existing aquaristic literature concerning this issue. He summarized taxonomy, keeping and breeding *Corydoras* spp. (Liebig 1924 a, b, c) und asks the right questions, e.g. questions concerning the reasons for the strange release of sperm (among others the body plan of armoured catfishes), the release of sperm (the specific contact of mates), when (exact time unclear) and how the fin pocket is formed (he mainly discusses inconsistent observations of several authors, the disadvantages of this pocket, which may even impede spawning on a flat substrate), and the way sperm may take to reach the pocket (Liebig 1924 d). The latter issue is dealt with in Liebig (1924 e).

Here, he discussed in great detail und critically the following options: (1) a portion of the water containing spermatozoa is collected by folding up the ventral fins (objection: collection of too little sperm, loss of too much sperm); (2) sperm directly swim from the male's genital pore towards the ventral fins directed by the male through bending his body or moving his caudal fin (objection: unfavourable position of the mates; a position, in which the male's ventral body surface is perpendicular to the ventral body surface of the female would be better); (3) the female takes up sperm with her mouth and spit them out before depositing the eggs (objection: the uptake of sperm by the mouth is possible, but according to the most observations not directly from the male's genital opening; spitting does not occur during egg deposition; eggs must be placed in a way that the micropyle can be reached by sperm); and again (4) the female drinks sperm and sperm are channelled via the accessory respiratory system to the fin pocket (objection: mates often eat during spawning, significant gill breathing, but no air breathing after spawning). Nevertheless, he continued to assume that sperm reach the fin pocket via the female's body.[7]

All in all, however, the author did not come to a final conclusion. He states: „After all these ... comments I conclude that nearly all what belongs to the reproduction of *Corydoras paleatus* ... remains undetermined and dark" („Nach allen diesen … Ausführungen bleibt somit das Fazit, dass so ziemlich alles, was zum Fortpflanzungsgeschäft von *Corydoras paleatus* gehört … noch ungeklärt und dunkel ist"; Liebig 1924, 231).

Between the first note of Liebig and his last summarizing remarks in 1924 also other aquarists have published their observations and conjectures. Wittig (1913) again described the female's attachment by suction near the ventral fins of the male and the deposition of eggs in the fin pocket. After a little rest, the female spit on a leaf and then she glued an egg on it. Wittig (l. c.) assumed that insemination and fertilization takes place on the leaf and eggs were glued on by secretions of the mouth. Further, he accurately described tone pitches produced

by the male, which obviously change depending on the degree of excitement.[8]

Mertens (1917) followed the view of Jürgens (see above) and acknowledges the merits of aquarists concerning the reproduction of *Corydoras* spp.[9] Meanwhile Dungan (1917) had bred *Corydoras paleatus* successfully in the USA. The author says nothing about courtship and mating, but in an appendix entitled "Notes on the Panzerwels" attached to this note the editor of the journal reports on the above mentioned article of Wittig, which is not easy to identify at first glance on the basis of the given bibliographic information. Friebe (1924) favours insemination and fertilization after the final deposition of eggs. Dörschel (1925) believes that the female is surrounded by a cloud of sperm that moves along her body up to her fin pocket due to the quivering male. Roelicke (1933) describes the spawning behaviour very accurately, excludes an internal insemination and favours the oral uptake of sperm and their passage through the intestine, arguing that, because the air easily and rapidly passes the intestine, the same may apply for sperm. Seleuthner (1938) does not know how insemination and fertilization may take place, but excludes oral uptake of sperm as he never has seen the female's mouth near the male genital opening. However, later, he favours the intestinal passage of sperm (Seleuthner 1950). Rohrbach (1939) describes the spawning behaviour of *Corydoras hastatus*, recognizes heavy movements of the gill covers of the female during the putative oral uptake of sperm and discusses whether sperm leave the gill openings or whether they pass the intestine to reach the fin pocket.

Finally, the strange and fully deviating speculation of Ada Latham (1935) should be mentioned herein for the sake of completeness. She describes the clasping (=interlocked position), but otherwise cannot confirm previous studies suggesting that the female's relatively long pectoral fin may have a tube that pick up sperm to channel them into the fin pocket.

From around 1939 there are no real new observations; and the discussion – only conjectures and speculations – goes round in circles. Principally, the scenarios listed in table 2 are checked again and again often without acknowledging previous providers of ideas. However, some of them should be mentioned briefly (see also tab. 2). Breitling (1940) argues against the oral uptake of sperm and the intestinal passage in *Corydoras hastatus*, because the female did not adhere to the male's anus and because she has eaten between deposition of the eggs in the fin pocket and the final deposition of eggs. Card (1949) mentions a broad spectrum of possibilities how to inseminate and fertilize the eggs, e.g. immediately when the spawn is deposited on the glass by sperm released onto the female's ventral fins, when the male chases the female (his own suggestion), the oral uptake of sperm by the female and their discharge before or after deposition of eggs, and that the male releases sperm in certain areas and then guides the female there. Stettler (1950) speculates that the (invisible) cloud of ejaculated sperm is sucked in by the sudden opening of the fin pocket, which process he considered more probable than the oral uptake of the ejaculate. Feigs (1954) again rejects the intestinal sperm passage, thinks to have observed oral uptake of sperm and postulates their discharge from the gill opening and their transport along the female's body to the fin pocket. Nieuwenhuizen (1955) referring only to Seeleuthner (l.c.) and Feigs (l.c.) agrees, with Feigs' view and considers the intestinal way of sperm unlikely. Last not least Pinter (1955) assigns active roles to both mates, observes that the female adheres (by suction) to various parts of his body, occasionally also to the genital opening, but thinks the oral uptake of sperm wrong. Further, he believes that sperm might be highly mobile in the water and brings chemoattractants into play.

The secondary literature before Knaack's articles recapitulates previous views, e.g. of Liebscher (l. c.) and Carbonnier (l. c.) (e.g. Bade 1931) or favoured insalivation and deposition of sperm before deposition of eggs (Innes 1935, Arnold & Ahl 1936). Innes (l .c.) also mentions clasping the female's barbels by the pectoral fin of the male.

Really new insights in the reproductive behaviour of *Corydoras* spp. based on pure observations

could not longer be expected. This changed in 1955, when KNAACK started a series of articles, of which especially the first one takes an experimental approach to the subject (KNAACK 1955 ff.).

2.2. The publications of KNAACK (1955-1964)

From 1955 to 1964, KNAACK published four articles on the reproductive behaviour of various *Corydoras* spp. (*C. paleatus*, *C. hastatus*, *C. aeneus*, *C. elegans,* and *C. caudimaculatus*). Of course, also the publications of KNAACK do not meet current scientific standards as he says for instance too little about the methods he used[10], probably not to overtax his readers. However, his articles differ substantially from previous (popular) publications in so far as he observed carefully conducting inventive experiments. In addition, the photos he added to his articles were really excellent for that time.

The most important article dates from 1955 (KNAACK 1955). Here KNAACK described very detailed courting and spawning of *Corydoras paleatus* (without touching, however, previous observers) as a sequence of relative stereotyped activities**.** He distinguishes:

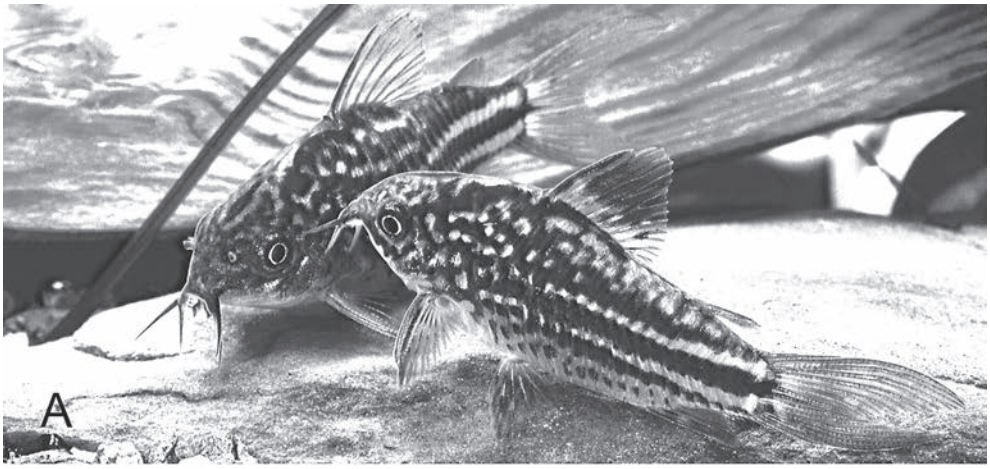
(1) restless swimming of mates and "cleaning" of putative egg laying places by the female;
(2) males tickle the female with their barbels and pectoral fins starting from her tail and then going to her head;
(3) a kind of wedding dance, in which the male performs a variety of movements;
(4) the male blocks the female in T-position by clasping her barbels with his pectoral fin (mostly near the substrate) (see fig. 2) and mates sink to the bottom and remain here for 50 bis 60 s until separation;
(5) discharge of sperm and their distribution into the water (see below);
(6) deposition of eggs into the fin pocket;
(7) insemination and fertilisation of eggs in the pocket;
(8) egg deposition on the substrate.

This process may be repeated several times.

Then KNAACK pays special attention to the way sperm take to reach the fin pocket. In his survey of what has been previously suggested, he confines himself to secondary aquaristic literature. KNAACK dissected a female of *Corydoras paleatus* ready to spawn to exclude internal fertilization and did not found developing egg in the ovary. Further, when he separated the mates during courtship or during spawning, females continued to lay eggs that, however, were unfertilized, but eggs removed from the pocket were fertilized (see REITZ 1910 b). Using a pipette with a finely drawn-out tip he applied a solution of concentrated sodium fluorescein (the amount was comparable to that of the respiratory water) directly in front of the female´s mouth, which rapidly spread, but did not reach the fin pocket. The procedure was repeated at the time the male discharges his sperm, i.e. when he had caught the female with the spine of the pectoral fin. In this case a "cloud" of the fluorescein solution (and in that very probably sperm) spreads in the water through the movements of the mates (fig. 3). In addition, during different stages of mating he removed water at different body sites (genital opening of the male, mouth and gill slit of the female) to check it for sperm. Detection of sperm seemed to have succeeded, but he does not give any further details formulating this result somewhat cryptically.[11] He noticed that spermatozoa in freshwater remained viable for 15 min.

In the following years KNAACK (1956, 1961, 1964) extended his studies to various *Corydoras* species. Apart from minor probably species-specific differences the observation of their

Fig. 2: Reproductive behaviour. **A** Courtship (*Corydoras napoensis*), male in front (Photo: H.-J. RICHTER). T-Positon. **B** *Corydoras paleatus*. **C** *Corydoras aeneus*. Note clasping of the female's barbels by the male's pectoral fin (B drawing: Ramona ALLSTADT-TORRAS after a photo by R. ZUKAL (1973 b). C Photo: H.-J. RICHTER).
Abb. 2: Fortpflanzungsverhalten. **A** Balz (*Corydoras napoensis*), Männchen vorne (Foto: H.-J. RICHTER). T-Stellung. **B** *Corydoras paleatus*. **C** *Corydoras aeneus*. Man beachte die Brustflosse des Männchens, die die Barteln des Weibchens einklemmt (B Zeichnung: Ramona ALLSTADT-TORRAS nach einem Foto von R. ZUKAL (1973 b). C Foto: H.-J. RICHTER).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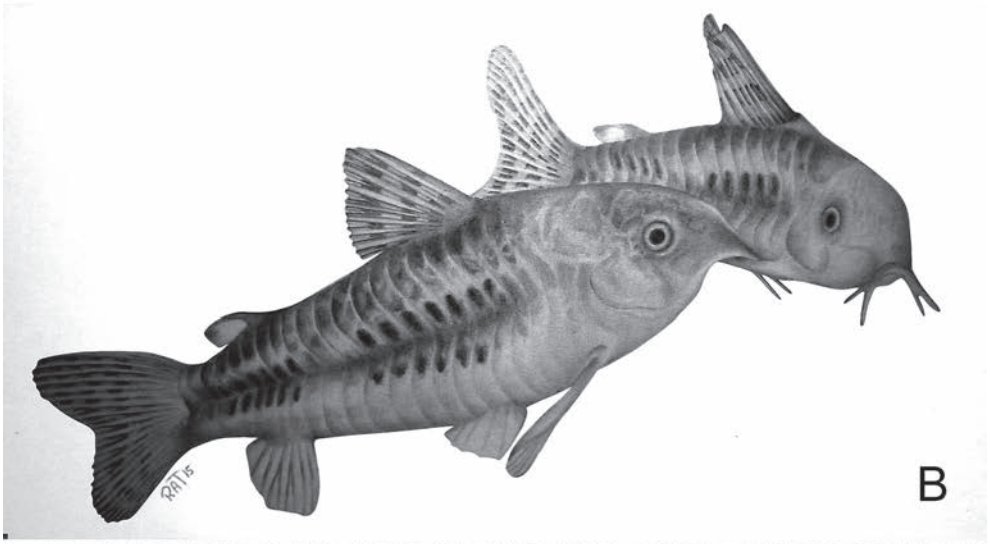
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reproductive behaviour confirmed the general sequence of the events given above.

In the 1964 article, in which he also introduces *Corydoras aeneus* he gives a kind of summary and deals with selected articles from the aquaristic literature.

In conclusion, KNAACK, partially confirming and partially disproving previous views, showed on the basis of photos, film sequences and some experiments

(1) that the reproductive behaviour of several *Corydoras* spp. is broadly the same,
(2) that the male is the more active partner,
(3) that the male blocks the female during the T-position by clasping her barbels with its pectoral fin,
(4) that sperm are released into the free water, and
(5) that eggs become fertilized in the fin pocket.

His articles have brought an endless debate to a temporary conclusion.

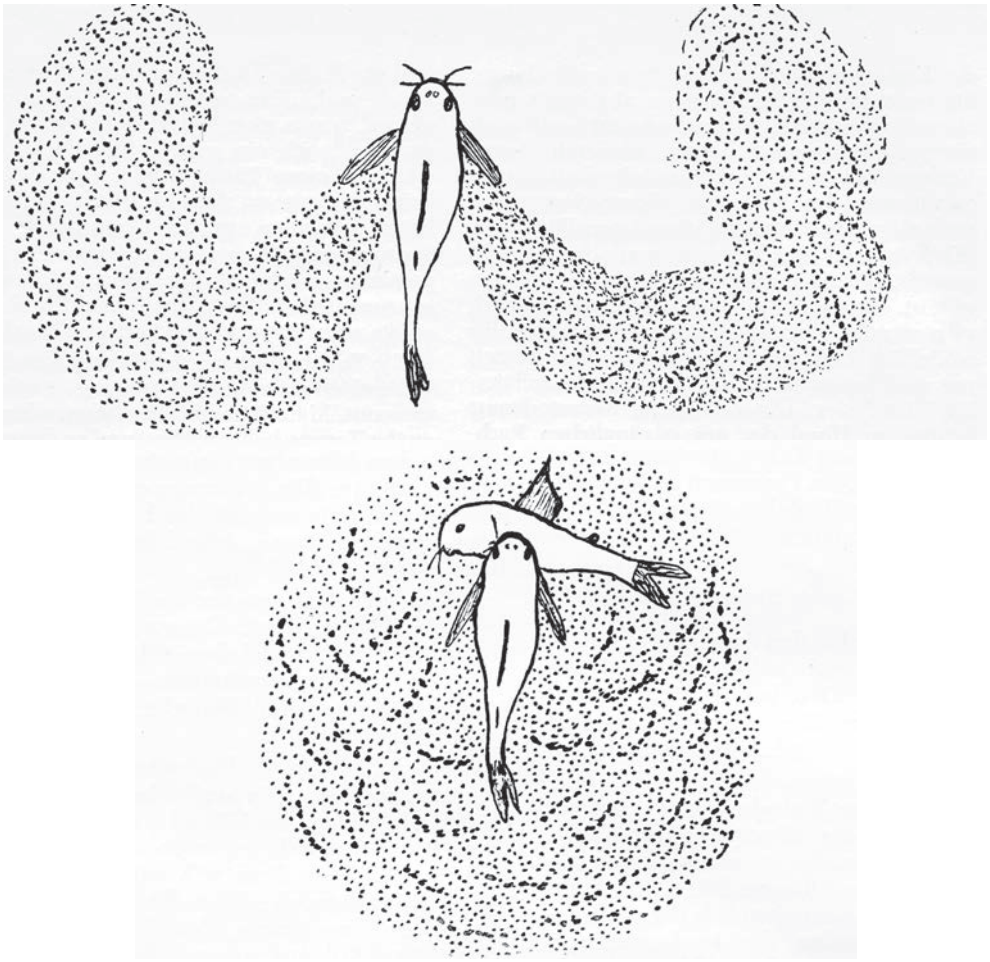


Fig. 3: Distribution of the breathing water of *Corydoras paleatus* after application of a fluorescein solution. On the top: a single female; below: in a couple in T-position during spawning. Note the different distribution of the fluorescein. For further explanations see text (from KNAACK 1955).
Abb. 3: Verteilung des Atemwassers bei *Corydoras paleatus* nach Applikation einer Fluorescein-Lösung. Oben: bei einem einzelnen Weibchen. Unten: bei einem Paar in T-Stellung. Man beachte die unterschiedliche Verteilung des Fluoresceins. Weitere Erklärungen s. Text (aus KNAACK 1955).

Knaack's observations have been appreciated relatively early also in non-German magazines (e.g. van Ramshorst 1957) and later Finley (1995) acknowledges his studies, when commenting the study of Khoda et al. (1995) in the magazine „Tropical Fish Hobbyist". Finley quotes a statement of Klee from a 1963 article, in which he does not want to consider "the ridiculous suggestion that she (the female *Corydoras*) swallows the sperm and later passes it through her vent" (Finley 1995, p. 110). However, his note "American aquarist Albert Klee later reported repeating the experiments in the early 1960s with similar results" (Finley 1995, p. 109) is not quite correct. Albert Klee reported on Knaack's experiments in Tropicals Magazine, September-October 1963, and did not add anything new, but stated at the end of the article: "As a postscript, it should be mentioned that I have tried the pipette-dye technique myself (also experimenting with other dyes) and have found it most effective. Patience is needed (as well as the proper equipment) but water currents and flows can be pinpointed quite nicely." (Klee 2015, pers. comm.) In 1970, Klee published a *Corydoras*-booklet for beginners, in which he briefly touches "sperm drinking" and transport of sperm by the female's barbels to fertilize eggs after deposition, but then he goes on to say: "The true story is much simpler one. The T-formation (and this is not to be taken too literally … the T, at times, may even degenerate almost into two parallel lines) serves to trigger the release of the male's sperm at the exact time the eggs are cupped in the female's pelvic fins. The close proximity of male with female during this process virtually insures proper fertilization." (Klee 1970, p. 7/8) This is entirely consistent with Knaack's experiments, but Klee regrettably does not name any source of this information.

Vogt (1970) summarized courtship and mating of armoured catfishes in „Grzimeks Tierleben" (at that time a famous multi-volume work with several editions and translations in many languages, also in English) notably appreciating the findings of Knaack.[12] His findings appeared to be largely accepted until the publication of the study of Khoda et al. (1995). It was put in several manuals for catfish keepers and breeders (see especially the contributions of H.-J. Franke in Sterba 1978, 1983; Franke 1985; Matschke & Matschke 1986; Hieronimus 1985). Especially Franke (in Sterba 1983, p. 175-176) expresses this issue briefly and precisely: "When mating, the male clamps the barbels of the females fast with the P and releases sperm at the same time. At the same moment the female produces 3–5 eggs and puts them in the Vs which have folded to make a bag. Then she swims though the cloud of sperm to fertilize the spawn and sticks this firmly after a short search." Currier & Smith (1969, p. 70) stated: "The other long standing myth concerns the manner in which *Corydoras* eggs are fertilized. Although scientific proofs have been available since 1955 the discussion still ranges in many quarters."

Breder & Rosen (1966) summarizing the reproductive behaviour of Callichthyidae in their well-known synopsis "Modes of reproduction in fishes" considered most of the above mentioned aquaristic literature until 1957, but obviously were not aware of Knaack's studies. However, authors describe the sperm transfer through the female's intestine as "surely an untenable conclusion", but do not give reasons for this statement (p. 268). Burgess (1987, 1989) describes the clasping of the female's barbels with the male's pectoral spines, favours the idea of a cloud of sperm surrounding the mates, and considers other theories "to be less plausible" (p. 348), but does not mention either the suggested intestinal transfer of sperm or any relevant literature concerning this issue.

2.3. The study by Khoda et al. (1995) and its consequences

From the above results and discussions nothing can be found in Khoda et al. (1995). This is strange, as the authors quote the synopsis of Breder & Rosen (1966), which summarizes most of the previous aquaristic literature concerning this issue (see above). Rather they extracted three hypotheses from popular books (among others Burgess 1989) how eggs are

inseminated "Insemination occurs (a) by sperm spread in the aquarium at various times after spawning; (b) on the egg attachment site by sperm, and there discharged from the mouth of the female held from the time of T-position, and (c) inside her pouch by sperm coming from a male in the T-position" (p. 3) or to formulate the relevant questions (1) Which male does fertilize the eggs? (2) Where fertilization does take place? (3) How sperm enter the pocket formed by the female's fins? Hypotheses 1 and 2 were disproved in favour of hypothesis 3 for a long time (see above).

In the abstract author's state: "We report on unique reproductive behaviour and a new mode of egg insemination in a small catfish *Corydoras aeneus* (Callichthyidae). A male courts a female by presenting his abdomen to her. Before releasing eggs, the female attaches her mouth to the male's genital opening and directly drinks his sperm. The sperm pass through her intestine and are discharged together with eggs into the "pouch" formed by her pelvic fins. Thus eggs are mixed with fresh non-dispersed sperm in an enclosed space, ensuring effective insemination. This mode of insemination is novel to fishes, but likely not restricted to catfishes of the genus *Corydoras*." (p. 1).

The brief description of courtship and spawning of *Corydoras aeneus* corresponds largely to that what is known from previous descriptions including ejaculation of sperm that according to general opinion takes place when mates are in the T-position. However, their description differs in two crucial details from previous observations: (1) Authors describe that the female attach her mouth to the male's anal region or genital opening instead of clasping her with his pectoral fin (interestingly, figure 1 in their article illustrating the sequence of behaviour during reproductive of *C. aeneus* shows in section figure d that the male clasps the barbels of the female with his pectoral fin), and (2) that the female closed her gill covers tightly for approx. 7 s, i.e. approximately the time the attachment of mates takes.

To clarify the way of sperm authors performed three experiments. In experiment I they used different strains of mates (albino and normal type) what shows that all eggs of one clutch were inseminated by sperm of the given mate. Results disproved the above mentioned hypothesis 1. In experiment II they collected eggs at various times after release 1 and showed that eggs are inseminated inside the fin pocket rejecting hypothesis 2. These results confirmed experimentally what was already expressed in earlier opinions (see above). In view of the above mentioned observations, experiment III is of specific interest.

Authors pipetted an aqueous solution of methylene-blue at the mouth of a female in T-position and describe their observations as follows: "After 4.2 s (± 0.8 SD, n=22) of the release of the solution, blue water appeared from her anus and was funnelled into her ventral pouch. During the time that the gill covers were closed (about 7 sec), the blue solution did not flow from her gills. The blue solution remaining around the mouth of the female did not reach the abdominal area (…). The flow of the blue water clearly indicates that the female drinks sperm together with some water from around the anal region of the male and discharges this into her pouch" (p. 4). With this experiment, authors obviously excluded a "sperm flow or swim along the outside of the body of the female" (p. 4). Unfortunately, authors did not state how and by what means they obtained such exact measurements of time.

Conclusions are as follows: "The reproductive behaviour of *Corydoras aeneus* includes a female's mouth attachment to a male's anal region in the T-position and releasing eggs into her pouch formed by ventral fins as in congeners (…). The flow of the blue water strongly indicates that while the gill covers of the female of *C. aeneus* are closed during the T-position, she directly drinks the sperm with some water, which is transported quickly through her intestine and discharged into her pouch. Eggs are released just after the discharge of sperm and will be inseminated inside her pouch, while she remains still on the bottom. Although fishes exhibit a variety of reproductive behaviours (…), this mode of egg insemination in *C. aeneus* is novel among fishes,

and perhaps in the animal kingdom (KHODA et al. 1995, p. 4-5).

Presence of a short gut length, frequent gulping air and its rapid passage through the gut, a fin pocket near the anus and the T-position during mating, all these features typical for many Callichthyidae prompted the authors to assume a wider distribution of sperm drinking among catfishes. Generally, "sperm drinking" has been considered as highly adaptive as this strategy may ensure a high insemination rate in turbulent habitats.

Critical responses to this study were primarily published in aquarist magazines, whereas reaction of the scientific community was reserved or scientists simply accepted the study (see above and below). Here we refer only to two articles. One study focusing on sound production of *Corydoras paleatus*, briefly describes the courtship sequences based on video sequences, and gives a drawing that shows a male clasping the female's barbels (PRUZSINSZKY & LADICH 1998). Authors cite KHODA et al. (1995), but did not take any further notice of clasping.

The second study, a review on the reproductive biology of the catfish *Hoplosternum littorale* (HOSTACHE & MO 1988) describes the contact of the female's mouth with the male's genital opening, while mates are in the T-position. During this time the female obviously collects the sperm in her mouth. After that she rests up to 60 sec on the bottom. According to GAUTIER et al. (1998; see also BREDER & ROSEN 1966), the female of *H. littorale* simultaneously release sperm (collected in her mouth) and eggs (deposited in her fin pocket) in the foam nest. In view of the study of KHODA et al. (1995), HOSTACHE & MO (1998) think that "sperm drinking" in *H. littorale* is possible.

3. Are there arguments against "sperm drinking"?

Results and their interpretation presented by KHODA et al. (1995) are, indeed, highly suggestive. Nobody doubts today that only one male fertilizes the eggs per clutch and that eggs are fertilized in the female's fin pocket. Regarding "sperm drinking", two observations by KHODA et al. (1995) cannot be confirmed or denied at present. These are (1) the release of the methylene blue solution applied to the female during T-position through the female's anus, and (2) the tight closure of the gill covers during the period the female may take up the sperm. By the way many of the above mentioned observers noted heavy movements of the gill covers during this time. Concerning the distribution of colour solutions a contrary study exists (KNAACK 1955), whereas the closure of the gill cover has been never mentioned before to our knowledge.

Provided that sperm do really pass the intestine as described by KHODA et al (1995), it is reasonable to interpret the results of other studies on the biology of armoured catfish within the meaning of this phenomenon. Thus, KHODA et al. (2002) argued in a follow-up study that the strikingly small gonadosomatic index of *Corydoras aeneus*, an obviously missing contest competition and, thus, sperm competition correspond with the small testis (see also STOCKLEY et al. 1997).

A similar approach is evident in two studies on the seminal vesicles published in the same year. Seminal vesicles are accessory glands of the male genital tract of a variety of non-related teleost taxa, whose secretions containing a variety of substances contribute to the seminal fluid. Secretions contain a variety of substances, of which various glycoproteins ("mucins") constitute the largest part, which are assumed to have a variety of functions such as ensuring sperm viability, immobilization of sperm, nutrition of sperm etc., but strictly speaking functions are not clear (for further readings see MAZZOLDI et al. 2007). FRANCESCHINI et al. (2007) studying the seminal vesicles of *C. aeneus* by conventional histochemistry speculate that their secretions might protect the sperm cells during the passage through the gut "forming a gelatinous environment" (p. 114) that also keeps sperm aggregated and immobile. In a broader study MAZZOLDI et al. (2007) found that within the Callichthyidae *Corydoras* spp. and *Hoplosternum littorale*, both assigned to the "sperm drinking"-type, possess seminal vesicles, whereas *Callichthys*

callichthys ascribed to the classic type of external spawners did not have this structure. Again they assume that the viscous mucus secreted by the seminal vesicles may reduce sperm dispersal (of significance for males with a low investment in gonads, see above) and protect the sperm in the gut. To our knowledge there is no experimental evidence for the suspected protective role of seminal vesicle secretion.

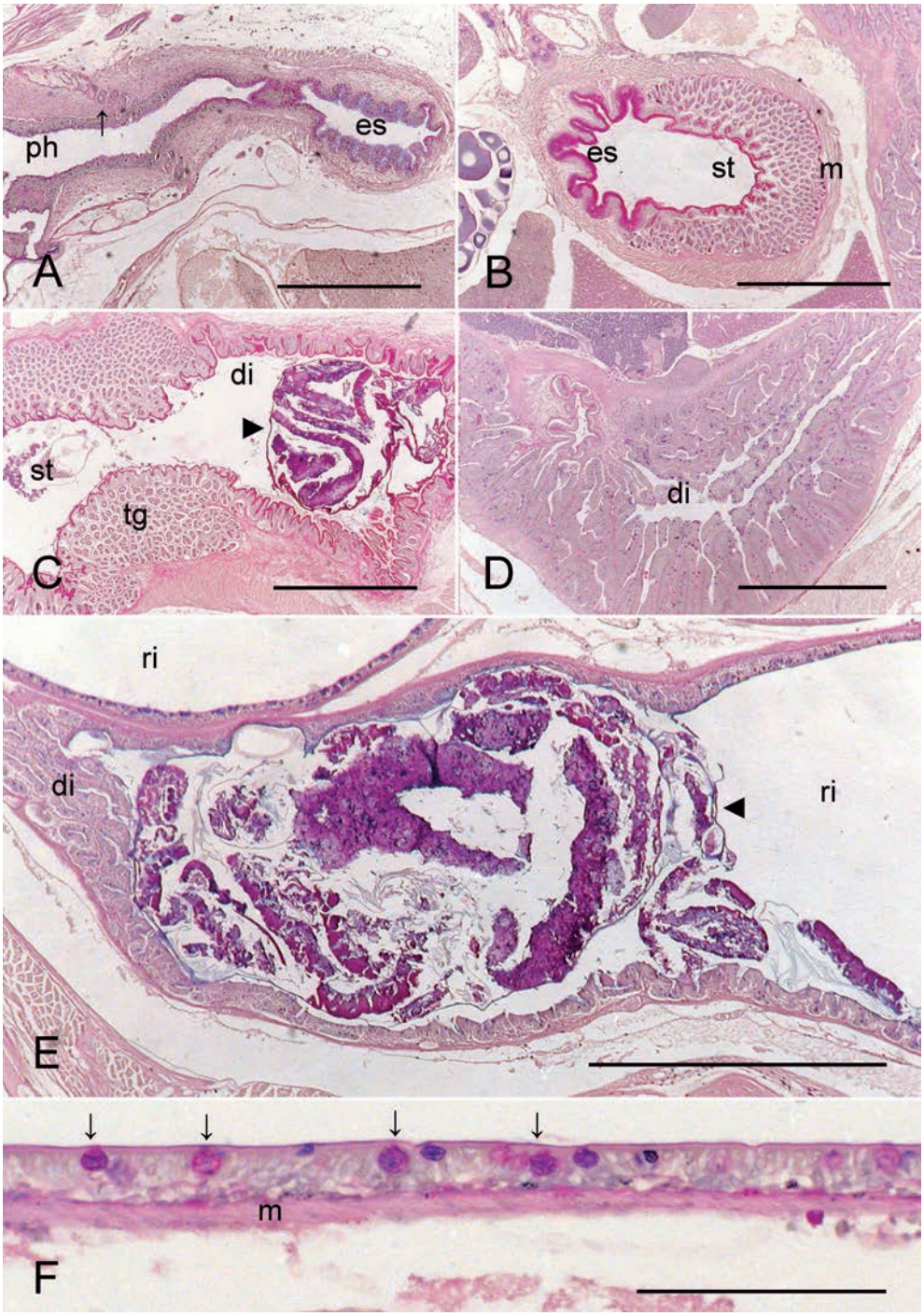
Aside from references to previous studies and a general feeling of suspicion (see introduction) some inconsistencies arising from the article of Khoda et al. (1995) should be commented more detailed.

Since 1881 courtship and mating of catfishes of *Corydoras* spp. have been observed countless times. Therefore the general sequence of behavioural events as described above is sufficiently proven. As a result it is unquestionable that the male blocks the female by clasping her barbels during the T-position, in which, and this is the overall opinion, sperm are discharged by the male. Clasping has been documented repeatedly by photos (s. Knaack 1955, 1964; Frey 1957; Burgess 1987; Zukal 1973 b) and drawings (e.g. Prudzinski & Ladich 1998) and even Khoda et al. (1995) depict this event (see their fig. 1 d), using, however, the ambiguous word "attaches" to the genital opening (p. 1) or "attachment" to the anal region (p. 5) to describe the contact between female and male. Therefore it is questionable, whether females do place her mouth over the genital opening of the male to suck in sperm. If so, drinking of discharged sperm would be extremely ineffective, if at all possible.

The time (approx. 4 s) for passage of sperm through the gut has caused surprise. *Corydoras* spp. are benthivores (Khoda et al. 2002) specialized primarily on aquatic invertebrates (Ibanez et al. 2007). Intestines of *Corydoras* spp. (mean standard length 51 mm) measures 28 mm on average (distance from the beginning of the esophagus to the anus) (Ibanez et al. 2007) and of *C. aeneus* 1.3-1.6 times the standard length (Kramer & McClure 1980) or 5.4 cm (Khoda et al. 1995; measured distance and standard length of specimens are not given). The mean forward velocity spermatozoa of freshwater teleost's may reach is 135-164 µm/s and longevity is within the range of a few seconds up to several minutes depending on the species (Alavi et al. 2005; see also Browne 2015). The maximum travel distances of fish sperm is relatively short (2.3–14.0 mm), because their high velocity ranging from 65 to 250 µm/s failed to compensate for their motility period of seconds to minutes (for review see Browne et al. 2015). Although relatively short, it is clear that spermatozoa are not able to cover this distance on their own.

The digestive tract of *Corydoras* spp. consists of the pharynx, a short, straight esophagus, a small muscular stomach, a thick anterior intestine with a highly folded mucosa, a thin-walled translucent posterior intestine with a flat and highly vascularized mucosa (fig. 4 A-F), and the rectum. Anterior and posterior intestine form some loops in the body cavity. The posterior intestine, approximately 21-69% of the entire intestine, serves as an accessory respiratory organ. It is unsuitable for digestive functions and is generally found to be devoid of digesta (Kramer & McClure 1980; Podkowa & Goniakowska-Witalinska 2002; Persaud et al. 2006; Nelson & Dehn 2011). The specific organisation of

Fig. 4: The various parts of the digestive tract of *Corydoras aeneus*. **A** Transition from the pharynx (ph) to the esophagus (es). Note pharyngeal teeth (arrow). **B** Transition from the esophagus (es) to the stomach (st); muscles (m). **C** Transition from the stomach (st) to the digestive intestine (di); note digesta in the lumen (arrowhead), tubular glands (tg). **D** Digestive intestine with high folding of the mucosa (di). **E** Transition from the digestive intestine (di) to the respiratory intestine (ri). Digesta (arrow). **F** Flat epithelium of the respiratory intestine with several goblet cells (arrows); muscle layer (m). Staining: AB-PAS for the demonstration of various glycoconjugates that are dyed in various red-blue shades. Scale bar: A-E = 1 mm, F = 100 µm.
Abb. 4: Die verschiedenen Abschnitte des Verdauungstraktes von *Corydoras aeneus*. **A** Übergang von Pharynx (ph) zu Ösopagus (es), man beachte die Pharynxzähne (Pfeil). **B** Übergang vom Ösophagus (es) zum Magen (st); Muskulatur (m). **C** Übergang vom Magen (st) zum verdauenden Darmabschnitt; man beachte



die Nahrungsreste (Pfeilspitze), tubuläre Drüsen (tg). **D** Verdauender Darmabschnitt mit starker Auffaltung der Mukosa (di). **E** Übergang vom verdauenden (di) zum respiratorischen Darm (ri). **F** Flaches Epithel des respiratorischen Darms mit Becherzellen (Pfeile); Muskellage (m). AB-PAS-Färbung zum Nachweis verschiedener Glykokonjugate, die in blauroten Farbschattierungen gefärbt sind. Maßstab: A-E = 1 mm, F = 100 µm.

the posterior intestine, which allows to digest and breath simultaneously by channelling (see below), may serve as tool for explaining the rapid passage of sperm through the gut (see HELFMAN et al. 2007). KHODA et al. (1995) even suggested that intestinal breathing may be one of the preconditions enabling the evolution of "sperm drinking".

As gut air breathers callichthyid catfishes frequently gulp air, which then passes quickly through the gut leaving the anus as an air bubble. To ensure efficient gas exchange, digesta in the posterior intestine are quickly removed by the unidirectional transport of air rather than by peristaltic movements. However, to create a more or less permanent air channel a transitional muscular zone between the digestive and respiratory portion compacts the digesta and possibly encases it with mucus, which results in a string of compressed boluses (PERSAUD et al. 2006). Obviously, formation of compressed boluses does not occur in the stomach and the digestive (anterior) intestine, which are often filled to some extent as *Corydoras* spp. are opportunistic feeders eating more or less continuously also between the single batches (see also fig. 4 C, E). This means that according to the view of KHODA et al. (1995) the water (with sperm) sucked in by the female must find its way through the esophagus, the stomach, the anterior intestine (filled at least in part) and the column of air present in the posterior intestine within seconds. These issues have not yet been sufficiently considered.

4. Conclusions

Comparing the observations and experiments of amateurs done in the last century on reproduction of callichthyid catfishes with that of the only scientific publication on this matter some questions and problems have arisen that need to be clarified before "sperm drinking" in catfish can count as a "proven" fact. However, before it makes sense to approach this problem again, novel experimental strategies and designs should be developed. In this context, it is noticeable that within the last 20 years apparently no one has made a serious effort to experimentally reprocess this "novel" and "unique" mode of egg insemination.

Another issue we only touch here is the fact that the most important data summarized by us have been published at the beginning and the middle of the last century in magazines, which we would today call at best „gray" literature. However, at that time aquarium fishes appeared to swim more easily across the boundaries between amateurs and professionals bringing considerable knowledge in their train.

According to today's usage, the term "gray" literature denotes not only conference proceedings, institutional reports not peer-reviewed, but generally "unconventional" (scientific) literature outside of the book trade, but also conventional informational material, e.g. magazines for hobbyists that usually do not contain original scientific contributions. Especially the latter are ignored to the largest extent by the scientific community. This is quite understandable considering the almost unmanageable amount of publications issued annually, and in view of the fact that these contributions mostly do not meet scientific standards (e.g. precise description of the methods used, plausible interpretation supported by the existing (scientific) literature, etc.), that "gray" literature is generally harder to access (for many people the inaccessibility is enough reason why it should not be cited), that those articles are published in national or even local magazines and, thus, are entirely unknown, or/and that they are written in languages not the easiest to understand. These disadvantages are not compensated by the often high circulation, good print quality and the low subscription rate. However, although mostly published in this kind of literature, experience and careful observations made by numerous aquarists significantly contributed and still contribute to the knowledge of the biology of (ornamental) fishes just as it was illustrated above. However, we have to ask ourselves whether these contributions are always acknowledged properly.

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Appendix

In the following we literally quote some passages from articles of aquarium magazines that to our opinion are particularly informative and original. Further, we add an translation into English maintainig all inconsistencies such as imprecise information on anatomical details etc.

[1] „Séduits et encouragés sans doute par la déclaration qui venait de leur être adressée par la femelle, deux ou trois mâles des plus entreprenants se précipitèrent vers celle-ci; ils s'agitaient sur ses côtés tout le long de l´abdomen, un autre se plaça sur son dos, un plus audacieux encore se posa en travers, au-dessus de la tête et à l'aide du premier rayon osseux de sa nageoire pectorale, comme avec une main, il étreignit avec force la femelle par ses barbillons. Accroché ainsi et posé dans le sens transversal, il se laissa glisser jusque sous la tête de la femelle, en émittant avec force dans la direction de l'abdomen de cette dernière ses principes fécondants… Au moment même où elle se sentait étreinte par le mâle, elle rapprochait l'une de l'autre ses deux nageoires ventrales à la façon de deux éventails ouverts qu'on réunirait par leurs bords, formant ainsí une sorte de cul-de-sac dont son abdomen et les membranes des nageoires formaient les parois, et au fond duquel se trouvait l'ouverture des ovaires. Les principes fécondants du mâle se trouvent ainsi emprisonnés, sans pouvoir s'échapper, dans cette sorte de sac membraneux, et lorsqu'une minute après les œufs vont y arriver expulsés par les contractions abdominales de la femelle, ils se trouveront en contact immédiat avec un liquide riche en spermatozoaires et par suite fécondés." (Carbonnier 1881, p. 106/107) [Seduced and encouraged by the female's declaration of love, two or three more enterprising males approached her moving to her abdominal side; another male positioned himself over the female's back and an even more bolder male placed himself transversely directly over her head vigorously clasping (like a hand) the female's barbels with the first bony spine of his pectoral fin. Attached in this way and in the transversal position he slipped under the head of the female, where he released his fertile principles (= sperm) towards her abdomen with great power … At the same moment she felt clasped by the male, she brought close

to each other her two pelvic fins like two open fans touching one another at the edges. Thus, she formed a kind of pocket, whose walls consisted of the the abdomen and the membranous fins, while the ovaries opened on its floor. Sperm of the male are stowed in this kind of membranous sac, without being able to run out, and if a minute later the eggs, expelled through the female´s abdominal contractions, arrive there they come into direct contact with a fluid rich ine sperm and become thereby fertilized ...]

[2] „Jetzt packte das Weibchen das quer vor ihm liegende Männchen mit dem Maule dicht über der Bauchflosse in die Seite und sog sich an ihm fest. Das Männchen bog sich halbkreisförmig unter fortwährend zitternden Bewegungen, so daß die konkave (S. 217) Seite dem Weibchen zugekehrt war, und zuckte konvulsivisch zusammen. Während dem hatte das Weibchen die gespreizten Bauchflossen zusammengefaltet und daraus eine Tasche gebildet, die den After, welcher zugleich als Geschlechtsöffnung dient, vollständig umschloss. Gleich darauf sah ich kurz hintereinander etwa ein halbes Dutzend weiße Eier in die glashelle Flossentasche fallen. Während dieser Vorgänge ließ das Männchen öfter ein knurrendes Geräusch hören,…Trotz größter Aufmerksamkeit habe ich nicht wahrnehmen können, daß das Männchen die Eier erst nach dem Ablegen befruchtet. Die Befruchtung derselben wird vielleicht schon in dem Moment erfolgen, wo das Männchen vom Weibchen angesogen wird und in konvulsivische Zuckungen gerät. Wahrscheinlich wird das mit den männlichen Spermatozoen geschwängerte Wasser, welches von der Flossentasche des Weibchens aufgefangen wird, im Innern der Tasche die Befruchtung der Eier bewirken".(Jürgens, 1900, S. 218)
[Now the female grabbed the male that lies across her with her mouth just above the pelvic fin and firmly adhered to him by suction. The males formed a semicircle while constantly shivering his body, the curved side facing the females, and twitching convulsively. Meanwhile the female has folded up the pelvic fins to form a pocket that completely enclosed the anus, which serves also as a genital porus. Shortly after this I saw how about half a dozen white eggs dropping in quick succession into the bright fin pocket. During these operations, the male make a croaking noise ... Despite the utmost attention I could an not observe fertilsaten by the male after dropping the eggs. Their fertilization probably takes place at the moment the male is sucked in by the female and twitches convulsively. Perhaps the water filled with sperm and captured by the female's fin pocket, will fertilize the eggs in the pocket.]

[3] Die Eier werden aber nicht erst nach dem Absetzen der Eier befruchtet, sondern dieser Akt ist schon vorher vollzogen. Der Befruchtungsvorgang ist nur so zu erklären, daß durch den Reiz des Ansaugens beim Männchen ein geringer Teil Sperma austritt und das Weibchen unmittelbar darauf durch Zusammenklappen der Bauchflossen ein Teil des mit Spermatozoen geschwängerten Wassers abfängt. Die Befruchtung geschieht demnach schon in der Flossentasche. Es scheint, daß durch die in einem Ruck erfolgende halbkreisförmige, seitliche Biegung, die der Körper des Männchens im Momente des Ansaugens einnimmt, wobei die konkave Seite dem Weibchen zugekehrt ist, die Spermatozoen nach der Mitte des Bauches des Weichens dirigiert und mit den zusammenklappenden Bauchflossen aufgefangen werden". (Jürgens, 1906, S. 368-369)
[The eggs become fertilized not after their dropping (on the substrate), but fertilization has taken place already previously. The fertilization process can only be explained by the fact that the females triggers the release of a small amount of sperm by sucking on the male and that the female catches portions of water loaded with sperms by folding up her ventral fins. Thus, fertilization takes place already in the fin pocket. It seems that the sperm is directed towards the middle of the female's belly and captured with the folded up pelvic fins, while the male abruptly bends his body laterally in a semicircle during the sucking, his curved side directed against the female.]

[4] „Die Befestigung des Laiches erfolgte in der Weise, daß das Weibchen zunächst eine Stelle mit dem Samen des Männchens, den es von ihm angesaugt hatte, einspeichelte, sodann je ein Ei darauf klebte … Die Befruchtung des Laiches erfolgt demnach nicht, wie bisher angenommen wurde, in der Flossentasche, sondern außerhalb derselben dadurch, daß das Weibchen die Eier mit dem vom Männchen ausgesaugten Samen einspeichelt" (Schubert, 1907, S. 546).
[Fixing the spawn was carried out in such a way that the female first insalivated a site with the male's sperm sucked in before and then attached a single egg there…Thus, fertilization of the spawn does not take place in, as previously thought, but outside the fin pocket by the fact that the female insalivates the eggs with male sperm sucked in before.]

[5] „Direkt nach einem Paarungsakt fing ich das betreffende Weibchen mit voller Flossentasche aus dem Zuchtbehälter und bemächtigte mich mittels eines Pflanzenstengels der Eier, die ich in einem gesonderten Behälter unterbrachte. Dieselben waren mit dem

Maule des Weibchens absolut nicht in Berührung gekommen und fielen trotzdem ordnungsgemäß aus, … Es darf also als einwandfrei gelten, dass die soeben ausgestoßenen Eier schon in der Flossentasche des Weibchens befruchtet werden." (Reitz, 1910 b, S. 375)
[Immediately after mating I removed the respective female, whose fin pocket was full, from the breeding tank, seized the eggs by means of a plant stem and brought them in a separate container. They definitely did not come in contact with the mouth of the female, but developed properly ... It is certain that the just ejected eggs are fertilized already in the fin pocket of the female.].

[6] „Ich überlegte mir nun, weshalb eigentlich das Weibchen die Eier in der Bauchflossentasche festhält, da dies zum Zwecke des Anheftens doch nicht erforderlich ist, wie zum Beispiel die Cichliden zeigen. Ich kam deshalb auf den Gedanken, daß es vielleicht doch nur zum Zwecke der Eibefruchtung geschieht und daß möglicherweise das Sperma denselben Weg nimmt wie die akzessorische Atmung. Es ist dies natürlich nur eine Vermutung." (Liebig, 1912 a, S. 427)
[Now I was wondering why the female holds the eggs in the bag formed by the pelvic fins, because this is not required for the purpose of adhering them, as, for example, is shown in cichlids. I therefore had the idea that this might happen only for the purpose of fertilization of eggs and that sperms possibly take the same route as the accessory breathing. This is of course just a guess.]

[7] „Die von mir 1912 ausgesprochene Vermutung, daß das Sperma den gleichen Weg durch den Körper des Weibchens nimmt wie die der akzessorischen Atmung dienende Luft, beruhte auf dem Glauben, daß neben dem Verdauungsdarm noch ein Atmungsdarm herliefe. Heute bin ich in solchen Sachen vorsichtiger, leider über den Bau des akzessorischen Atmungsorgans auch nur insoweit unterrichtet, daß ein Teil der Darmschleimhaut hierzu dient. Trotzdem komme ich aber auch jetzt wieder zu einem ähnlichen Schluß." (Liebig, 1924, S. 230)
[My assumption from 1912 that sperms take the same route through the female's body as the air for accessory respiration was based on the idea of a "respiratory gut" paralleling the digestive gut. Today I am more cautious in such matters; unfortunately I know only that a portion of the intestinal mucosa serves for this purpose. However, again I come to a similar conclusion.]

[8] „Plötzlich drehte das Weibchen den Spieß um. Mit einer schnellen Bewegung hatte es das Männchen an der Seite gepackt und heftete sich unter kräftigem Saugen an das Männchen in der Gegend der Bauchflossen, wo neben dem After die Geschlechtsöffnung mündet. Mit zitternden Bewegungen hafteten so die Tiere eine Weile, 10 bis 20 Sekunden, aneinander, wobei das Männchen sich etwas auf die Seite legte und dem Weibchen den Bauch zukehrte. Während dieses Vorganges traten 3-4 Eier aus der Genitalöffnung des Weibchens in eine Tasche, die durch Zusammenlegen der Bauchflossensäume gebildet wurden. Auf diesen Akt folgte ein kurzer Zustand der Schwäche besonders für das Weibchen … Nachdem es sich dann erholt hatte, schwamm es zwischen den Pflanzen umher, suchte sich ein geeignetes Blatt der *Ludwigia* aus und berührte es auf der Unterseite mit speienden Bewegungen des Maules, wobei es jedenfalls einen klebenden Stoff absonderte und an die Blätter heftete. Dann legte sich das Weibchen … auf den Rücken, … drückte schnell die Eier an das Blatt, wo sie gleich festhafteten … Wann die Befruchtung stattfindet, … habe ich nicht genau feststellen können. Entweder erfolgt sie in der Flossentasche oder dann, wenn die Eier an die Blätter geheftet werden. Das letztere ist mir wahrscheinlicher. Daß die Samenflüssigkeit in die Flossentasche aufgenommen wird, ist bei der zu einander senkrechten Lage der Tiere während dieses Aktes vollständig ausgeschlossen. Dagegen wäre es möglich, daß durch die saugenden Bewegungen des Weibchens die Samenfäden zwischen den Kiemen hindurch gegen die Bauchflossen geschleudert würden und hier die Eier befruchteten. Allein dagegen spricht wieder der feste Zusammenschluß der Flossensäume. Es hat wohl wenig Wahrscheinlichkeit für sich, daß das Saugen allein ein Reizmittel für den Austritt der Samenflüssigkeit ist, denn dann wären gerade die Eier möglichst weit von der männlichen Geschlechtsöffnung entfernt und da gelegen, wo sie die geringe Aussicht auf Befruchtung hätten. So bleibt nur noch der Fall übrig, daß das Weibchen die Spermatozoen aufsaugt und sie dann gegen das Blatt speit, wo nun erst die Eier befruchtet werden (Wittig 1913, S. 286-287).
[Suddenly, the female turned the tables. With a quick movement she grasped the male's side whilst vigorously sucking adhering to the area of his pelvic fins near the anus, where the genital opens. With continuous quivering mates adhered to each other for a while, 10 to 20 seconds; during this event … the male slightly lay on his side turning his belly towards the femael. Meanwhile 3-4 eggs were expelled from the female's into a pocket formed by folding the edges of the pelvic fins … After that followed a short condition of weakness, especially

for the females … When she had recovered, she swam among the plants searching for a special leaf of *Ludwigia*, which she touched on the underside with a spitting motion of the mouth, whereby a adhesive substance was exuded and fastened to the leaves. Then, the female turned on her back and quickly pressed the eggs on the leaf, where they adhere immediately. When fertilization takes place … I could not exactly see. Either it takes place in the fin pocket or when the eggs are fastened on the leaves. The latter is more probable. That the sperm is admitted into the fin-pocket is completely excluded due to the animal's perpendicular position to each other during this act. On the other hand, it could be that through the sucking operation of the female the spermatozoa are drawn through the gills and thrown back on the ventral fins to fertilize here the eggs. Against this speaks the fact that the fin edges are tightly closed. It appears unlikely that the sucking alone stimulates ejaculation for at that time the eggs are farthest away from the male's genital opening and placed where they would have the least chance of being fertilized. So the theory only remains that the female sucks out the sperm and spits it against the leaf, where the eggs are fastened, and here fertilization takes place.]

[9] „Das Interessanteste, was *Corydoras paleatus* dem Beobachter zu bieten vermag, ist ohne Zweifel seine Fortpflanzung. … Das Verdienst, diesen Vorgang entdeckt zu haben, kommt der Aquarienkunde zu." (Mertens, 1917, S. 211).
[The most interesting thing *Corydoras paleatus* offers the observer is undoubtedly its reproduction. The spawning of this fish is in fact very peculiar and unique among fishes. The merit of having discovered this matter goes to aquarists.]

[10] „Um den Weg des Spermas und damit die Befruchtung kennenzulernen, habe ich eine Reihe von Versuchen durchgeführt, die ich im Rahmen dieses Aufsatzes nicht ausführlich besprechen kann. Lediglich einige wichtige Beobachtungen und Ergebnisse sollen mitgeteilt werden" (Knaack 1955, S. 165).
[To get to know the way of sperm and with that fertilization, I performed some experiments that I can not discuss in detail within this article. Only some important observations and results shall be communicated here.]

[11] „Als Ergebnis kann gesagt werden, daß, nachdem das Weibchen vom Männchen festgeklemmt ist und gegen die Geschlechtsorgane des Männchens gedrückt wird, die Spermatozoen aus der Genitalöffnung ins Wasser treten." (Knaack, 1955, S. 166)
[To conclude, spermatozoa are discharged from the genital opening into the water, after the female is clamped by the male and pressed against the reproductive organs of the male.]

[12] „Bis vor wenigen Jahren sind über die Fortpflanzung der Panzerwelse falsche Angaben gemacht worden. Seit die erste Zucht dieser Tiere im Aquarium gelang, hieß es über Jahrzehnte hinweg immer wieder, daß sich das Weibchen in der Geschlechtsgegend oder gar an der Genitalpapille des Männchens festsauge und dabei den Samen absauge und verschlucke, so dass es zu einer Art von „innerer Befruchtung" komme. Es gab schon immer eine Reihe anatomische Beweisgründe, die gegen diese Annahme sprachen; aber erst 1955 hat Knaack eine Richtigstellung vorgenommen. Er beobachtete und fotografierte die Panzerwelse bei der Paarung und fand schnell heraus, daß die Weibchen sich nicht ansaugen. Die Männchen legen sich zur Paarung vor das Weibchen, umfassen dann die gegen ihre Körperseiten stoßende Partnerin mit den kräftigen Strahlen der Brustflossen unter den Bartfäden und klemmen sie am eigenen Körper fest. Dann gibt das Männchen seinen Samen einfach in das Wasser ab, während das Weibchen ein oder zwei Eier austreten läßt und mit den Bauchflossen auffängt. Nun löst das Männchen seine Klammerung; und das Weibchen schwimmt mit der aus den Bauchflossen gebildeten, nach vorn offenen Tasche, in der die Eier kleben, durch die Wolke von Spermien, um den Laich zu befruchten." (Vogt, 1970, S. 405/406)
[Incorrect statements about reproduction of the armored catfish have been made until a few years ago. Since the first successful breeding of these animals in the aquarium it was published again and again over decades that the female adheres to the male's genital area or even to his genital papilla sucking in and swallowing the spermlieding to a kind of "inner fertilization". There have always been several anatomical reasons against this suggestion, but only Knaack has corrected this view in 1955. He observed and photographed armoured catfishes during mating and soon he become aware that the females do not adhere by suction. During mating the males lie before the female, then he clasps the barbels of the female that pushes against the side of his body with his strong rays of the pectoral fins and anchors her firmly to his body. Then, the male discharges sperm into the water, while the female lays one or two eggs, which she collects with her pelvic fins. Now the male releases the female that swims through the cloud of sperm to fertilize the eggs stacked in the pocket that is formed by the pelvic fin and open anteriorly.]