

Tentative findings on the phylogenetic relationship within the genus *Xiphophorus* with regard to the frequency distribution of sexual behavior patterns

(Pisces: Poeciliidae)

by

Wolfgang HEINRICH *) and Johannes Horst SCHRÖDER *) **)

(Institut für Biologie der Gesellschaft für Strahlen- und Umweltforschung, Neuherberg bei München, West Germany *) and Institut für Zoologie, Universität Innsbruck, Austria **)

Vorläufige Befunde über die phylogenetische Verwandtschaft innerhalb der Gattung *Xiphophorus* bezüglich der Häufigkeitsverteilung von Merkmalen des Sexualverhaltens (Pisces: Poeciliidae)

Synopsis: Eine vergleichende Untersuchung zur Analyse des Sexualverhaltens von 17 verschiedenen *Xiphophorus*-Arten wurde durchgeführt. Mögliche phylogenetische Verwandtschaftsverhältnisse zwischen diesen Arten bezüglich der Häufigkeitsverteilung von 23 sozialen Verhaltensweisen legen die Unterteilung der Gattung *Xiphophorus* in zwei Abstammungslinien nahe, nämlich in eine ohne präkopulatives Balzverhalten und in eine zweite mit einem wohlentwickelten präkopulativen Balzverhalten. Diese Befunde wurden im Zusammenhang mit den Resultaten von FRANCK (1964, 1968) und den taxonomischen Untersuchungen von ROSEN (1960, 1979) diskutiert.

Introduction:

According to ROSEN (1979), among the live-bearing fish family of Poeciliidae the Middle-American genus *Xiphophorus* represents one of the best defined groups with respect to the complexity of their external male genital organ ('gonopodium') and associated modifications of the male pelvic fins. Conventionally, the species of *Xiphophorus* are subdivided into two lineages, the platyfishes or platies (formerly *Platypoecilus*), and the swordtails (*Xiphophorus* sensu stricto). The male swordtails develop a sword-like appendix, formed by the elongation of the ventral rays of the caudal fin, while the male platyfish normally do not form such an appendix but are able to do so after artificial testosterone treatment (ZANDER and DZWILLO, 1969).

Following ROSEN's (1979) intense discussions concerning the implications of the zoogeographical distribution of the genus *Xiphophorus*, it firstly should be stated that no xiphophorin species

*) Present address: P.D. Dr. W. Heinrich, Universität Bern, Zoologisches Institut, Ethologische Station Hasli, Wohlensstraße 50a, CH-3032 Hinterkappelen, Switzerland.

**) Reprint requests should be sent to Prof. Dr. J.H. Schröder, Institut für Biologie, GSF, Ingolstädter Landstraße 1, D-8042 Neuherberg nr. München, West Germany (GFR).

has a Pacific slope occurrence in coastal drainages. All populations of this genus seem to be strictly confined to the river systems of the Atlantic slope.

In the case of roughly coincident distributions, platyfishes prefer the slower flowing downland parts of the rivers and their coastal drainages, whereas swordtails occur in the faster flowing portions of the same waters. There are, however, also endemic forms in *Xiphophorus* such as *X. milleri*, coastward in the Río Papaloapan region (in Laguna Catemaco), and an endemic species of swordtail, *X. clemenciae*, which is sympatric and syntopic with the wide-spread swordtail species (or species complex), *X. helleri*, in the upland portions of the Río Coatzacoalcos (in the Río Sarabia). A species pair of platies, viz. *X. couchianus* and *X. gordonii*, are confined to isolated water systems north from the Río Grande watershed in northern Mexico. *X. couchianus* is confined to spring-fed pools near Monterrey, Nuevo León, and *X. gordonii* is confined to the isolated lagunas of the intermontane Cuatro Ciénegas basin, Coahuila. Further endemic taxa occur in the Río Panuco watershed and in waters somewhat north and south of it: *X. cortezi*, *X. evelynae*, *X. montezumae*, *X. nigrens*, *X. pygmaeus*, *X. variatus*, and *X. xiphidium*. South of these taxa and slightly overlapping them in distribution, the genus *Xiphophorus* is represented by the widespread species or species complex *X. helleri*, that extends along the Atlantic versant of Mexico to the base of the Yucatan Peninsula in Mexico, Guatemala and Belize. With respect to the species pair of swordtails, *X. helleri* and *X. signum*, the populations from the Río Polochic, Río Motagua, and Northern Honduras are slightly different from both species, but are most closely related to both *X. helleri* and *X. signum*, and were described as putative natural hybrids between both species, designated as "PMH" (ROSEN, 1979). Despite of the roughly coincident distributions of the two major lineages of *Xiphophorus*, platyfishes occur somewhat farther north in the Río Soto la Marina basin (*xiphidium*) and swordtails somewhat farther south in Honduras (*helleri*) (ROSEN, 1960).

As compared to the last revisionary study of *Xiphophorus* (ROSEN, 1979), the present investigation includes two additional species of platyfishes, viz. *X. andersi* (MEYER and SCHARTL, 1980) and *X. meyeri* n. sp. (SCHARTL and SCHRÖDER, 1986). With respect to the experimental investigation of the sexual behavior, both the platyfish species *X. andersi*, *X. evelynae*, and *X. gordonii*, and the swordtail species *X. alvarezii*, *X. clemenciae*, and *X. signum* were analysed ethologically for the first time in the present study. It should be emphasized, however, that these tentative findings can only lead to preliminary conclusions of possible phylogenetic relationships within the genus *Xiphophorus*. A more comprehensive study including statistical considerations of a more quantitative ethological comparison of all xiphophorin species is now in progress.

Material and Methods:

1. Maintenance and Origin of the Fish:

The fish were kept in aquaria of 8, 25, 50, 100, or 200 liter volume at a temperature averaging 25°C. They were fed on TETRAMIN[®], nauplia of *Artemia salina*, *Daphnia* and *Tubifex*. The artificial illumination was set to a 12-h rhythm, but daylight itself was not excluded. Mated couples, dead and newborn fish were routinely checked by daily examination of all basins in the morning. Because the broods were sometimes born over a period of several hours and because some females might have been cannibalistic, all fry were immediately removed from their parents to small glass vessels and later transferred to rearing aquaria. Aquatic plants, *Fontinalis*, *Riccia* and/or *Myriophyllum*, were grown in aquaria where broods were anticipated, to enable the newborn fish to hide from their parents.

To obtain virgin females which are receptive to male courtship activities, females and males of broods were separated from each other immediately after initiation of the transformation of the anal fin into a gonopodium in males. In inbred lines of *X. helleri* and *X. maculatus*, the fish were exclusively mated to sib-mates of the same brood.

The natural distribution and the first introduction to laboratory maintenance from their natural habitats of the 17 *Xiphophorus* species (Photo 1 - 17) used in the present study are listed in Table 1. The abbreviations of different species as given by Table 1 (ALV, AND, CLE, COR, COU, EVE, GOR, HEL, MAC, MEY, MIL, MON, NIG, PYG, SIG, VAR, and XIP) will be used in the present paper.

2. Scoring Sexual Behavioral Traits:

The social behavior patterns of 11 out of 17 different *Xiphophorus* species were analysed by FRANCK (1964, 1968). CLARK et al. (1954) studied the mating behavior in the two sympatric xiphophorin fishes, *X. helleri* and *X. maculatus*, and its inheritance by interspecific hybridization of these two species. FRANCK (1970) improved this method of behavior-genetic analysis and gave

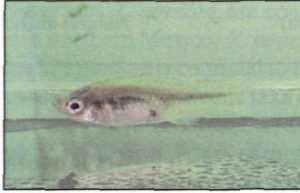
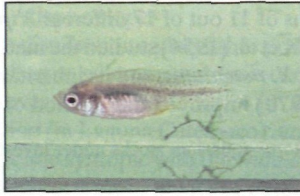
Table 1: Description of the *Xiphophorus* aquarium stocks under investigation.

Species (abbreviation)	Natural distribution of aquarium stocks	Laboratory maintenance since
<i>X. alvarezii</i> ROSEN* (ALV) (= <i>X. helleri alvarezii</i> ROSEN, 1960)	Río Chacamax, Chiapas, Mexico	1980
<i>X. andersi</i> MEYER and SCHARTL, 1980 (AND)	Río Atoyac, Veracruz, Mexico	1979/1980
<i>X. clemenciae</i> ALVAREZ, 1959 (CLE)	Arroyo La Cascada, Río Sarabia, Oaxaca, Mexico	1968
<i>X. cortezi</i> ROSEN* (COR) (= <i>X. montezumae cortezi</i> ROSEN, 1960)	Río Axtla, San Luis Potosí, Mexico	1981
<i>X. couchianus</i> (GIRARD)* (COU) (= <i>Limia couchiana</i> GIRARD, 1859)	La Huasteca, Huasteca Canyon, Nuevo León, Mexico	1961
<i>X. evelynae</i> ROSEN* (EVE) (= <i>X. variatus evelynae</i> ROSEN, 1960)	Río Teco Iutla near Necaxa, Puebla, Mexico	1979
<i>X. gordonii</i> MILLER and MINCKLEY, 1963 (GOR)	Laguna St. Tecla, Coahuila, Mexico	1981
<i>X. helleri</i> HECKEL, 1848 (HEL)	Subspecies <i>X. h. guentheri</i> , inbred strain Bx, Db ¹ from New York; Belize River, Belize	1949
	Subspecies <i>X. h. guentheri</i> , stock Db ² from Hamburg; Río Lancetilla, Honduras	1951
<i>X. maculatus</i> (GÜNTHER)* (MAC) (= <i>Platyopocilus maculatus</i> GÜNTHER, 1866)	Inbred strain Jp 163A from New York; Río Jamapa, Veracruz, Mexico	1939
<i>X. meyeri</i> n. sp. SCHARTL and SCHRÖDER, 1986 (MEY)	Headwaters near Musquiz, Coahuila, Mexico	1982
<i>X. milleri</i> ROSEN, 1960 (MIL)	Laguna Catemaco, Río Papaloapan basin, Veracruz, Mexico	1963
<i>X. montezumae</i> JORDAN and SNYDER, 1900 (MON)	Río Salto de Agua, Río Panuco basin, San Luis Potosí, Mexico	1965
<i>X. nigrensis</i> ROSEN* (NIG) (= <i>X. pygmaeus nigrensis</i> ROSEN, 1960)	Río Choy, Río Panuco basin, San Luis Potosí, Mexico; dimorphism of males	1972
<i>X. pygmaeus</i> HUBBS and GORDON, 1943 (PYG)	Río Axtla, Río Panuco basin, Luis Potosí, Mexico; population with yellow males	1980
<i>X. signum</i> ROSEN and KALLMAN* (SIG) (= <i>X. helleri signum</i> ROSEN and KALLMAN, 1969)	Río Chajmaic, Río de la Pasión basin, Alta Verapaz, Guatemala	1979
<i>X. variatus</i> (MEEK)* (VAR) (= <i>Platyopocilus variatus</i> MEEK, 1904)	Río Tamesi, Tamaulipas, Mexico	1957
<i>X. xiphidium</i> (GORDON)* (XIP) (= <i>Platyopocilus xiphidium</i> GORDON, 1932)	Arroyo Marmelejos, Sierra San Carlos, Río Soto la Marina basin, Tamaulipas, Mexico	1965

* according to ROSEN, 1979

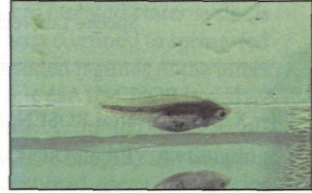
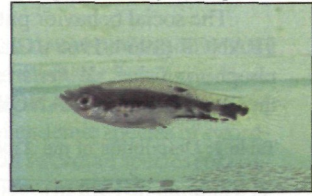
Fig. 1 - 17: *Xilophorus*-species
in both sexes.

◇ Fig. 3a: *X. evelynae* ♂



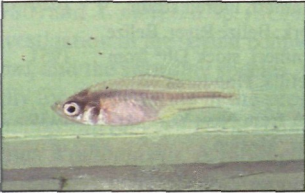
◇ Fig. 3b: *X. evelynae* ♀

◇ Fig. 6a: *X. meyeri* n. sp. ♂



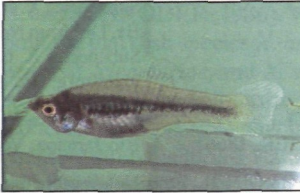
◇ Fig. 6b: *X. meyeri* n. sp. ♀

◇ Fig. 1a: *X. andersi* ♂



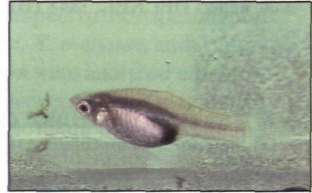
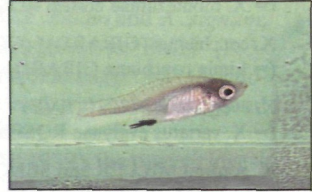
◇ Fig. 1b: *X. andersi* ♀

◇ Fig. 4a: *X. gordonii* ♂



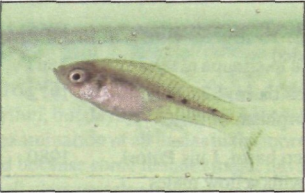
◇ Fig. 4b: *C. gordonii* ♀

◇ Fig. 7a: *X. milleri* ♂



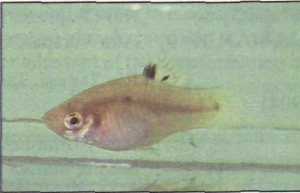
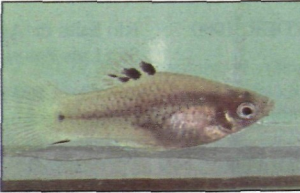
◇ Fig. 7b: *X. milleri* ♀

◇ Fig. 2a: *X. couchianus* ♂



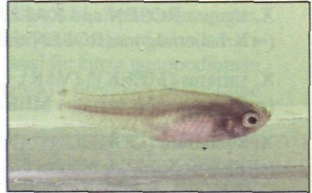
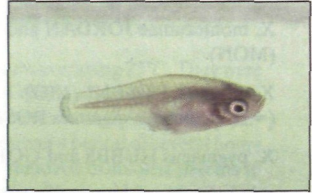
◇ Fig. 2b: *X. couchianus* ♀

◇ Fig. 5a: *X. maculatus* ♂



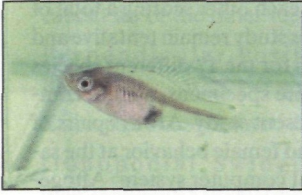
◇ Fig. 5b: *X. maculatus* ♀

◇ Fig. 8a: *X. variatus* ♂

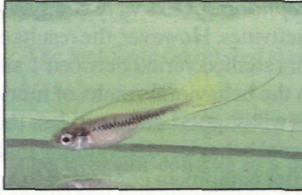


◇ Fig. 8b: *X. variatus* ♀

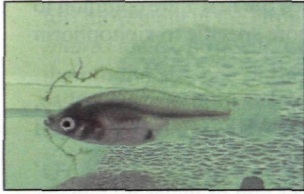
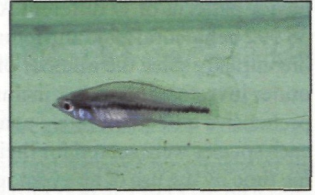
◇ Fig. 9a: *X. xiphidium* ♂



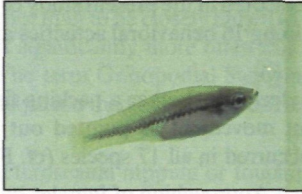
◇ Fig. 12a: *X. cortezi* ♂



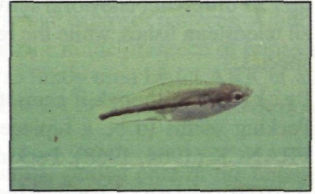
◇ Fig. 15a: *X. nigrensis* ♂



◇ Fig. 9b: *X. xiphidium* ♀

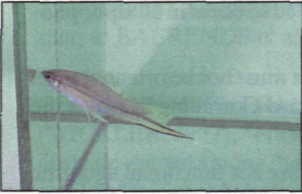


◇ Fig. 12b: *X. cortezi* ♀

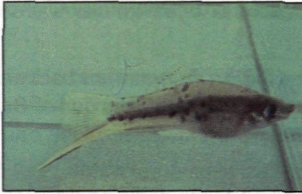


◇ Fig. 15b: *X. nigrensis* ♀

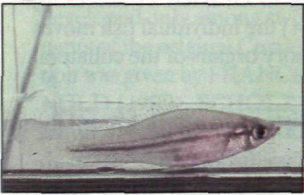
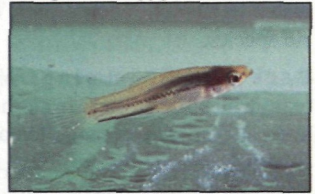
◇ Fig. 10a: *X. alvarezii* ♂



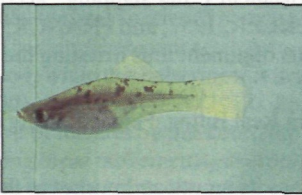
◇ Fig. 13a: *X. helleri* ♂



◇ Fig. 16a: *X. pygmaeus* ♂



◇ Fig. 10b: *X. alvarezii* ♀

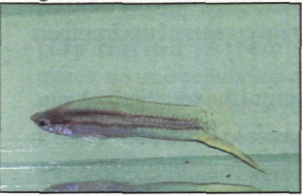


◇ Fig. 13b: *C. helleri* ♀

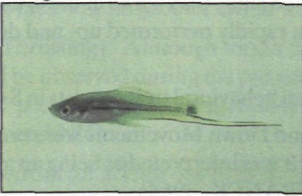


◇ Fig. 16b: *X. pygmaeus* ♀

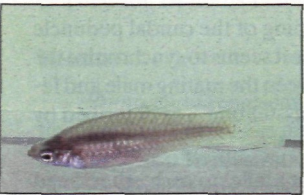
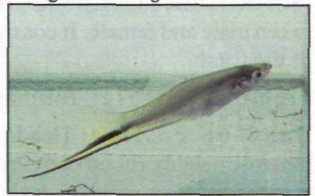
◇ Fig. 11a: *X. clemenciae* ♂



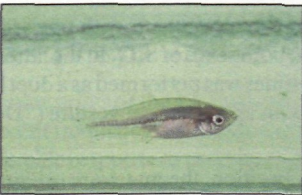
◇ Fig. 14a: *X. montezumae* ♂



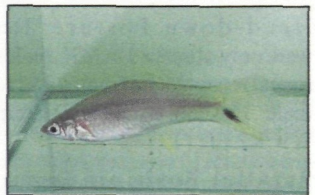
◇ Fig. 17a: *X. signum* ♂



◇ Fig. 11b: *X. clemenciae* ♀



◇ Fig. 14b: *X. montezumae* ♀



◇ Fig. 17b: *X. signum* ♀

more examples of species-specific inheritance within this genus. In the present study, the sexual behavior patterns of 17 different *Xiphophorus* species were compared to each other scoring a total of 58 992 behavioral male and female activities. However, the results of this study remain tentative and incomplete, since the number of pairs studied varied between 1 and 16 for the 17 different species under investigation. After inclusion the behavioral results of much more specimens, a more comprehensive and quantitative analysis will support and complete the present study. Always pairs of each species were scored for their sexual behavior, determining male and female behavior at the same time by the use of an event recorder equipment connected to an LSI computer system. Altogether 23 different behavioral activities scored in the present study of which the first 7 are common to all teleostean fishes, while the remaining 16 behavioral activities are more specific to xiphophorin species.

Pecking: Although it cannot be decided whether a pecking fish intakes food or does not so, Pecking seems to be a replacement movement as pointed out by CLARK et al. (1954) and FRANCK (1964, 1968). Pecking occurred in all 17 species (cf. Fig. 1).

Approaching: Like Pecking, also Approaching of females by males and of males by females could be observed in all 17 species.

Leaving: Opposite to Approaching, a leaving male withdraws from the female and a leaving female from its male counterpart. This universal behavior trait was observed to occur in all xiphophorin species.

Backward Swimming: When a *Xiphophorus* swims backward, it must not be oriented to its mate which thus differs from the exclusively male behavior of Backward Corraling in which the male always orients to the female mate.

Tail Beating: Like the following two behavioral traits, Tail Beating is a functional agonistic behavioral pattern. During this movement ("tail-slapping" according to CLARK et al., 1954; "Schwanzschlag" according to WICKLER, 1957, and FRANCK, 1964) the individual fish moves rapidly its caudal peduncle toward its opponent thus irritating the sensory organs of the collateral line.

Feigned Biting: Different from Real Biting, Feigned Biting consists of an attack toward the opponent without touching its skin.

Real Biting: The biting fish opens its mouth and pushes to the surface of its adversary sometimes wounding it (WICKLER, 1957).

Rapid Head Jerking: Like Pecking the behavioral trait designated as Rapid Head Jerking (SCHRÖDER and HEINRICH, 1985) may play a role in the synchronization of the courtship between male and female. It consists in rapidly performed up- and down movements of the frontpart of the trunk.

Sigmoid Posture: This universal behavioral trait consists in S-curving of the vertebral column.

Head-up Posture: Head-up and Down Movements were only registered when performed in the close neighborhood of the mate. It was interpreted as being an appeasement gesture during agonistic encounters of MAC males (FRANCK, 1964).

Head-down Posture: Head-down movements with upward sloping of the caudal peduncle were only observed in MIL males and both sexes of SIG. In the latter case it seems to synchronize the sexual receptivity of mates and sometimes was performed as a duet between the mating male and female. This movement also resembles an appeasement gesture ("Demutsstellung") as described by WICKLER (1957).

Parallel Position: During this position, the mates are orientated parallel to each other, head by head and caudal fin by caudal fin.

Antiparallel Position: During this position, the head of one mate is orientated opposite the caudal fin of the other mate and vice versa.

Perpendicular Position: The mates are orientated at right angles to each other, mostly head to flank.

Escape Response: One of the two mates darts away from the other.

Gonopodial Swinging: This behavior consists of a down- and forward movement of the male copulatory organ (gonopodium) and was assumed by BAERENDS et al. (1955) to be a comfort movement in the guppy rather than to be closely linked to the sexual behavior patterns. *Xiphophorus* males, however, exhibit significantly more often this behavior in the presence of females than in the absence of them. The term Gonopodial Swinging was firstly used by CLARK et al. (1954) but was already previously described by SCHLOSSBERG et al. (1949) as "isolated flexion of the gonopodium".

Genital Nipping: The heterosexual nipping or touching on the genital pore of the female mate is a wide-spread behavior trait among poeciliid tooth-carps. It might be directed to all parts of the body but is restricted to the female genital region in the case of Genital Nipping. Then the male touches or bites at the genital region of the female ("nipping" according to SCHLOSSBERG et al., 1949, and to CLARK et al., 1954; "Maultupfen" according to WICKLER, 1957; "biting" according to BAERENDS et al., 1954).

Forward and Backward Corraling: The movements described as "Wiegen" (LATTERMANN, 1957; FRANCK, 1964), "arcing" (CLARK et al., 1954), "Rückwärtsschwimmen" (WICKLER, 1957), "Forward and Backward Swimming" (SCHRÖDER and HEINRICH, 1985) are wide-spread among the species of the genus *Xiphophorus*. The intensity and velocity of the forward and backward phases of this behavior are quite different from species to species and are highly developed only among swordtails. In some species of platyfish (AND, COU, VAR, XIP) only remnants of the original Corraling (backing) behavior seem to be developed. A more detailed description was given by FRANCK (1964) while this behavior was firstly mentioned and described by ARNOLD (1909), SCHOLZ (1909), and LANGER (1913). Since it seems as if swordtail males attempt to limit the liberty to move of females by this courtship behavior, the present authors introduced the term Corraling. During these movements, swordtail males curve their swords toward or away from the female (Sword curved toward ♀, Sword curved away from ♀) giving the impression that the female's motility is hindered by the male's body axis elongated by its sword-like appendix.

Courtship Jump: After Copulation or Copulation Attempts the male leaves rapidly the female by darting away from it, which was only observed in MON, PYG and SIG.

Copulation Attempt (Thrusting): Although virgin females were mostly used as female mates, no true copulation could be observed during the present experiments. Gonopodial Thrusts, directed to the female's genital pore, however, were relatively often recorded except for AND, EVE, GOR, VAR, XIP, COR, and NIG.

All experiments were carried out for at least one hour in 25-liter tanks. Males and females were isolated for 24 hours before beginning the behavioral observations.

Results:

Photo 1 - 17 represent the color prints of the 17 *Xiphophorus* species (cf. Table 1) under investigation. Fig. 1 expresses the percent frequency distribution of the 23 social behavioral activities for the 17 species. To illustrate the female response to male courtship activities, the ratio of relative frequencies for 12 responsive behavioral patterns expressed as male activities/(male + female activities), $\sigma\sigma/(\sigma\sigma + \text{♀}\text{♀})$, is given in Table 2.

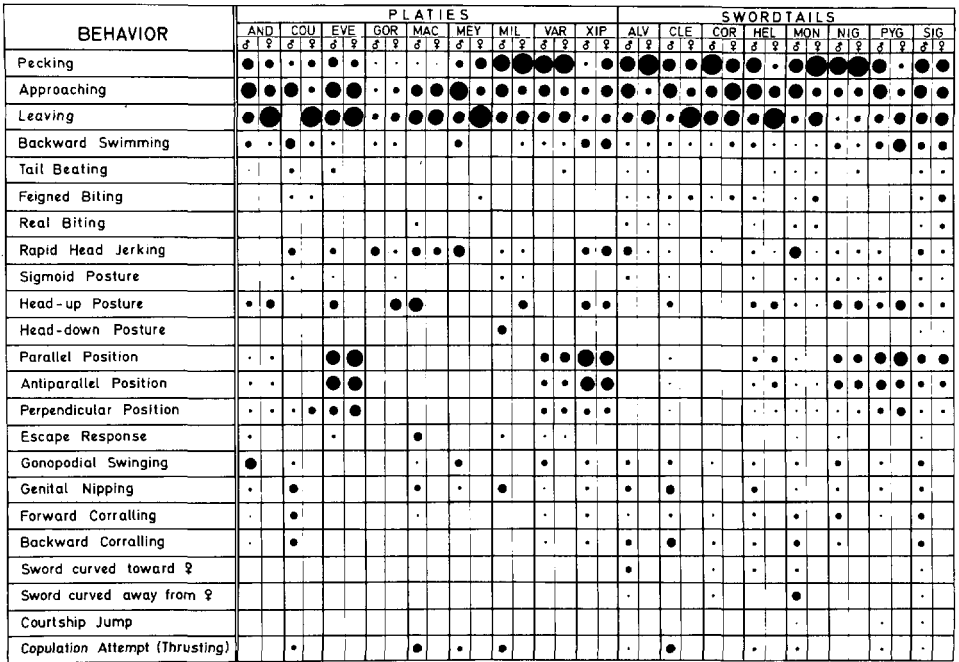


Fig. 1: Percentage frequency distribution of 23 social behavioral activities within the genus *Xiphophorus*.

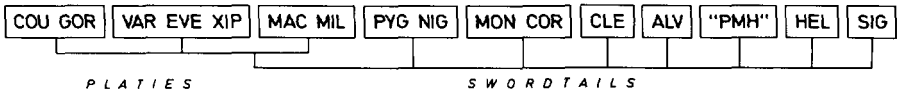
Table 2: Ratio of male to male + female ($\delta\delta/\delta\delta + \text{♀♀}$) relative frequencies for 12 responsive behavior patterns.

Behavior/Species	AND	COU	EVE	GOR	MAC	MEY	MIL	VAR	XIP	ALV	CLE	COR	HEL	MON	NIG	PYG	SIG
Pecking	0.59	0.26	0.66	0.29	0.43	0.34	0.36	0.45	0.03	0.36	0.48	0.68	0.90	0.32	0.45	0.90	0.56
Approaching	0.66	0.90	0.52	0.65	0.38	0.81	0.83	0.62	0.14	0.82	0.71	0.25	0.64	0.64	0.48	0.79	0.58
Leaving	0.17	0.01	0.42	0.42	0.38	0.17	0.48	0.52	0.40	0.25	0.12	0.42	0.17	0.32	0.24	0.39	0.36
Backward Swimming	0.74	0.79	1.00	0.71	0.00	1.00	0.00	0.45	0.64	0.82	0.74	0.32	0.86	0.50	0.75	0.28	0.58
Tail Beating	1.00	1.00	1.00	—	—	—	—	0.00	—	0.71	—	—	0.00	0.42	0.00	—	0.58
Feigned Biting	—	0.46	—	—	—	0.00	—	—	—	0.65	0.87	0.49	1.00	0.14	—	—	0.15
Real Biting	—	—	—	—	1.00	—	—	—	—	0.88	1.00	—	1.00	0.41	—	—	0.09
Rapid Head Jerking	—	1.00	1.00	0.87	0.65	1.00	—	0.64	0.51	0.95	1.00	1.00	0.58	0.98	0.55	1.00	0.63
Sigmoid Posture	—	1.00	—	0.63	—	—	—	0.81	—	1.00	—	—	1.00	0.95	0.50	1.00	0.81
Head-up Posture	0.39	—	—	0.45	1.00	—	—	0.00	0.58	—	1.00	—	0.32	0.92	0.03	0.29	0.58
Head-down Posture	—	—	—	—	—	—	—	1.00	—	—	—	—	—	—	—	—	0.64
Escape Response	1.00	—	—	1.00	1.00	—	1.00	0.38	—	—	1.00	—	—	1.00	—	—	1.00

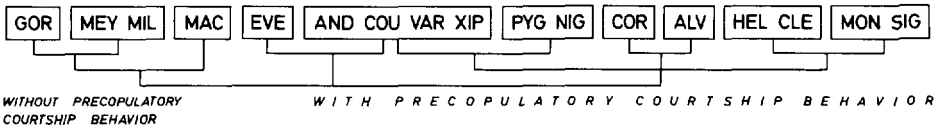
Considering Fig. 1, GOR possesses the fewest behavioral activities while SIG was most active. Between these two extreme values, the remaining 15 species can be ranked according to increasing number of behavioral activities in males as follows: MEY < MIL < MAC = COR < EVE = VAR < XIP < COU < AND = NIG = PYG < ALV < CLE < HEL < MON. If one compares each of the 17 different *Xiphophorus* forms with respect to the total number of behavioral activities they share with

the remaining 16 species, the following rank order of increasing number of common activities was found: GOR < MEY < MIL < MAC < XIP < VAR = CLE < COU < AND = COR < HEL < EVE < NIG < ALV < PYG < MON < SIG.

As to the responsiveness between male and female behavioral activities (Table 2), the ratio of $\sigma\sigma/(\sigma\sigma + \text{♀♀})$ may occupy all values between 0 and 1. It equals 0 when the male value equals 0 and will become 1 when the female value equals 0. Accordingly, a value of 0.5 represents equal male and female activity. If one regards all values of Table 2 with approximately similar female response to male courtship, i.e. all values varying between 0.4 and 0.6 (0.5 ± 0.1), the 12 behavioral activities rank as follows according to a decreasing number of that kind of value (0.5 ± 0.1): Pecking = Leaving > Approaching = Backward Swimming = Rapid Head Jerking = Head-up Posture > Tail Beating = Feigned Biting > Real Biting = Sigmoid Posture > Head Down Posture = Escape Response. Rank-ing the 17 species under the same aspect, the following order will be found: SIG > NIG > VAR = XIP = MON > EVE = GOR > AND = COU = MAC = MIL = CLE = HEL > MEY = ALV = PYG.



Upper part of the synapomorphy diagram for the species *Xiphophorus* (after ROSEN, 1979)



Interspecific relationship according to the frequency distribution of sexual behavior patterns

Fig. 2: Tentative phylogenetic relationships within the genus *Xiphophorus*.

Discussion:

Taking altogether (Fig. 1, Table 2), the possible phylogenetic relationship within the genus *Xiphophorus* might be tentatively extracted from these results (Fig. 2) which need further confirmation by more quantitative studies now in progress. The present findings agree partly with the last revisionary systematic investigation of the genus carried out by ROSEN (1979) in as much as GOR and SIG occupy the endpoints of a linear scale representing the interspecific relationship in both studies (Fig. 2). Further agreements consist of a close neighborhood between MAC/MIL and PYG/NIG, and, more far distant, between ALV/HEL. Differences then exist with respect to the remaining 9 species. "PMH" populations were not included in the present study and ROSEN (1979) could not yet regard the recently described species AND and MEY. The present investigation revealed closer relationships between MIL/MEY, AND/COU/VAR/XIP, PYG/NIG, HEL/CLE, and MON/SIG.

Although it seems still premature to discuss all the possible relationships in detail and compare our outcomes with those of FRANCK (1964, 1968) and ROSEN (1960, 1979), it should be stated that GOR represents the species with the least developed sexual behavior patterns while SIG represents the species which shows the largest repertory of sexual behavior. In agreement with FRANCK (1968), we cannot find any dichotomy within the swordtails. However we are unable to follow

FRANCK in demonstrating a split of the genus into two major lineages, the platyfishes and sword-tails. Instead of this a division of xiphophorin fishes into two groups will be proposed, viz. one group of *Xiphophorus* without precopulatory courtship behavior (GOR, MEY, MIL, MAC, EVE) and a second group with a well-developed precopulatory courtship behavior (AND, COU, VAR, XIP, PYG, NIG, COR, ALV, HEL, CLE, MON, SIG) following the behavioral dichotomy in the subgenus *Limia* as found by FARR (1984). The borderline between species with and without precopulatory behavior consists of the presence or absence of both the forward and backward phase of Corraling ("backing" behavior, "Wiegebalz"). Again we agree with FRANCK's opinion that the only poorly developed sexual behavior patterns of the second group of xiphophorin fishes may be considered as remnants of the original corraling behavior of the first group with a distinct precopulatory behavior. If so, the first group does not represent the primordial state of evolution but rather a secondarily reduced evolutionary state. That is to say, SIG should more resemble the primordial state of *Xiphophorus* than, e.g., GOR or MEY. Evolutionary transitions would then take mainly by regulatory mutations leading to repressions of different behavioral patterns, i.e. to secondary simplifications as found for the *Xiphophorus* group without precopulatory courtship behavior. Inter-specific breeding experiments now in progress should provide further evidence for this hypothesis.

S u m m a r y : A comparative study was carried out to analyse the sexual behavior of 17 different species of *Xiphophorus*. Possible phylogenetic relationships between these species with respect to the frequency distribution of 23 social behavioral patterns revealed a subdivision of the genus *Xiphophorus* into two major lineages, viz. one without a precopulatory courtship behavior and a second one with a well-developed precopulatory courtship behavior. These findings were discussed in terms of the behavioral results of FRANCK (1964, 1968) and the revisionary studies of ROSEN (1960, 1979).

A c k n o w l e d g e m e n t s : The *Xiphophorus* species used in this study were kindly provided by the late Prof. Dr. Dr. h.c. mult. C. Kosswig, Prof. Dr. K.D. Kallman, Mr. M.K. Meyer and Dr. M. Schartl. The authors are gratefully indebted to Mdmes. E. Neubner, L. Kern and A. Sedlmeier for preparing the drawings and careful breeding of the fish. For both critical correction and formal improvement of the manuscript, the help of Dr. J. Favor is gratefully acknowledged. Furthermore, we have to thank Mr. G. Goddeng for taking the photos from the live fish. The present investigation was partly supported by a grant of the Deutsche Forschungsgemeinschaft (DFG Schr 219/2-3) to Prof. Schröder.

References:

- ARNOLD, P. (1909): *Xiphophorus helleri* var. *guentheri*. — Wschr. Aqua.-Terrark., 6: 433 - 435.
- BAERENDS, G.P., R. BROUWER and H.T.J. WATERBOLK (1955): Ethological studies on *Lebistes reticulatus*. I. An analysis of the male courtship pattern. — Behaviour, Supplement, 1: 1 - 243.
- CLARK, E., L.R. ARONSON and M. GORDON (1954): Mating behavior patterns in two sympatric species of xiphophorin fishes: Their inheritance and significance in sexual isolation. — Bull. Amer. Mus. Nat. Hist., 103: 135 - 226.
- FARR, J.A. (1984): Premating behavior in the subgenus *Limia* (Pisces: Poeciliidae): Sexual selection and the evolution of courtship. — Ztschr. Tierpsychol., 65: 152 - 165.
- FRANCK, D. (1964): Vergleichende Verhaltensstudien an lebendgebärenden Zahnkarpfen der Gattung *Xiphophorus*. — Zool. Jb. Physiol., 71: 117 - 170.
- (1968): Weitere Untersuchungen zur vergleichenden Ethologie der Gattung *Xiphophorus* (Pisces). — Behaviour, 30: 76- 95.
- (1970): Verhaltensgenetische Untersuchungen an Artbastarden der Gattung *Xiphophorus* (Pisces). — Ztschr. Tierpsychol., 27: 1 - 34.
- LANGER, W.F. (1913): Beiträge zur Morphologie der viviparen Cyprinodontiden. — Gegenbaurs Morphol. Jb., 47: 193 - 307.
- LATTERMANN, S. (1957): Beobachtungen zur Verhaltensweise des Schwerträgers *Xiphophorus helleri*. — Unpublished Thesis, Universität Hamburg, Zoologisches Staatsinstitut.
- MEYER, M.K. and M. SCHARTL (1980): Eine neue *Xiphophorus*-Art aus Vera Cruz, Mexico. — Senckenbergiana Biologica, 60: 147 - 151.

- ROSEN, D.E. (1960): Middle-American poeciliid fishes of the genus *Xiphophorus*. – Bull. Florida State Mus., **biol. Sci.**, **5**: 57 - 242.
- (1979): Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative geography. – Bull. amer. Mus. nat. Hist., **162**: 267 - 376.
- ROSEN, D.E. and K.D. KALLMAN (1969): A new fish of the genus *Xiphophorus* from Guatemala, with remarks on the taxonomy of endemic forms. – Amer. Mus. Novitates, **2379**: 1 - 29.
- SCHARTL, M. and J.H. SCHRÖDER (1986): *Xiphophorus meyeri* n. sp., eine neue Poeciliiden-Art aus Coahuila, Mexico. – (In preparation).
- SCHLOSSBERG, H., M.C. DUNCAN and B.H. DAITCH (1949): Mating behavior of two live-bearing fish, *Xiphophorus helleri* and *Platypoecilus maculatus*. – Physiol. Zool., **22**: 148 - 161.
- SCHOLZ, E. (1909): Bericht über die Generalversammlung der Vereinigung der Breslauer Aquarien- und Terrarienfreunde. – Wschr. Aquar.-Terrark., **6**: 624.
- SCHRÖDER, J.H. and W. HEINRICH (1985): Genetic alterations as determined by quantitative morphological, viability and social behavioral traits in postirradiation generations of an inbred strain of the platyfish, *Xiphophorus maculatus* (GÜNTHER) (Pisces: Poeciliidae), induced by 1000 R of X-rays to spermatogonia and oogonia. – Biol. Zbl., **104**: 125 - 143.
- WICKLER, W. (1957): Das Verhalten von *Xiphophorus maculatus* var. Wagtail und verwandten Arten. – Ztschr. Tierpsychol., **14**: 324 - 346.
- ZANDER, C.D. and M. DZWILLO (1969): Untersuchungen zur Entwicklung und Vererbung des Caudalfortsatzes der *Xiphophorus*-Arten (Pisces). – Zeit. wiss. Zool., Leipzig, **178**: 275 - 315.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Berichte des naturwissenschaftlichen-medizinischen Verein Innsbruck](#)

Jahr/Year: 1986

Band/Volume: [73](#)

Autor(en)/Author(s): Schröder Johannes Horst, Heinrich Wolfgang

Artikel/Article: [Tentative findings on the phylogenetic relationship within the genus Xiphophorus with regard to the frequency distribution of sexual behavior patterns \(Pisces: Poecillidae\). 187-197](#)