

## Courtship and mating of *Nomorhamphus liemi* Vogt, 1978 (Zenarchopteridae)

Balz und Kopulation von *Nomorhamphus liemi* Vogt, 1978 (Zenarchopteridae)

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**Summary:** Courtship and mating of the males of the viviparous halfbeak *Nomorhamphus liemi* includes various elements such as watching the female, approach, swimming towards the female, nipping, checking, copulatory events, emerging, retreat and escape) and of females such as resting, cooperative behaviour (if any), evasion, retreat, threatening, biting. Males courted virgins (presumably receptive) and gravid (presumably unreceptive) females. Starting copulations or copulation attempts, the male swims alongside the female, rapidly bends his body and flicks his genital region towards the female urogenital aperture. Distinction between cooperative copulations, sneak copulations and copulation attempts is nearly impossible due to the rapidity of the process. However, some indirect evidence is given by the receptivity state of the female (non-receptive, but also otherwise reluctant females may attack males) and her cooperative behaviour. Presumably receptive females did not escape and occasionally appeared to tilt their genital opening towards the male's genital. We were not able to visualize the immediate physical contact of mates with the technique used, which probably is < 40 ms. The male's modified anal fin is capable to perform a slight lateral movement, but does not appear to act as intermittent organ.

**Key words:** halfbeaks, courtship, mating, high speed shutter, modified male anal fin

**Zusammenfassung:** Während der Balz und Paarung des viviparen Halbschnabelhechtes *Nomorhamphus liemi* sind verschiedene Verhaltenselemente (Männchen: Ruhe und/oder Beobachten des Weibchens, Nähern, Anschwimmen, Nippen, Prüfen, Kopulationen im weitesten Sinn, Rückzug, Flucht; Weibchen: Ruhe, evtl. kooperatives Verhalten, Flucht, Zurückziehen, Drohen, Beißen) zu erkennen. Die Männchen balzen jungfräuliche (sehr wahrscheinlich rezeptive), aber auch trächtige (sehr wahrscheinlich nicht-rezeptive) Weibchen an. Bei einer Kopulation oder einem Kopulationsversuch krümmt sich das Männchen rasch und schlägt mit seiner Genitalregion heftig gegen die des Weibchens. Die Unterscheidung zwischen einer kooperativen Kopulation, einer Vergewaltigung oder einem Kopulationsversuch ist kaum möglich, weil die Dauer des körperlichen Kontaktes nur etwa 40-60 ms beträgt (abgeschätzt nach Videoaufnahmen mit der Sportschaltung). Indirekte Hinweise geben evtl. die mögliche Rezeptivität des Weibchens (nicht rezeptive, aber auch unwillige Weibchen attackieren balzende Männchen) und sein kooperatives Verhalten. Nur in ganz wenigen Fällen schwamm das Weibchen deutlich langsamer und schien seine Genitalöffnung in Richtung des Männchens zu neigen. Die modifizierte Afterflosse des Männchens kann leicht in Richtung des Weibchens gebeugt werden, wird aber wohl nicht in die weibliche Genitalöffnung eingeführt.

**Schlüsselwörter:** Halbschnabelhechte, Balz, Kopulation, Sportschaltung, modifizierte Analflosse des Männchens

### 1. Introduction

Among the internally inseminating halfbeaks, which form the monophyletic clade Zenarchopteridae (the clade Hemirhamphidae, in which these genera were previously included, was re-

cognized as paraphyletic, see LOVEJOY et al. 2004), species of the viviparous genera *Nomorhamphus* and *Dermogenys* and here and there *Hemirhamphodon pogonognathus* are popular "ornamental" fish. However, detailed studies on their social organization and behaviour and even on

their morphology are rare or anecdotal at best, which may be attributed at least in part to the fact that behavioural experiments with halfbeaks are not easy to perform (for review see GREVEN 2006, in press).

*Dermogenys* and *Nomorhamphus* spp. are sexually dimorphic; females are larger than males and males possess a modified anal fin, called andropodium by some authors (e.g. BREMBACH 1976, DOWNING MEISNER 2001). In the wild, species live in more or less large groups; males show courtship and compete for females. Copulations (= mating) are not often seen and their duration appears extremely short (*Dermogenys pusilla*: GREVEN & NEHRIG 2004; see GREVEN 2006, in press).

In the present article we report on courtship elements in *Nomorhamphus liemi* focusing on the immediate mating of this species as revealed by high-speed shutter videography.

## 2. Material and methods

Groups of adult *Nomorhamphus liemi* with changing numbers of individuals were kept in 160 l aquaria fitted with some plants (e.g. *Vallisneria* sp., *Ceratophyllum submersum*). The water temperature was approximately 25 °C. Fish were fed daily with flakes, *Chironomus* sp. and *Daphnia* sp. Under these conditions males showed display and animals breed more or less regularly. The offspring was reared separately until maturity.

To analyze courtship and especially mating more detailed we used three males (M1 = 3.5 cm TL, M2 = 3.8 cm TL, M3 = 4.5 cm TL), two virgins (F1 and F2) approximately 6 months old and two gravid females (F3 and F4). Females were larger than the biggest male.

1. The two virgins (F1, F2) were isolated for two days; then, each female was confronted with the three males, one after the other in a 25 l aquarium. The adaptation time to the new environment was 12 h. Courtship and mating behaviour of each pair was observed for 30 min. Encounters of M1 with F1 and M1 with F2 were videotaped.

2. Two gravid females (F3, F4) were isolated for two days and then confronted with the same males as described. The behaviour of the pairs was observed for 30 min and one encounter (M2 with F4) was videotaped.

For videotaping we used a Sony Digital Handy cam DCR-VX 1000 E with a high-speed shutter (1/6000 exposure time, operating distance 40 cm), a recorder Sony QSVT-1008 and for illumination two Primal spotlights (1250 W each). For analysis of the rapid actions we generated half frames (for details see BRENNER & GREVEN 1999).

## 3. Results

### 3.1. Behavioural elements

The behavioural elements described in the following could be observed in the aquarium, where a group of halfbeaks was housed, as well as in the tanks, where fish were kept in pairs. However, intensities were different depending on both, the males and the females.

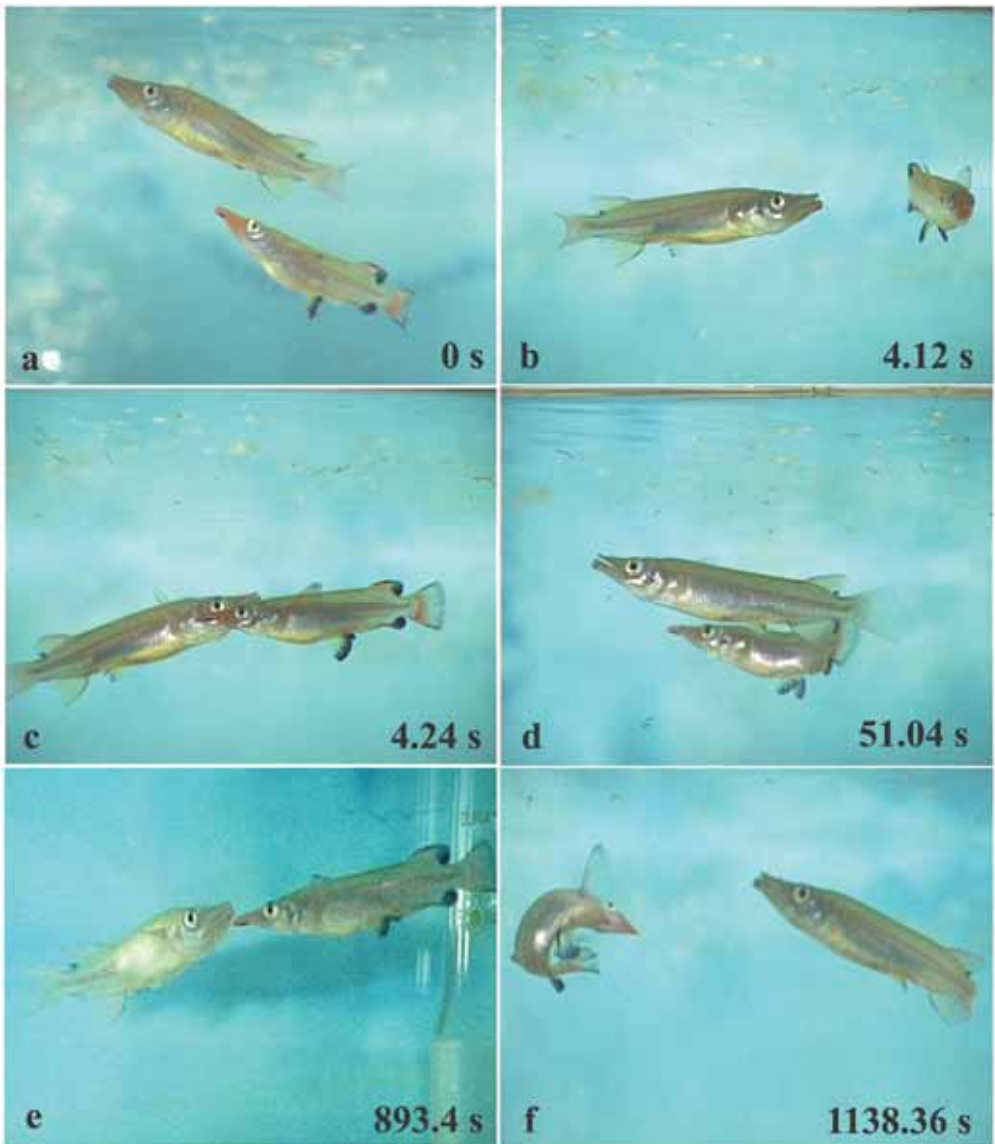
#### 3.1.1. Male

We distinguished watching (the female); approach, swimming towards the female, nipping, checking, copulation (attempt), emerging, leaving, and escape (figs. 1 a-f).

Watching: The male's distance to the female is more than one body length. Pectoral fins and caudal fin move slowly and constantly and ventral fins are flattened.

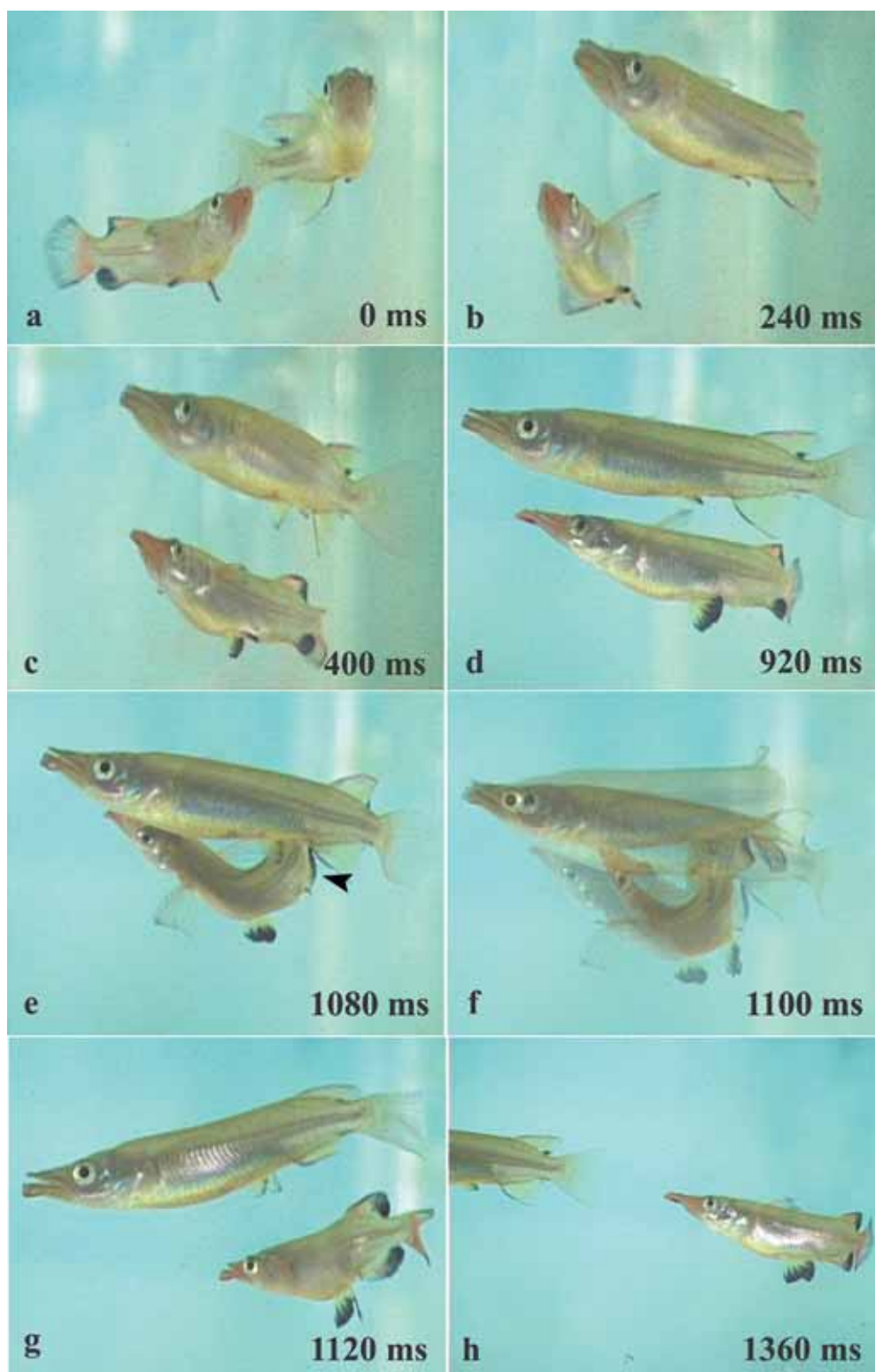
Approach: The male reduces the distance to the female. If the female swims away, the male may stop, may reduce the distance again or may straight approach her.

Swimming towards the female: The male swims towards the female either from behind (fig. 1 a) to bring his jaws near the female's genital region (this position may be the starting point for nipping), alongside the female to bring his anal fin near her genital region (fig. 1 d; figs. 2 b-d) and to start a copulation (attempt), head-on (often seen after checking; see below) stopping alongside the anterior portion of the



**Figs. 1 a-h:** Courtship (M1 and F1); the male with black fin margins. **a** Swimming towards the female from behind; **b** checking; note the spread fins (ventrals, pectorals) of the male; **c** swimming towards the female head-on; **d** alongside swimming towards the female; **e** frontal nipping; **f** the male has overshot the female from a position shown in fig. 1 a, turning now to swim again towards the female.

**Abb. 1 a-h:** Balz (M1 und F1); das Männchen mit schwarzen Flossensäumen. **a** Anschwimmen des Weibchens von hinten; **b** Sperren; man beachte die gespreizten Flossen (Ventrales, Pectorales) des Männchens; **c** Anschwimmen frontal; **d** Parallelschwimmen; **e** frontales Nippen; **f** das Männchen hat das Weibchen aus einer Position wie in Abb. 1 a überholt, wendet abrupt und schwimmt erneut an.



female (fig. 1 c) or behind her, or from the side at about a right angle (fig. 3a). In this case the male has to repeat the approach to come alongside the female. Once we observed that a male coming from behind overshot the female, turned abruptly and swam again to the female (fig. 1 f).

**Nipping:** When the male has brought his lower jaw near the female's genital region (fig. 1 a), he often rapidly opens and closes his mouth spreading ventral and pectoral fins. Nipping at the head of the female was seldom (fig. 1 e); a direct touch of the female body including the genital aperture was never seen. The male remains in this position for some seconds or follows the female in case she swims away.

**Checking:** The male may prevent evasive actions of the female by checking her. He persists in front of the female presenting his broadside (fig. 1 b). Checking often took place after nipping or in the case the female was not cooperative. During this action the male's frequency of breathing increases his ventral fins as well as the dorsal and the anal fin are spread widely and the mouth may be open. If the female moves on, the male may follow and approach her again. An excited male may heavily beat with his caudal fin towards the female.

**Copulation or copulation attempt:** This is a very rapid event accompanied by a strong bending of the male's body. Mating takes place from the left or the right side of the female. Details are not visible to the naked eye. It will be described below.

**Emerging:** A male may emerge to the water surface from all positions under the female and after presumptive copulation attempts.

**Retreat:** After a failed copulation or if the female is aggressive, the male swims away.

**Escape:** This is a hasty retreat regularly seen, when a reluctant female threatens (fig. 3 h) or bites the male. In this case phases of display may alternate with phases of escape.

### 3.1.2. Female

We distinguished resting, cooperative behaviour, evasion, retreat, threatening and biting.

**Resting:** Ventral fins are flattened against the body, pectoral fins and caudal fin move slowly. The female may ignore an approaching male or the female swims away (fig. 1 a).

**Evading:** Both, presumably receptive and non-receptive females, change their swimming direction or turn away from the courting male to undermine copulation (attempts)(figs. 4 c, d). Occasionally, the female threatens the male after such an action.

**Retreat:** This is another way to prevent copulations. In contrast to evasive actions, the female swims away slowly or more jerkily after copulation (attempt) to gain a larger distance to the male.

**Threat:** All females threaten, if they feel harassed by males, especially, however, large, dominant females (fig. 3 h). Threatening females spread ventral and pectoral fins, lift the gill covers and open the mouth widely. If the male does not escape, the female tries to bite him.

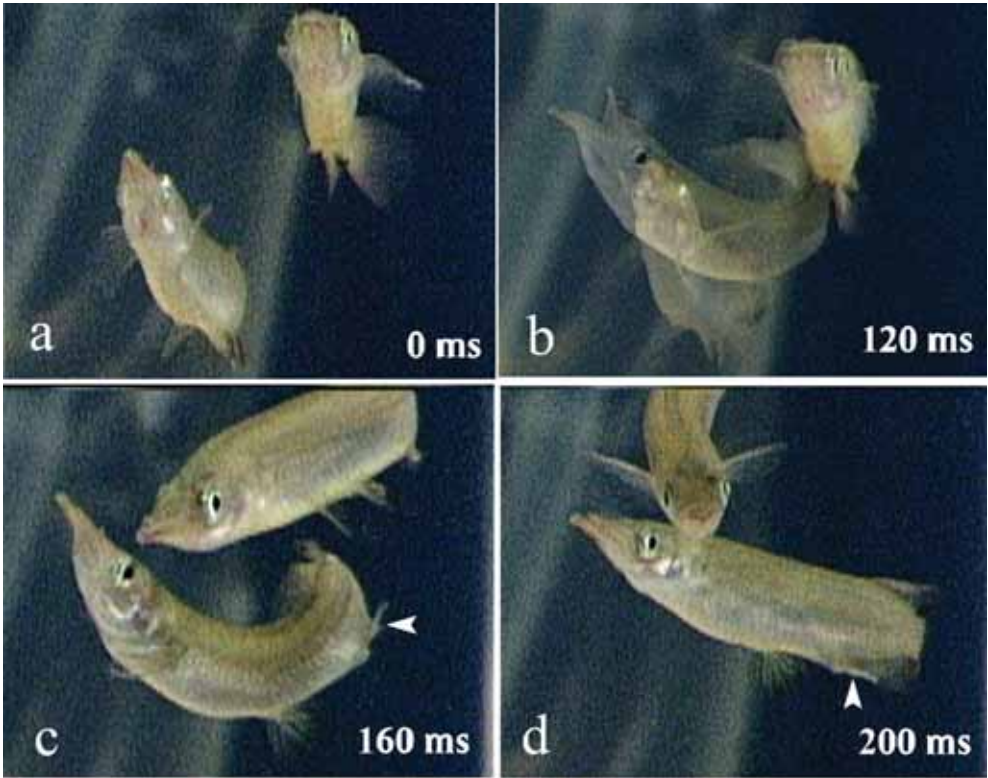
**Biting:** Biting is rarely seen and takes place when the male does not escape, e.g. after threatening. Females seem to prefer the male's jaw as point of attack.

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**Figs. 2 a-h:** Courtship and presumptive cooperative copulation with a virgin (M1 and F1). **a** Swimming towards the female and nipping; **b** mates change their direction; **c** alongside swimming; **d** the male has come closer to the female; **e, f** copulation; **g** the male bends his body away from the female obviously flicking thereafter his genital region towards that of the female; note flexion of the male anal fin (arrow); **g** mates are separated; **h** the female (left side) swims away.

**Abb. 2 a-h:** Balz und vermutlich kooperative Kopulation mit einem jungfräulichen Weibchen (M1 und F1); **a** Anschwimmen von hinten und Nippen; **b** die Fische ändern die Schwimmrichtung; **c** paralleles Anschwimmen; **d** das Männchen hat sich dem Weibchen noch mehr genähert; **e, f** Kopulation; das Männchen krümmt sich vom Weibchen weg und schlägt offensichtlich danach seine Genitalregion an die des Weibchens; man beachte die Krümmung der Afterflosse des Männchens (Pfeil); **g** die Partner haben sich getrennt; **h** das Weibchen entfernt sich.





**Figs. 3 a-d:** Presumptive copulation attempt and/or sneak copulation, virgin female (M1 and F2); **a** the male is under the female; **b** the male bends his body to come in contact with the female genital region; note the open mouth; **c** the female draws aside; note the laterally deflected anal fin (arrowhead) of the male; **d** anal fin (arrowhead) of the male in resting position.

**Abb. 3 a-f:** Vermutlicher Kopulationsversuch und/oder Vergewaltigung, jungfräuliches Weibchen (M1 mit F2); **a** das Männchen befindet sich unter dem Weibchen; **b** das Männchen krümmt seinen Körper, um in Kontakt mit der Genitalregion des Weibchens zu kommen; man beachte das geöffnete Maul; **c** das Weibchen weicht aus; man beachte die lateral gekrümmte Analflosse des Männchens (Pfeilspitze); **d** Analflosse des Männchens wieder in Ruhestellung (Pfeilspitze).

### 3.2. Interactions of couples

M1 showed courtship (fig. 1). Courting F1 and F2 was very intense. One copulatory event was seen with F1 after 2 and 10 min (see fig. 2); termination after 24 min. F2 was never aggressive against M3, but avoided two copulation attempts after 16 min (see fig. 3); termination after 18 min. M3 was interested in F3 and in F4, but showed only nipping; termination after 10 min.

M2 courted eagerly. Courtship was very intense in presence of F1 or F2, but no copulatory event was observed. F3 was not cooper-

ative; a single copulatory event was seen and the male stopped courting after 15 min. F4 was very aggressive, but was courted intensely; copulatory events were seen after 3 and 11 min (see fig. 4); termination after approximately 13 min.

The following descriptions are based on the videotaped actions and consider primarily copulatory events.

Contrary to the behaviour in a group M1 practically did not court under the experimental conditions. Towards F1 and F2 no reactions were seen; termination after 13 and 9 min, respectively. Towards F3 and F4 he was some-

what aggressive; occasionally he nipped F3; termination after 8 min and 7 min, respectively.

### 3.2.1. Male and virgin female

M1 and F1 (fig. 2): Only the first copulatory event was suitable for description. Behavioural elements before this action were swimming from behind, nipping, checking, head-on swimming and swimming alongside the female to start copulation and repeated checking, because the female swam away. Finally, the male swam towards the female from behind, nipped her and swam alongside bringing his genital region at the level of the female's urogenital aperture. Male and female seemed to stop for a short moment (ca. 140 ms); then the male bent his body towards the female, head and tail away from the female and the mouth closed, obviously flicking his genital region towards the female for approximately 40 ms (figs. 4 c-d). The immediate physical contact of mates could not be visualized, but should require less than 40 ms (see time intervals in figs. 2 e-g). We had the impression that the female slightly tilted her body towards the male. Perhaps this action was a true copulation, as the virgin female was stationary for a very short moment, not aggressive and showed perhaps some cooperation.

M1 with F2 (fig. 3): The two copulatory events observed in this encounter were similar, but differed from that described above. First M1 swam towards F1 from the side without nipping; he brought his head in front of the ventral fins of the still stationary female, turned and swam then alongside the female (fig. 3 a). Frequency of the male's breathing was markedly increased and his ventral fins were spread. The male quickly bent his body as described (see above), but with a widely opened mouth and head upward. He apparently did not touch the female urogenital aperture (fig. 3 b). The videotape clearly shows a lateral movement of the anal fin towards the female (fig. 3 c). After this action the fin returns to the resting position (fig. 3 d). The female showed no cooperation and turned away from the male during the action (fig. 3 c, d).

Both events observed in this encounter may be regarded as copulation attempt or more probably as sneak copulation due to the absence of the nipping behaviour, the missing cooperation and the obvious evasive action of the female.

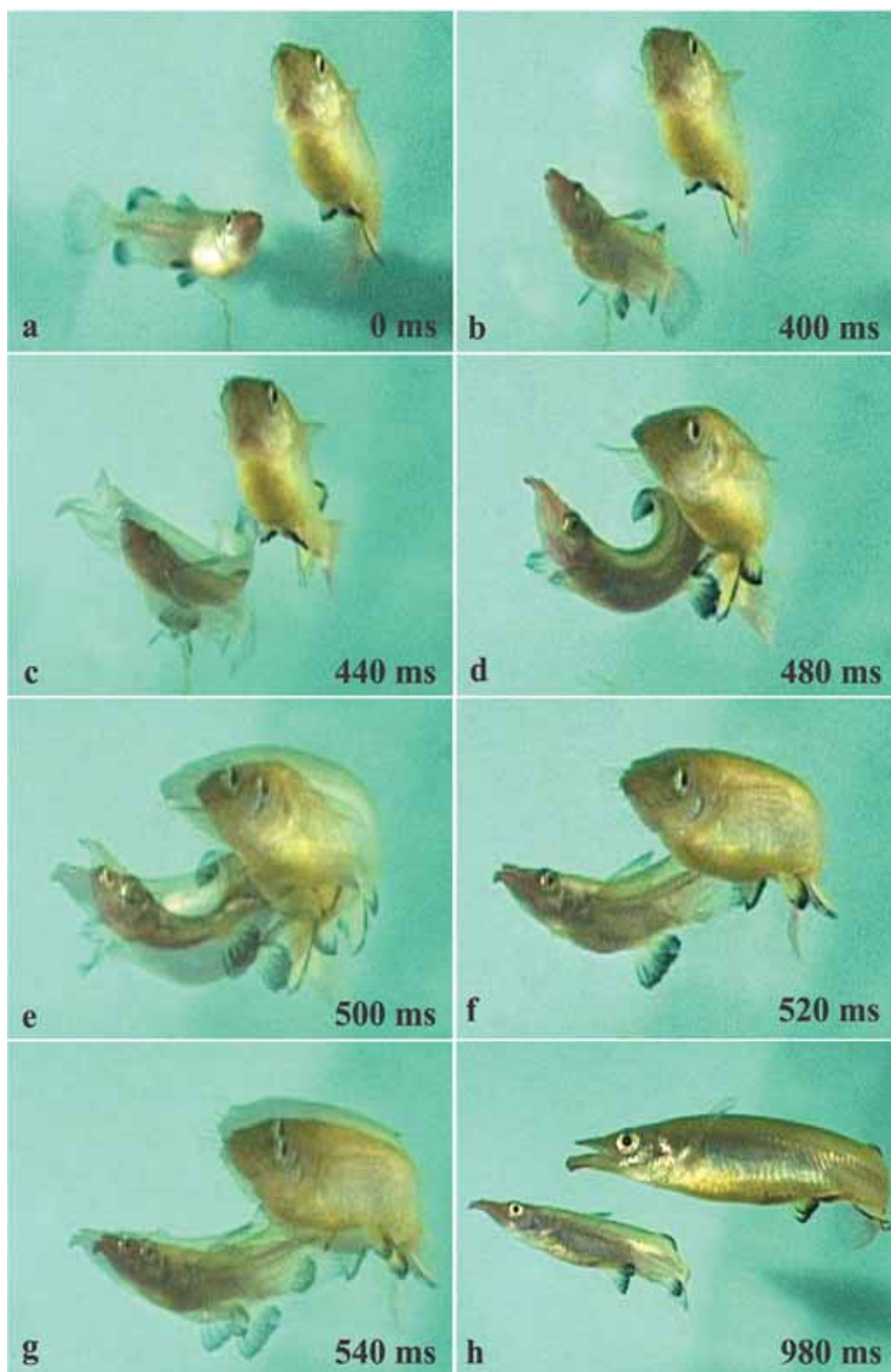
### 3.2.2. Male and gravid female

M2 and F4 (fig. 4): M2 approached F4 from the side at about a right angle, swam then alongside the female, stopped there with spread ventral and highly beating pectoral fins and started copulation with a strong bending of his body presenting his genital region towards the female for approximately 60 ms; during his action the mouth was open (figs. 4 c-d.) Whether the genitals of mates touch one another could not be seen. Already during the male's presentation, the female turned slightly towards the male (compare figs. 4 d and e-f) and threaten the male immediately after (fig. 4 h). M2 stopped courtship after 13.32 min due to the high aggressiveness of the female. The two copulatory events observed in his encounter were nearly identical. We consider both as sneak copulations due to the fact that the female was pregnant, showed no signs of cooperation and responded aggressively to the male's effort.

## 4. Discussion

Although essentially descriptive, the present study broadens the few anecdotal reports on courtship and mating behaviour of *Nomorhamphus liemi*. Data from the wild concerning this matter do not exist either of *N. liemi* or related species; at least some *Dermogenys* spp. live in shoals, which are probably dominated by the largest female, and males, on average smaller than females, permanently try to gain copulations (see GREVEN in press).

Distinction of various behavioural elements during courtship and mating is a somewhat subjective matter, but the present observations and previous studies show the large degree of similarity in reproductive behaviour of the hitherto studied *Nomorhamphus* and *Dermogenys* spp. (see also GREVEN 2006, in press) and revealed





the most “complete” succession of elements, when a male encounters a cooperative virgin. Reproductive behaviour of males includes different kinds of swimming towards the female, nipping, checking and finally rapid copulation (attempts) (see GREVEN & NEHRIG 2004; this article). Females often appear prudish and choosey and cooperation might be indicated when they are stationary for a short time and/or tilt their body towards the male, but these elements are hardly seen with clarity. Behavioural elements described herein are known from various livebearers of different taxa, e.g. poeciliids (for review see FARR 1989). With regard to halfbeaks, these elements are discussed more detailed elsewhere (e.g. GREVEN & NEHRIG 2004, GREVEN 2006, in press).

Nipping is widespread in livebearers, e.g. in poeciliids, and allows the male to check receptivity of the female obviously by means of pheromones produced in their ovaries (for review see LILEY 1983). This is very likely true also for female *Nomorhamphus* and *Dermogenys* spp. Males may detect pheromones by chemoreceptors located on their elongate jaws and by their nasal barbels (see the discussion in GREVEN 2006, in press). A physical contact of the male’s jaws and the female’s urogenital pore could not be observed in *N. liemi* and seems not to be necessary as the “receptivity” pheromone may work either from distance or by contact as shown in poeciliids (summarized in GREVEN 2005). Although nipping is shown in the first phases of courtship and is reduced in a later phase of display, males nipped the virgin female also just before inseminating. Checking was shown when a female tried to

swim away from a courting male. However, males are always in an inferior position when checking a large female.

Mating in *N. liemi* (and *D. pusilla*) is extremely rapid. Copulations or copulation attempts surely last < 25 ms as roughly estimated for *D. pusilla* (GREVEN & NEHRIG 2004), but obviously is much shorter as indicated by the herein used high speed shutter videography. To our knowledge this is the shortest time hitherto estimated for the copulation of livebearers (see GREVEN 2005, 2006, in press). Due to this rapidity the herein used technique could not resolve the action in full detail, namely the direct physical contact of mates and its duration. The way the male takes up speed and power to suddenly strike the female with the posterior part of his body is largely confirmed by high-speed videography. The strong flexion of the male creates a power that pushes away at least somehow dazed females (see GREVEN 2006, in press, unpublished).

Due to the relatively few conspicuous courtship elements, which sometimes resemble harassment rather than a “persuading” courtship, the extreme rapidity of copulatory events and the poor signs of female cooperation, distinction between cooperative, “true” copulations, copulation attempts and sneak copulations appears difficult. However, there are good reasons to assume that virgins and females immediately around parturition are receptive and most susceptible for courtship, as their presence increase the efforts of the male, whereas gravid females, which should be non-receptive, are less attractive (unpublished). This is also the case in other livebearers (for review see FARR

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**Figs. 4 a-h:** Swimming towards the female and presumptive sneak copulation, gravid female (M2 and F4); **a** Swimming towards the female from the side; **b** the male in a parallel position underneath the female; **c, d, e** the male strongly bends his body towards the female attempting a copulation; note the open mouth of the male; the female slightly bends its body apparently to avoid contact with the male (d, e); **f, g** mates are separated; the male sprawls again; **h** the female threatens the escaping male.

**Abb. 4 a-h:** Anschwimmen und vermutlicher Vergewaltigungsversuch, trächtiges Weibchen (M2 und F4); **a** Anschwimmen von der Seite; **b** das Männchen steht parallel unter dem Weibchen; **c, d, e** das Männchen krümmt sich stark in Richtung des Weibchens und versucht eine Kopulation; man beachte das geöffnete Maul des Männchens; das Weibchen wendet sich dem Männchen zu; **f, g**, die Partner sind getrennt; das Männchen streckt sich wieder; **h** das Weibchen droht dem fliehenden Männchen.

1989). Therefore, we tentatively consider at least one copulatory event (M1 with F1) as true copulation (virgin, cooperative behaviour), a further event (M1 with F2) appeared to be a copulation attempt or even a sneak copulation (virgin, but the female tried to avoid the copulation), and all copulatory events with gravid females (M2 and M4) may be regarded as sneak copulations (gravid females were always uncooperative and either avoided the male's approach or threatened or bit him).

Successful sperm transfer by any copulatory event, sneaky or cooperative, has to be otherwise checked, e.g. by histology or by flushing out the urogenital sinus.

Receptivity does not necessarily include willingness to copulate and cooperation (for discussion see GREVEN 2005). Females of *Nomorhamphus* and *Dermogenys* spp. appear choosy and even virgins do not accept any male (see above) and not only non-receptive females answer the nearly permanent sexual harassment with escape or aggressiveness. In a small group of an undetermined *Dermogenys* species, kept for a while in our lab, non-pregnant females were so aggressive that we never saw a copulation attempt much less a true copulation (unpublished). Traits for female choice may be the size, length of the "halfbeak", colouring etc. (see GREVEN 1999, 2006, in press), but have not proved as yet.

Nevertheless, we think that males of *N. liemi* (and of *Dermogenys* spp.) use two mating tactics (see GREVEN 2006, in press): 1) courting with presumably most receptive females, i.e. virgins or females a short time before and after parturition, as known also from poeciliids (e.g. LILEY 1983, GREVEN 2005), 2) probably further reduction of the unspectacular display anyway, when females are presumably non-receptive and/or non-cooperative or when a dominant male impedes access to females, leading to "sneak copulations". This latter tactic was used by a male of *N. liemi* introduced in a group of five females and a male (unpublished). It is unknown, whether such sneak copulations are successful. Males do not show a behaviour indicating sperm transfer (com-

pare the postcopulatory jerking, e.g. of *Poecilia reticulata*). However, females of *Nomorhamphus* and *Dermogenys* spp. are able to store sperms in their oviducts and ovaries (GREVEN 1995, MEISNER & BURNS 1997, GREVEN 1999, 2006, in press).

The definitive role of the complex modified anal fin of male *Nomorhamphus* spp. (and *Dermogenys* spp.) is unclear (for some suggestions see GREVEN in press). Its size and limited mobility as well as the smallness of the female urogenital aperture do not allow the anal fin to clasp or grip the female or to act completely as an intromittent organ (GREVEN 2006, in press). A slight lateral movement of the anal fin was seen in our video sequences (see also BREMBACH 1976, GREVEN & NEHRIG 2004), when the male bent towards the female. The tridens flexibilis, a characteristic element of the male's anal fin (BREMBACH 1976, 1991, DOWNING MEISNER 2001) may help to establish a somewhat firmer contact between the mates for a very short time, but more intricate functions have been suggested, too (see BREMBACH 1976). Also the urogenital papilla (or genital palp) of the male is unsuitable to serve as intromittent organ as suggested (MEISNER & BURNS 1997, DOWNING MEISNER & BURNS 1997). In contrast to the urogenital papilla in *Hemirhamphodon* spp., in *Dermogenys* and *Nomorhamphus* spp. this organ does not stand freely or is provided with muscles (GREVEN in press).

The few data of the reproductive behaviour in internally inseminating halfbeaks, i.e. species that give birth to competent fry (viviparous species) (*Dermogenys pusilla*: GREVEN & NEHRIG 2004, for review see GREVEN 2006, in press) and those shedding fertilized, very probably embryonated eggs (*Hemirhamphodon tengah*: DORN & GREVEN 2007) come from aquarium observations. Field observations of two inseminating *Zenarchopterus* spp. have been published by KOTTELAT & LIM (1999). In spite of the poor knowledge two or three types of reproductive behaviour appear to emerge from these and the here presented observations:

1. *Zenarchopterus gilli* and *Z. buffonis* seem to lack a distinct display (this might be owed, how-

ever, to the difficulty to observe this action in the field); male *Z. gilli* swim alongside the female clasping her tail region with the modified dorsal and anal fin rays, whereas male *Z. buffonis* swim alongside the female flicking their genital region slightly upward and against the female (see figures 3 and 4 in KOTTELAT & LIM 1999),

2. *Hemirhamphodon* spp., which include superfetating species and a single embryoparous species, show a short lasting (?) display and the immediate mating resembles that of *Z. buffonis* at least in *H. tengah* (DORN & GREVEN 2007),

3) *Nomorhamphus* and *Dermogenys* spp., which exhibit diverse modes of viviparity including superfetation (MEISNER & BURNS 1997) and the most modified male anal fin, show a largely identical courtship followed by very rapid copulations, which is clearly dissimilar from courtship and mating of *Zenarchopterus* spp. (KOTTELAT & LIM 1999) and *Hemirhamphodon* spp. (BREMBACH 1978, DORN & GREVEN 2007).

This grouping, which has to be substantiated in further studies, obviously fits the clades currently distinguished among internally inseminating halfbeaks (ANDERSON & COLETTE 1991), i.e. Zenarchopteridae (LOVEJOY et al. 2004).

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