The Genus *Xiphophorus* in Mexico and Central America

KLAUS D. KALLMAN\(^1\) and STEVEN KAZIANIS\(^2\)

ABSTRACT

The genus *Xiphophorus* is found from northeastern Mexico (Coahuila) for about 2200 Km as far as Honduras. There are 26 species, of which 21 occupy headwaters on the eastern slope of the Sierra Madre Oriental and continuing Cordillera to the southeast. Virtually all the species in the headwaters occupy limited ranges, often in rivers traversing karst country that are separated from lowland streams by underground passages. Only the three forms in the coastal plain are more widely distributed. Nineteen taxa occur within 400 Km of the Mexican Trans Volcanic Belt, suggesting that the genus may have evolved in this region. In many localities two species are sympatric, but natural hybrids are only known from three or four sites. Four monophyletic groups have been identified: the northern platyfish and the northern swordtail groups, north of the Mexican Trans Volcanic Axis, and to the south the *helleri* and the *clemenciae* swordtail groups. The status of the three southern platyfish is still not resolved and the phylogenetic relationship of the different groups to each other is still not fully understood.

INTRODUCTION: PLATYFISH AND SWORDTAIL

The fish of the genus *Xiphophorus* are known by the common names of platyfish and swordtail. Until the early part of the last century, only five forms of the genus were known. Three species were platyfish, *maculatus*, *couchianus*, and *variatus*, which lacked swords and were united by certain gonopodial characters. They were placed in the genus *Platypoecilus*, meaning the "broad variable one," a reference to the body shape and the many color patterns of the southern platyfish. Two species were swordtails much larger and more elongate and with long caudal appendages or swords. They also shared a number of gonopodial traits that set them apart from the platyfish. They were placed in the genus *Xiphophorus*: the etymology is derived from Greek and means "carrier of the dagger," a reference to the dagger-like gonopodium, the modified anal fin of adult males, and not to the long sword as is sometimes supposed (reviewed in Refs. 1 and 2).

As more species were described, it became apparent that the distinction between *Platypoecilus* and *Xiphophorus* could no longer be maintained. There were forms that showed gonopodial traits of either group and there were platyfish with short swords and swordtails without. *Platypoecilus* became *Xiphophorus*.\(^{1,2}\)

The vernacular terms of "platyfish" and "swordtail" have never been defined and thus have no scientific standing. Researchers make a virtually unconscious decision whether to call a *Xiphophorus* a platy or a swordtail. It is a Gestalt idea drawing upon size, shape, and pigment patterns. Only Rosen\(^2\) once expressed doubt when he pointed out that *X. milleri*, a "platyfish," really has a body shape that is closer to that of a swordtail. Nevertheless, the vernacular terms are useful for discussion purposes and we think we should continue using

---

\(^1\)Department of Vertebrate Zoology (Ichthyology), American Museum of Natural History, New York, New York.


271
them. Other terms have been used, such as “northern platyfish, southern platyfish, Rio Grande platyfish, Pánico Basin swordtails, northern swordtails, and southern swordtails.” This terminology also has never been defined, and is rather loosely applied by different investigators. Thus, paradoxically, a platyfish (e.g., *xiphidium*), sometimes considered as “southern,” may live further north than the northern swordtails. We propose to use the Trans-Mexican Volcanic Belt in central Veracruz as a reference point for “north” and “south,” because it bisects the Atlantic coastal plain at Punta del Morro and it is an important divide and barrier to many groups of fish.³

Species of *Xiphophorus* that are north of this barrier become northern platyfish (*variatus, evelynae, xiphidium, couchianus, gordoni, and meyeri*) or northern swordtails (*pygmaeus, multilinatus, nigrensis, montezumae, nezahualcoyotl, contineus, cortesi, multirnche, and birchmanni*). A subset of the northern platyfish (*couchianus, gordoni, and meyeri*) can be referred to as “Rio Grande platyfish,” because they live in this drainage basin. South of the volcanic belt there are three southern platyfish (*milleri, andersi*, and *maculatus*) and eight southern swordtails. Because it is known that the southern swordtails are not monophyletic,⁴ we propose that these fish be referred to as the *helleri* (*helleri, alvarezi, signum, nayae*, and *kallmani*) and the *clemencie* groups (*clemencie, monticulus, and mixel*). This proposed terminology is being used in this text. It must be emphasized that the use of these vernacular terms is strictly for discussion purposes and does not imply that members of a section (e.g., “platyfish”) constitute a monophyletic group, although they very well might so.

**NORTHERN PLATYFISH**

Three species of *Xiphophorus* are known from the Rio Grande drainage in Mexico (Fig. 1). All of them have extremely limited distributions. The most northerly form, *Xiphophorus meyeri*, occurs in a few springs in and around the town of Melchor Muzquiz, Coahuila.⁶⁷ This site (approximately 200 Km west of Nuevo Laredo on the United States–Mexican border) is located along the base of the Sierra Madre Oriental and at the edge of the Chihuahuan Desert. Many individuals of this species are polymorphic for a prominent black pattern that consists of large clusters of melanophores distributed along the flank and primarily arranged in the lower parts of the dermis, in the myoseptae, and along major blood vessels. Individuals lacking this pattern possess a few small elongated spots of subdermal melanophore on the caudal peduncle and along major blood vessels. This faint pattern, “the deep lying spot trait,” is also present in the other *Xiphophorus* species inhabiting the Rio Grande drainage, but absent from all other members of the genus.

The difference between the two color morphs of *X. meyeri* is controlled by a single autosomal locus (homozygous recessive is absence of spots). When a homozygous recessive *X. meyeri* with only faint traces of this pattern is crossed with an unsotted *X. milleri*, a species lacking this pattern, *F₁* hybrids are produced that all exhibit this pattern to a moderate degree. When backcrossed to *X. milleri*, the expression of this trait in the *Bc* hybrids ranges from complete absence to one comparable to that seen in the *F₁* fish. In Mendelian terms this means that the deep lying spot pattern is caused by a polygenic system present in all *X. meyeri*. A dominant autosomal factor is required to bring it to its full expression. *X. milleri* lacks the polygenic system for this pattern, but it has a genotype that permits expression of the polygenic *meyeri* system.

About 120 km to the southwest of Melchor Muzquiz, *X. gordoni* inhabits a few small springs in the Cuatro Ciénagas Basin, Coahuila.⁸ Population size is rather limited. The fish exhibit a greatly reduced form of the “deep-lying” melanophore pattern, faintly visible above the midlateral line of the caudal peduncle.⁹

The third species, *X. couchianus*, inhabited springs around what has now evolved into the metropolis of Monterrey, Nuevo León. It was the second *Xiphophorus* to be described and it was discovered by Lt., later Major General, Couch. The type location appears to have been a spring pool at a location, Cadarecta (perhaps a misspelling of Cadareyta), now obliterated by a skyscraper in Monterrey. The species became
extinct in its natural habitat around 1964 when excessive pumping lowered the water table, and the springs in the Huasteca Canyon about 10 Km upstream from Monterrey failed. These springs were the last known refuge of this species. The small isolated populations in the canyon, like those of *X. gordonii*, had a depauperate gene pool.

In subsequent years, a number of populations of *Xiphophorus* have been discovered in some spring-fed pools in the formerly dense thorn forest about 20 Km northeast of the center of Monterrey (e.g., Apodaca). This area has now become engulfed in the urban sprawl of Monterrey and all of these undescribed populations have become lost either by hybridization with released domesticated swordtails and platyfish of the hobby trade or because of failure of the springs. Like *X. meyeri*, individuals of these populations exhibited similar large melanophore spotting on the flank. There can be no question that this undescribed form is closely allied to the *meyeri-gordonii-couchianus* group. The possibility that it might represent a spotted variety of *X. couchianus* (just like *X. meyeri* that has spotted and unspotted individuals) cannot be rejected until formally examined.

The type specimens of *X. couchianus* have not been located and are apparently lost, and a direct comparison between the “Monterrey-Huasteca” and the Apodaca forms is not possible. Moreover, some doubt persists about the exact type location of *X. couchianus*, because there is also a town called Cadereyta, 35 Km east of Monterrey. Thus some uncertainty exists as exactly where and which kind of *Xiphophorus* Li. Couch collected.
Xiphophorus couchianus from the Huasteca Canyon does not phenotypically resemble the Apodaca form. It does exhibit “deep-lying” melanophores to a slightly greater degree than X. gordonii but it does not even faintly resemble the bold pattern present in Apodaca fish and X. meyeri. Gordon, who in 1930 and 1939 was the second investigator to collect X. couchianus, did not mention any specimens with black blotches.11 Kallman, who studied these fish in the Huasteca Canyon and in the Río St. Catarina (its outflow), saw and collected only unspotted fish in 1960 and 1961.

The Río San Fernando, which is the next river to the south of the Río Grande system, is the only river on the Atlantic slope of Mexico, Belize, and Guatemala that has no Xiphophorus. The next river system to the south, Río Soto La Marina, is inhabited by X. xiphidium (Fig. 1). This species is commonly found in small springs and streams that arise at the base of the Sierra Madre from Ciudad Victoria (Tamaulipas) northwards. At least one population, perhaps an undescribed form allied to xiphidium, is known from a spring at an elevation of 1000 m near Aramberri, San Luis Potosí.2 The species occurs also in springs at the foot of the Sierra San Carlos, an isolated mountain range in front of the Sierra Madre. Two sex-linked macromelanophore patterns and a number of autosomal tail spot patterns have been described for this species.13 The lower ventral caudal fin rays in males are slightly elongated to form a colorless sword.

Separated from this river system by basalt capped mesas to the south is the large Río Pánuco Basin inhabited by ten species of Xiphophorus. X. variegatus has the widest distribution (Fig. 2) and is found throughout the coastal plain and foothills and extends southwards in the ever narrower coastal plain as far as the Río Nautla. Only in two places does X. variegatus occur in the Sierra Madre: in the Jamauve Valley, an arid intermontane basin and in the headwaters of the Río Cazones, areas from which other Xiphophorus are absent. This species possesses a number of sex-linked macromelanophore and autosomal tail spot patterns.13,14

The macromelanophore patterns of the Río Pánuco X. variegatus are distinct from those of fish in the Río Tuxpan, Río Cazones, Río Tecolutla, and Río Nautla to the south. Populations with these different patterns are encountered within 200 m of each other across a low Río Tuxpan–Pánuco Basin divide, about 20 Km south of Chicontepec (Veracruz). One macromelanophore pattern, spotted caudal (Sc), is restricted to the Río Tuxpan and Río Cazones populations. The tail spot patterns appear to be identical to those of X. xiphidium. Mature males develop a yellow dorsal fin and the caudal fin becomes either red or yellow. The caudal fin polymorphism is controlled by an autosomal locus. Other yellow and red patterns are present in the populations south of the Pánuco Basin.

A form closely resembling X. variabilis, restricted to the headwaters of the Río Tecolutla at Nacaxa (at 1200 m, see Fig. 1) (Puebla) above the falls at Patla, has been described as X. evelynae.2 This form has been poorly studied and is little known. Xiphophorus variabilis in the headwaters of the Río Cazones, found at an elevation of ~1000 m, superficially resembles X. evelynae.

NORTHERN OR RÍO PÁNUCO SWORDTAILS

Nine northern swordtails inhabit different tributaries of the Río Pánuco Basin, draining the eastern slope of the Sierra Madre Oriental and the Sierra Potosina and Sierra San Martín, low mountain ranges immediately to the east (Tamaulipas, San Luis Potosí, Hidalgo). None of them occur in the coastal plain (Figs. 1 and 3). The three species of the pygmaeus clade (X. pygmaeus, X. multilineatus, X. nigrensis) live in three short swiftly flowing streams (Río Huichihuayán, Río Coy, and Río Choy), all in San Luis Potosí. These streams arise within 50 Km of each other and originate from large springs between 40 to 100 m above sea level at the foot of the Sierra Madre. The headwaters of the Río Huichihuayán (pygmaeus) and Río Coy (multilineatus) come within 3 Km of each other in the narrow level valley between the Sierra Madre to the west and the Sierra Potosina to the east. The Río Coy joins the Río Tampón on its southern bank, whereas the Río Choy (mi-
**Xiphophorus** in Mexico and Central America

![Map of Mexico and Central America](image)

**FIG. 2.** Distribution of the three wide-ranging *Xiphophorus* species. (A) *X. variatus*, (B) *X. helleri* and *X. maculatus*. The range of *X. helleri* completely encompasses that of *X. maculatus*, but the latter is restricted to the coastal plain. The area along the base of the Yucatan peninsula is poorly collected. The range of *X. helleri* and *X. maculatus* may extend somewhat further to the north than indicated on the map.

*grensis*) flows into the Río Tampáon further downstream on the opposite bank. Mature males of the three species are laterally compressed and assume an iridescent blue sheen.

The *X. montezumae* clade is found north of the Río Tampáon–Río Santa María Axis (San Luis Potosí and Tamaulipas). The rivers and streams that drain the eastern folded front ranges are inhabited by *X. nezahualcoyotl*, whereas those in more interior valleys are occupied by *X. montezumae*. *Xiphophorus continens* is restricted to a single short headwater stream (Río Ojo Frío) where it is sympatric with *X. montezumae*. Different sections of each of the two main rivers occupied by *X. nezahualcoyotl* are separated from each other by high waterfalls and cataracts, but these do not represent barriers to the species' distribution. The species is found from an elevation of 100 m at Nacimiento del Río Nacimiento to 1200 m at Gallitos (Tamaulipas) and Francia Chica (San Luis Potosí).

The three species differ from each other in standard length, body proportions, and pigment patterns. The males of *X. montezumae* develop one of the longest swords in the genus, whereas in the diminutive *X. continens* a sword is lacking.

The *cortezi* clade is found south of the Río Tampáon–Santa María Axis (Fig. 3). The rivers that drain the Sierra Madre between the Río Santa María and the Río Moctezuma (San Luis Potosi) are occupied by *X. cortezi*. This species also occurs in the streams of the relatively low Sierra Potosina and Sierra San Martin that are in front of the Sierra Madre. Beyond the Río Moctezuma, the streams of the Sierra (Hidalgo Anticline) are inhabited by *X. birchmanni*. Its
range extends southeastward into the adjacent Rio Tuxpan drainage. At higher elevation this species is replaced by *X. malinche*, but its range is incompletely known, because this region is poorly collected. Members of this clade are robust, deep-bodied fish. The males of *X. birchmanni* lack swords, but in the other two species the caudal appendage is moderately well developed. The three species share a number of pigment patterns.

**SOUTHERN PLATYFISH AND SWORDTAILS**

About 70 Km northwest of the city of Veracruz, the Atlantic coastal plain disappears momentarily where the Trans-Mexican Volcanic Belt runs into the Gulf of Mexico. Further to the east, the gulf coastal plain widens to 100 Km in the Rio Papaloapan and Rio Coatzacoalcos Basins and to 250 Km in the Rio Usulacinta drainage in the Peten and Alta Verapaz districts of Guatemala. About 130 Km east of the city of Veracruz, a volcanic range, Sierra de los Tuxtlas, is bordered on the north by the Gulf of Mexico and surrounded on the other sides by the coastal plain. A large lake, Lago de Catemaco, fills the 14 Km wide caldera. Numerous small streams drain into the lake; its outflow drops over El Salto de Eyipantla into the Rio Papaloapan drainage.

Two species, *X. maculatus* and *X. helleri*, occur from this volcanic belt southeastward for about a thousand kilometers as far as Guatemala and Honduras (Fig. 2). The southern platyfish, *X. maculatus*, is restricted to the coastal plain and ranges inland as far as the
foothills, whereas X. helleri is also present in mountain streams near Jalapa as high as 1500 m elevation. This platyfish is a rather short, small species with a large number of color patterns. As far as pigmentation is concerned, it is the most variable vertebrate known. The green swordtail is a rather large, somewhat elongate fish with a long sword, with red stripes along the flank. A large number of pigment patterns are present, usually of rather local distribution, which have been neither studied nor catalogued. In general, X. maculatus is the more common fish in the coastal plain.

Two forms of Xiphophorus are endemic to the Lago de Catemaco Basin. Little is known about the distribution of X. kalbmani (Fig. 1), recently described from a small stream entering the lake near Tebanca and its possible sympatry with X. helleri. The other endemic, X. milleri, a rather slender, diminutive platyfish, is found in every stream that drains into the lake and is also present in its outlet (Fig. 1). X. maculatus is found below the waterfall.

Another endemic form, X. andersi, also of limited distribution, is restricted to the headwater of the Rio Atoyac (elev. 550 m), just east of Cordoba, Veracruz, above the falls and cataracts at Atoyac (Fig. 1). This species is relatively small and deep bodied and the only pigmented polymorphism present concerns the pseudogravity spot that is lacking in the smaller males. The presence or absence of the pattern is under sex-linked control. The genetic basis for the pseudogravity spot is analogous to that of the deep-lying spot pattern of X. meyeri. All males develop a very short unpigmented sword.

The members of the clemenciae group (clemenciae, monticolus, mixei) are endemic to the upper Rio Coatzacoalcos Basin, the Isthmus of Tehuantepec (Fig. 4b; Veracruz and Oaxaca). Xiphophorus helleri and X. clemenciae exhibit a complimentary distribution (Figs. 4a and 4b). In general, X. helleri occurs as far inland as the foothills and is then replaced by members of the clemenciae clade. Xiphophorus clemenciae has its heaviest concentration in the streams east of the center of the Isthmus (Fig. 4b). In some streams near the foothills both species are sympatric. To the west the other two members of the clade are found in headwater streams of the Rio Sarabia and Rio Jaltepec which are major Rio Coatzacoalcos tributaries. Only in the very center of the Isthmus where the elevation barely exceeds 250 m does one find X. helleri as far south as the continental divide and the clemenciae group is absent.

In the eastern part of its range, X. helleri is replaced by X. signum and X. alvarezi in headwater streams of the Rio Usumacinta drainage (Fig. 1; Chiapas, Mexico; Alta Verapaz, El Quiche, Huehuetenango, Guatemala). At least in Guatemala all of these rivers in this extensive karst area go either underground or are separated by waterfalls from coastal plain streams, and this may also hold true for Chiapas. In some areas, X. alvarezi and X. helleri are separated from each other by a barrier of only 1 kilometer. The populations of X. alvarezi from the isolated sections of the Rio Salinas system differ in several pigmentary and morphological traits from those further west. Xiphophorus alvarezi has a relatively wide distribution, approximately 125 Km inside the front ranges, whereas X. signum is restricted to the Chajmaic Valley. This form is the morphologically most distinct of all swordtails. It lacks any trace of red pigmentation and it is the only Xiphophorus with a subtriangular dorsal fin (the anterior dorsal rays are significantly longer than the posterior ones). All immature fish display the "grace" spot beginning at the age of about 3-4 weeks which in other swordtail species is restricted to males and does not develop until the onset of sexual maturation. The pattern gives rise to or is incorporated into the black dorsal margin of the sword in all Xiphophorus with a caudal appendage except X. andersi and X. xiphidium.

Near the eastern limit of the range of X. helleri in Guatemala and Honduras the gonopodial structure of the swordtails differs somewhat from that of other populations. Rather than describing these fish as still another taxon, Rosen referred to these fish as the "PMH" (Rio Polochic, Rio Motagua, Honduras) complex. Recently a new species of swordtail, X. mayae, was described from near Lake Izabal, Guatemala, but its distribution is not well understood (Fig. 1). The supposition of Meyer and Schartl that PMH and X. mayae are one and the same form is not supported by their results.
FIG. 4. (a) Collecting stations for X. helleri in the Río Coatzaalco Basin depicted in green circles. (b) Collecting stations for three species of the X. clemenciae clade in the Río Coatzaalco Basin. Red squares indicate X. clemenciae, yellow triangles represent X. mixel, and purple stars indicate collections of X. monticolus.
XIPHOPHORUS IN MEXICO AND CENTRAL AMERICA

The Rio Lancetilla stock of swordtails, a member of the PMH complex, is indistinguishable from "helleri" and distinct from X. mayae, according to the authors' own mitochondrial DNA data. The Rio Lancetilla stock of Meyer and Schartl, of Kallman, Walter, Morizot, and Kazianis (see below) and the specimens examined by Rosen and originated all from Dr. Myron Gordon's collection in Honduras in 1951.

SYMPATRY

In many regions two species of Xiphophorus occur together, but few sites are known where three species are present. Over its entire wide range X. maculatus is broadly sympatric with X. helleri (Fig. 2), but platyfish always greatly outnumber swordtails. Xiphophorus helleri is also sympatric with X. milleri in Lago de Catemaco and with X. andersi in the upper Rio Atoyac. Again, the swordtail is usually greatly outnumbered by the other two species. In the Rio Coatzacoalcos Basin there is a rather narrow zone where the ranges of X. helleri and X. clemenciae overlap (Figs. 4a and 4b). At one site (in the Río Nautla) X. helleri is sympatric with X. variatus. Not sufficient information is available to determine whether X. mayae and "PMH" are sympatric with X. helleri. Xiphophorus monticolor and X. mixei are sympatric in the Río del Sol (Fig. 4b, Oaxaca).

A more complex situation occurs in the Río Pánuco Basin where nine species of Xiphophorus are found. X. variatus is sympatric with six species (X. nezahualcoyotl, X. nigrescens, X. multilineatus, X. pygmaeus, X. cortezi, X. birchmanni) in parts of its range along the mountain front (Fig. 1). Xiphophorus cortezi is sympatric with X. birchmanni in the Río Santa Cruz near Oriztlan (Hidalgo), and X. malinche occurs together with X. birchmanni in the Río Cañali. The distribution of X. malinche is incompletely known; there could exist other areas of sympathy. Over its entire limited range in the Río Ojo Frío X. continens is found together with X. montezumae. The only locations where three species are present are in the Río Coy tributaries (X. variatus, X. multilineatus, X. cortezi) and in the Río Huichihuayán (X. variatus, X. pygmaeus, X. cortezi). Species that are not sympatric with any other Xiphophorus anywhere within their ranges are the three Río Grande platyfish, (X. meyeri, X. gordonii, X. couchanus), X. xiphiidum, X. alvarezi, and X. signum.

HYBRIDIZATION

In spite of the many areas of sympathy and the relative ease with which many hybrids are obtained in the laboratory, only three or four localities are known where two species of Xiphophorus hybridize with each other. Hybrids between X. malinche and X. birchmanni are common in the Río Calnali (Fig. 1; Hidalgo, Mexico) and in a nearby arroyo. These sites are close to the altitude (1000 m) that corresponds to the upper limit of X. birchmanni and the lower limit of X. malinche distribution. Hybrids between X. birchmanni and X. cortezi have been identified in the Río Santa Cruz east of Oriztlan, Hidalgo, by electrophoretic methods (Morizot and Kallman, unpublished observations). This rather disturbed site comprises a wide shallow river with innumerable rocks and boulders at a road ford. The third hybrid location is the source of the Arroyo Zarco (Tamaulipas, Mexico), a small headwater tributary to the Río Sabinas. The source of the arroyo are two small isolated spring-fed rock pools, perhaps not more than 1 m wide, 0.75 m deep, and 20 m long, virtual natural aquaria. The pools are inhabited by X. variatus and X. nezahualcoyotl, two rather dissimilar species in coloration but not in size, and their complex hybrids. There are males with the habitus of variatus but with short swords and nezahualcoyotl type males with long swords, red caudal fins and the tail-spot pattern "Cut-Crescent." Xiphophorus nezahualcoyotl is restricted to the two springs and does not occur in any of the pools further downstream. Electrophoretic data failed to reveal F1 hybrids. Instead the fish turned out to be complex hybrids with highly variable amounts of traits from either parental species, apparently a hybrid swarm that dates back many generations (Morizot and Kallman, unpublished observations). Gonopodial anatomy was just as variable. Many mature variatus or variatus-type males exhibited a heavy melano-
nosis in the region immediately above the insertion of the gonopodium. Such an abnormal pigmentation on this part of the lower flank has not been seen on any *X. variatus* over the entire range of this species. Even in the pools downstream from the two springs, no *X. variatus* has ever exhibited such a pattern.

A fourth hybrid location may occur in the upper Río Salinas or Río Chixoy (El Quiche, Alta Verapaz, Guatemala) where several populations of swordtails exhibit morphological features intermediate between those diagnostic for *X. helleri* and *X. alvarezi*. This situation, however, differs from the other hybrid sites in that only one parental species is present. *Xiphophorus helleri* is found in the lower Río Salinas, but as far as is known, *X. alvarezi* is present only in the nearby isolated Río Dolores. Rosen\(^{20}\) interpreted these populations as representing secondary intergrades.

Marcus and McCune\(^{23}\) suggested that body size could be a prezygotic barrier to interspecific fertilization (hybridization) and predicted that sympatric forms should be less similar in body size than allopatric ones. Indeed, adult size differs in eight to twelve sympatric species pairs (*pygmaeus*–*variatus* and *cortezii*; *milleri–hellerii*; *milleri–kallmannii*; *maculatus–hellerii*; *andersii–hellerii*; *mixei–monticulus*, and *continentes–montezumae*). The two species of pygmy swordtails, *X. nigriensis* and *X. multilineatus*, which are polymorphic for adult male size, could also be listed as living in sympathy with larger forms (*cortezii, variatus*), because most of their males are small. Adult male size in these taxa is controlled by a sex-linked polymorphism.\(^{24}\) Seven sympatric pairs do not differ significantly in size (*clementiae–hellerii*; all three forms of the *cortezii* clade are similar in size; *variatus–nezahualcoyotl*; *variatus–birchmanni* and *cortezii*). The three known hybrid situations all involve species of similar sizes.

With the possible exception of *X. signum*,\(^{20}\) all species of *Xiphophorus* can be hybridized with each other in the laboratory. Species hybrids are fertile and \(F_2\) and backcross generations can be obtained. Hybrids involving three species have also been bred. Hybridization has involved virtually every species except those that have been described during the last 4 years. The literature on hybridization is too numerous and scattered to be cited here. Three early useful summaries are those of Rosen.\(^{2,25,26}\) Hybrids develop many abnormalities that affect pigmentation,\(^{25–28}\) sex determination,\(^{29}\) physiology of the hypothalamo-pituitary axis,\(^{30}\) and morphology.\(^{1}\) Zander\(^{31}\) reported on hybrids involving members of the *pygmaeus* clade, species that are not often used in such experiments. Homospecific sperm has the advantage over heterospecific one.\(^{32}\) Recent studies also suggest that some hybrid combinations result in segregation distortion in selected regions of the genome.\(^{33}\)

Hybridization was originally performed to study melanoma development that occurs when the macromelanophore gene of *X. maculatus* is introduced into *X. helleri*. It is less well known that the expression of xantho-erythropore genes is also changed after hybridization, although not always in the same direction as the melanophore genes. Sporadic melanoma formation has also been observed within species.\(^{34,35}\)

**CONSERVATION AND ECOLOGY**

Urbanization and industrialization takes place in many parts of Mexico and is especially rapid in the arid northern region. All Río Grande platyfish are endangered and have been considered so for many decades (Fig. 1). These species live in a few small springs and these limited water resources are diverted increasingly for agricultural and human uses.\(^{36}\) The situation is especially serious in Melchor Muzquiz (Coahuila) where the springs are located within the city limits. In the Monterrey area (Nuevo León), *X. coulmanii* became extinct around 1963, and the last surviving population of the undescribed form east of the city near Apodaca was extirpated in 2005. A strain of *X. coulmanii* rescued from the Huasteca Canyon in 1961 is maintained at the *Xiphophorus* Stock Center, Southwest Texas State University, San Marcos, Texas, and a stock of the population from Apodaca is propagated at the Universidad Autonoma de Nuevo León. All *Xiphophorus* species that inhabit small ranges,
are of small population sizes, and are not considered endangered at the present, should be periodically monitored. Many of the species in the Cordillera live in long narrow valleys (Río Huichihuayán, X. pygmaeus; Río San Miguel, X. monticolus; Río del Sol, X. mixei and X. monticolus) that could be turned into reservoirs. *Xiphophorus continens* is abundant only in the nacimiento and is found in ever decreasing numbers downstream for 10 Km as far as Damian Carmona (San Luis Potosí). Although this semi-arid region is sparsely inhabited, agricultural use is quite intense and excessive withdrawal of water could eventually lead to the failure of the spring. The same consideration applies to *X. andersi* (Fig. 1) that is abundant only in the spring pool at Finca Santa Anita. A small dam has been constructed across the Río Attoyac, just downstream from the pool, from where the water is diverted to sugar cane fields. Further upstream some of the small tributaries to the Río Attoyac are heavily polluted from the effluent of a sugarcane mill. None of the three species of pygmy swordtails is threatened presently, but each one inhabits rather short streams and the area is under heavy agricultural use. The status of *X. milleri* (Fig. 1) should be reconsidered; it is considered threatened due to limited habitat, presence of exotic species, and small population size. But thriving populations exist in each of the many small mountain streams that drain into the lake. *Xiphophorus clemenciae* which had been considered a species of special concern, because of its apparent limited range, can now be removed from the list of threatened species (see Fig. 4). It is abundant and widespread in many streams in the uplands of the Río Coatzacoalcos Basin.

Many parts of southern Mexico and Central America were once covered by dense tropical forest that is now destroyed and replaced by pasture. The most obvious effects on aquatic habitat are more intense solar radiation leading to increased daylight water temperature, greater fluctuation of current and water level due to more rapid runoff. Although one does not know the condition before these changes took place, we fail to discern any effect of deforestation on the species' distribution. Over its wide range from Veracruz to Guatemala, *X. maculatus* (Fig. 2) is found consistently in the lowlands in small streams and stagnant bodies of water roughly to an altitude of 100 m, regardless of forest cover. The main requirements appear to be smaller bodies of water, stagnant or with light current, and submerged vegetation along the bank. It does not matter whether these habitats are in dense forests or in sun-drenched pasture. Gordon described the process by which intermittent pools are formed in arroyos during the dry season, their progressive shrinkage with time and the ever-increasing concentration of fish therein, and the ultimate extinction of the local populations. But this is a natural process and the streams and arroyos become repopulated by platyfish at the beginning of the rainy season from permanent spring-fed pools. With respect to platyfish species with which Gordon was most familiar, he wrote that all are found in relatively large number in the vicinities of springs. We like to add that this holds true for most, if not all *Xiphophorus* species. In the Río Tamesí drainage *X. nezahualcoyotl* (Fig. 1) occurs in the small source springs of the Arroyo Zarco, the densely shaded deep nacimientos of the Río Sabinas and Río Frio and also in the few pools in the boulder strewn, but otherwise dry Arroyo La Flor. In the interior Valley of Ocampo there is no body of water from where this species is absent. This includes the sun-drenched shallow pools in the middle of the mostly dry Río Ocampo and the small shallow rills just west of the town. Further west the species is also present in the deep pool at St. María de Guadalupe, the isolated spring at Calejones, and above a 400 m high escarpment in the isolated and shaded Río Gallitos at 1200 m. Upstream from Salto de Agua, the species is found in small brooks in narrow ravines between 1000 m and 1200 m at St. Barbara and even in man-made wells on steep hillsides. It appears as if geography is more important than habitat.

Only in some small streams in the Uxpanapa Valley (Veracruz) which has relatively recently been denuded of forest cover was the temperature at the critical level at which fish died (Kallman and Kazianis, unpublished observations).
PHYLOGENY AND GEOGRAPHY

Although the morphology, genetics, and taxonomy of these fish have been studied in considerable detail since 1927, a clear understanding of their phylogeny still eludes us. Any proposed phylogeny must also be placed into a geographic context. The genus ranges from northeastern Mexico to eastern Honduras. The species are found in parts of the coastal plain and on the eastern slopes the Sierra Madre Oriental and continuing mountain ranges to the southeast but never beyond the barrier range of the Mexican plateau. Of the 26 currently recognized species, 21 are restricted to the eastern slope of the Cordillera. If one disregards the five species in the coastal plain and in the isolated Sierra de los Tuxtlas, then one can envision a Xiphophorus distribution “band” about 2,200 Km long but never more than 25–50 Km wide (Fig. 1). Nineteen of the 26 species are found within 400 Km to the north and south of the Trans-Mexican Volcanic Belt, suggesting that Xiphophorus may have evolved in this region (as previously mentioned). Its sister-group, Priapella, is also found in this region (four species from the Rio Papaloapan to Rio Usamacinta). The taxa inhabiting the coastal plain are widespread (Fig. 2; over 1000 Km in the case of maculatus and helleri) whereas the mountain forms have rather restricted ranges (Fig. 1). This pattern of distribution indicates that the coastal plain offers no barrier to a species dispersal but the mountainous terrain does. Yet some species within their small geographic area extend across major ridges, escarpments, and perhaps waterfalls.

Four monophyletic groups have been identified (the northern platyfish group, the helleri group, the clemenciae group, the northern swordtail group). There is no agreement on the evolution of the three southern platyfish and how they are related to the other four groups. The phylogenetic position of these groups relative to each other is also not well understood. A phylogeny based on mitochondrial DNA data shows two main branches, one leading to the northern swordtails (north of the Trans-Mexican Volcanic Belt) and a second one to all other Xiphophorus. From the second one, the most basal branch leads to the helleri group followed by four branches leading to andersi, maculatus, milleri, and clemenciae, in this order. It should be noted that all five branches lead to taxa south of the Trans-Mexican Volcanic Axis. Thus according to this phylogeny, the southern platyfish plus the clemenciae group are basal to the northern platyfish and this makes very good geographic sense. The ancestral platyfish moved north from central Veracruz.

The habitus of X. clemenciae, however, differs radically from that of the platyfish that in our opinion its position as nesting among them should be reinvestigated. A phylogeny that is based upon a combination of morphological traits, AP-PCR results and the mitochondrial DNA data has all southern swordtails on one branch with the clemenciae group in the basal position. The southern swordtails comprise the sister-group to all platyfish. However, a phylogeny based upon nuclear DNA gave a different result. It also showed two clades, but one led to the helleri group and not to the northern swordtails and a second to all other Xiphophorus. These contradictions have to be re-examined with independent material.

The distribution of the four monophyletic groups is well correlated with major geographic features. The northern swordtails have been placed into three clades (montezumae, cortezii, pygmaeus). As discussed above, the distribution of the montezumae clade (Fig. 3) coincides with the folded ridges and valleys north of the Rio Tampón–Rio Santa María. The cortezii clade is associated with the Hidalgo anticline and the Sierra Potosina and Sierra San Martín south of the Rio Tampón and the pygmaeus clade with the small swift rivers that arise in front of the Sierra Madre. The synapomorphies (morphology and biochemical traits) uniting the pygmy swordtails are so numerous that the rather weak mitochondrial DNA evidence that places X. pygmaeus with the cortezii group is not convincing.

The northern swordtail group is restricted to the headwaters of the Pánico Basin (Fig. 3). In our interpretation, they evolved from an ancestral form that inhabited an ancient coastal plain located further to the west than the present one. This plain with the ancestral species was uplifted and in some places folded. As the fish became restricted to and subsequently iso-
lated in individual watersheds, they diverged and evolved into related endemic forms. The orogeny did not occur simultaneously in all places. This could also explain the presence of *X. variatus* and *X. evelynae* at high elevations above steep falls in the Río Cazones and Río Tecolutla, and of *X. variatus* in the arid Jamaquc Valley behind the high front ranges. As the sea receded and a new coastal plain was formed, another ancestral *Xiphophorus*, perhaps a proto-platypfish, invaded the new coastal plain from the south. This could explain why the northern swordtails are not closely related to any of the northern platyfish.

The Trans-Mexican Volcanic Belt eventually bisected the range of this new coastal form. This form spread in the coastal plain as far north as present day Coahuila and evolved into the northern platyfish group (Fig. 1). This group is monophyletic on the basis of biochemical and mitochondrial DNA data. There is a clear progression in the number of shared derived characters from south to north. Basalt-capped mesas just north of the Pánuco Basin then became the barrier that separated what became *variatus* from the northern populations. A further vicariant event split the Río Soto La Marina fish (now *xiphidium*) from the Río Grande platies. Climatic factors also must have played a role. As one proceeds north the climate becomes progressively cooler in winter with freezing temperatures of regular occurrence. *X. gordonii* and *X. meyeri* are relict populations that survive in isolated spring-fed pools that maintain a constant temperature throughout the year (Fig. 1). In historical times *X. coulanius* apparently was more widespread than the other two platyfish further north.

The mitochondrial DNA evidence shows *evelynae* as the most basal branch of the northern platyfish group. If this is correct, it would mean that a population of the platfish ancestor in the gulf coastal plain north of the Trans-Mexican Volcanic Belt was uplifted before the fish in the coastal plain differentiated into *variatus* and the remaining northern platyfish species. The overall close morphological similarity between *evelynae* and *variatus* suggests that the northern platyfish ancestor looked pretty much like these two species.

South of the Trans-Mexican Volcanic Belt there are two monophyletic groups of swordtails (*helleri* and *clernenciae*; Fig. 4) which are unrelated in spite of their overall gross morphological similarity. The taxonomic position of the three southern platyfish is poorly understood, but appear to be ancestral to the northern platyfish.

On geographical grounds a close relationship appears unlikely between *milleri* in the isolated Los Tuxtlas range along the coast and *andesi* on the slopes of the volcanic belt, two hundred kilometers to the northwest (Fig. 1). Both could have evolved independently from the coastal form. Phylogenies based upon mitochondrial DNA show the branch leading to *X. andesi* as the most basal one among the platyfish. Thus the vicariant event was the uplifting of a platyfish population as the Trans-Mexican Volcanic Belt arose, whereas the form that stayed in the coastal plain gave rise to all other platyfish. Like the northern swordtails the *clernenciae* group is endemic to a single river system and restricted to the headwater streams behind the front-range (Fig. 4). The region where *X. maculatus* and *X. helleri* on the one hand and *X. clernenciae* on the other meet appears to correspond to an old coast line. According to this view, the *clernenciae* group then represents the older taxon and *helleri* and *maculatus* are the new comers.

The widespread *X. helleri* group presents a problem. One species (*helleri*) extends over 1000 Km from the Trans-Mexican Volcanic Belt to Guatemala and possible Honduras and three or four taxa (*alvarezi*, *sigunum*, *maeqe*, PMH) each of rather limited distribution are found near the eastern limit of the group’s distribution (Fig. 1).

Two of these forms occur in the isolated rivers in the karst region of Guatemala and adjacent Chiapas, Mexico. Yet in the Río Coatzaocacos Basin, the *X. helleri* group is primarily distributed in the coastal plain, except in the very center of the Isthmus of Tehuantepec where the topography as far south as the continental divide is barely above 250 meters. The information concerning the uplands of the Río Papaloapan and Río Grijalva drainages (Mexico) is too sparse to determine the status of *X. helleri* in these regions. Near its western limit *X. helleri* is present on the southeast facing slope of the Volcanic Belt as high as 1500 m (near
Jalapa) and one small population made it across to the northwest flank of the Rio Nautla.2

The nuclear and mitochondrial DNA evidence is incomplete and provides conflicting interpretations as to how the members of the helleri group are related to each other. The nuclear DNA data show that the Lancetilla swordtail from Honduras (Rosen's "PMH") is most closely related to X. alvarezi. These two taxa cluster more closely with X. helleri from the Rio Coatzaocalcos and X. signum than with the northern X. helleri from Jalapa.4 The recently described forms, X. mayae and X. kallmani, were not tested. The phylogeny based on mitochondrial DNA identifies X. signum and X. mayae as one sister group and X. alvarezi and X. helleri (including the Lancetilla fish) as another.21 Swordtails from Jalapa were not included in this analysis.

Considering that the distributions of X. mayae and "PMH" are poorly known (Fig. 1), that in one of the analyses a possible confusion of Lancetilla fish with PMH or helleri (see above) exists and that in both studies key members of the group were not included, it is difficult to interpret these results. Rosen and Kallman9 were unable to decide whether signum evolved from a local helleri population in the lowlands after headwater isolation or whether it represents a remnant of an older fauna. The last idea cannot be rejected outright, because other endemic genera and species occur in the isolated karst basin of Guatemala31,41 and these have no close relatives in front of the Cordillera. A similar explanation could also apply to the evolution of X. kallmani in Lago de Catemaco (Fig. 1), were an helleri ancestor could have been uplifted and subsequently isolated. A secondary invasion by X. helleri is indicated, because this species is also present in the lake19 and in streams that drain outwards from the rim of the caldera (Fig. 2). The situation in Guatemala and Chiapas is similar to that in the Rio Pánuco and upper Rio Coatzaocalcos Basins where a multitude of taxa, members of a monophyletic group, have evolved in an extensive karst environment. However, in Guatemala and Chiapas a related form exist in the coastal plain which is absent in the other two regions. This might suggest that the helleri group has arrived in this region more recently.

ACKNOWLEDGMENT

The authors are indebted to Dr. Salvador Contreras-Balderas for introducing us to several of the northern platyfish populations and for pointing out the uncertainties that surround the type location of X. couchianus.

REFERENCES


Address reprint requests to: Klaus D. Kallman
Department of Vertebrate Zoology (Ichthyology)
American Museum of Natural History
Central Park West at 79th Street
New York, NY 10024

E-mail: xiphkallman@aol.com