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The Threespine Stickleback in Austria (*Gasterosteus aculeatus* L., Pisces: Gasterosteidae) - Morphological Variations

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Abstract

The threespine stickleback, *Gasterosteus aculeatus*, occurs regularly in Austria in the Rhine and Danube rivers. These populations are of allochthonous origin and trace back to introduction in the second half of the 19th century. Morphological differences between populations are most obvious in the occurrence of different plate morphs. The typical three morphs of *Gasterosteus aculeatus* - complete (trachura), partial (semiarmata) and low (leiura) - are reported for both large Austrian river systems, the Rhine (western Austria) and the Danube (eastern Austria). It is a significant morphological difference between threespine sticklebacks in these two river systems that only polymorphic populations had been found in the area of the Rhine, whereas in the region of the Danube polymorphic as well as monomorphic populations occur. We compare bony elements like the numbers of lateral plates and the elements of the defensive complex of low plated threespine sticklebacks from western Austrian polymorphic populations with those of a monomorphic low plated population from eastern Austria.

Key words. *Gasterosteus aculeatus*, body armour, plate morphs, River Rhine, River Danube, Austria.

Zusammenfassung

Gasterosteus aculeatus L., 1758 kommt in den österreichischen Abschnitten des Rheins und der Donau häufig vor. Diese Bestände des Dreistachligen Stichlings sind allochthonen Ursprungs und gehen auf Einschleppung in der zweiten Hälfte des 19. Jahrhunderts zurück. Morphologische Unterschiede einzelner Populationen zeigen sich am auffälligsten in den divergierenden Lateralplattenformen. Die für *G. aculeatus* typischen drei Plattenmorphen - vollständig (trachura), teilweise (semiarmata) und wenig (leiura) beschildet - sind für den Rhein (Westösterreich) und für die Donau (Ostösterreich) dokumentiert. Ein auffälliger Unterschied zwischen den Dreistachligen Stichlingen dieser Flüsse besteht darin, daß im Einzugsgebiet des Rheins bisher nur polymorphe, im Donauraum aber polymorphe und monomorphe Populationen nachgewiesen wurden. Wir vergleichen die Anzahl der Lateralplatten und die knöchernen Elemente des Defensivkomplexes wenig beschildeter Formen sowohl polymorpher Populationen Westösterreichs als auch monomorpher Populationen Ostösterreichs.

Introduction

Gasterosteus aculeatus L., 1758, the threespine stickleback, was introduced in Austria in the drainage systems of the Rhine and Danube rivers about 130 years ago, very likely by aquarists (AHNELT 1986 and authors summarized there; AHNELT & al. 1994). These allochthonous populations not only became established, but also spread along the course of both river systems. Today, *G. aculeatus* is regularly found in Austria along the Rhine and Danube rivers, as well as in Lake Constance (WAIDBACHER & al. 1991, BERG 1993, AHNELT & al. 1994).

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The threespine stickleback is known to develop different plate morphs, i.e. complete (trachura), partial (semiarmata) and low (leiura). The completely plated morph is generally accepted as the primitive form, from which the low plated morph has developed (WOOTTON 1984, BELL & FOSTER 1994). This complete form developed in the marine environment, from which anadromous populations and, subsequently, resident freshwater populations emerged. All three morphological forms occur in both marine and freshwater and may represent two ecological forms of the threespine stickleback, the anadromous and the resident freshwater form (for detailed information compare WOOTTON 1984, BAKKER & SEVENSTER 1988). Recent investigations support the view of ZIUGANOV (1983) that not only three plate morphs but also a fourth exist (BANBURA & BAKKER 1995): specimens may occur with plate numbers typical for the low plated form but with a keel on the caudal peduncle. To date, such phenotypes have only been reported from a few autochthonous populations. This fourth morph is separated from the partially plated and is designated as low plated with a keel (leiura with a keel) (ZIUGANOV 1983). Such a morph was not previously identified in an Austrian threespine stickleback population.

Autochthonous polymorphic populations are known to occur in Europe along the coasts of north-west and northern Central Europe; they are composed of all three plate morphs, although in different percentages (MÜNZIG 1962, 1964, GROSS 1977, 1978). Monomorphic populations of either complete or low morphs occur in marine (complete) or in freshwater (low) habitats (PAEPKE 1996 and authors summarized therein; for exceptions compare BANBURA 1994). It is therefore of interest that both polymorphic and monomorphic populations of threespine sticklebacks are documented in Austria (AHNELT 1986, AHNELT & al. 1994). Initial investigations by one of us (H.A.) revealed that the threespine sticklebacks from western Austria differ from those east and south of Vienna (eastern Austria) (1) in the number of lateral plates and (2) in the development and composition of the defensive complex.

Additional studies and a comparison of such polymorphic and monomorphic populations from western and eastern Austria were carried out in the framework of a thesis (POHL 1997). Of special interest is the development (number and dimension) of those external bony structures which serve as a functional unit against predation (HOOGLAND & al. 1956, GROSS 1977, REIMCHEN 1983, BAUMGARTNER 1992b).

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Material and methods

309 specimens of *Gasterosteus aculeatus* from five populations from natural waters in Austria have been investigated.

Rhine valley total 219 specimens: 46 spec. Harder Dorfbach, 200 m upstream before it enters Lake Constance, 23.IX.1993; 60 spec. Gillbach near Altach, 1.IX.1993 and 10.VII.

1995; 37 spec., Lustenauer Kanal near Lustenau, 11. and 23.VIII.1993; 76 spec. Rheintal Binnenkanal near Hohenems, 22.III. and 1.IX.1993. Collectors: E. & M. Amann, E. & O. Bösch and A. Lunardon.

Danube valley total 90 specimens: 23 spec., 25.VIII.1994 and 67 spec., 10.V.1995; Aiglbach near Fischamend. Collectors: H. Belanyecz , H. Keckeis, H. Ahnelt.

Material is deposited at the Natural History Museum of Vienna and the Institute of Zoology, University of Vienna.

To render the bony structures more visible, 192 specimens (133 with a standard length > 40 mm used for Figs. 2, 3) from two localities from western and one from eastern Austria were cleared and stained following the method of DINGERKUS & UHLER (1977). The terminology of the elements of the defensive complex follows REIMCHEN (1983). To characterize the three plate morphs of *G. aculeatus* and to distinguish its two basical ecological forms - anadromous and resident freshwater - we follow WOOTTON (1984).

Results

Plate morphs

All three typical plate morphs of *G. aculeatus* were found in both large Austrian drainage systems. These complete, partial and low morphs of threespine sticklebacks form populations that differ from each other, whether polymorphic or monomorphic. To date polymorphic and monomorphic assemblages have been documented only in the drainage system of the Danube in eastern Austria. In contrast, all populations of western Austria are polymorphic. These populations from the tributaries of the Rhine and Lake Constance consist of the three plate morphs, although not in the same percentage. In all investigated populations the complete morph dominates the two other morphs (AHNELT & al. 1994), by a ratio between 3:1 and 2:1. In contrast, the polymorphic populations, which at present are less well documented than those from western Austria, are apparently less dominated by the complete morph than those from western Austria (AHNELT 1986). All monomorphic populations from eastern Austria have been found in the vicinity of Vienna, in the Wiener Becken or close to the Danube. These threespine sticklebacks all belong to the low morph and may form groups with large numbers (AHNELT 1986, unpublished).

Body armour

All *G. aculeatus* specimens in Austria investigated to date have well developed dorsal and pelvic spines, whether they belong to the complete, partial or to the low morph. No distinct or complete reductions of these essential parts of the body armour as reported for populations from western North America (REIMCHEN 1994) or from Scotland (CAMPBELL 1985) have been observed. Nevertheless, the number of dorsal spines in *G. aculeatus* may vary between two and four in Austria, although three dorsal spines are clearly the standard (AHNELT & al. 1994). The pelvic girdle consists of a bilateral pair of plates, each with an anterior, posterior and an ascending process; these plates are always well developed.

These dorsal and ventral assemblages of bony structures - the first and the second dorsal spines with their basal plates and the pelvic girdle with the pelvic spines - form the median bony elements of the characteristic body armour of the *G. aculeatus*-complex. They are usually laterally buttressed by bony scutes forming together the so-called defensive complex (BAUMGARTNER 1992a, b), a functional unit that protects the abdomen against predation (GROSS 1977, 1978, REIMCHEN 1983, 1994).

Defensive complex

The defensive complex of *G. aculeatus* (Fig. 1) was extensively redescribed by REIMCHEN (1983), who showed how the different skeletal elements together function against gape-limited predators. Threespine sticklebacks in Austria have the same assemblage of bony structures as those described by REIMCHEN (1983) for the North American specimens, but their composition varies between the investigated populations.

This variation relates to the number of the bony elements forming the defensive complex and to some extent also their dimensions, i.e. the spine length (POHL 1997). As mentioned above, the median skeletal structures of this complex are present in their entirety and well developed in all investigated Austrian populations. Variation in number of these bony elements pertains to the lateral plates only.

Comparing the low plated specimens from the polymorphic populations of the Rhine with those of the monomorphic population from the Danube a distinct difference appears: while threespine sticklebacks in western Austria develop 5 - 8 lateral plates, the number varies from 1 to 6 in eastern Austria (Fig. 2a, b). The latter result means that some specimens from the Danube lack any plate either on the left or the right side.

The lateral plates become part of the defensive complex if they touch the ascending branches of the pelvic plates and/or the basal plates of the first and the second dorsal spines (Fig. 1a). They occur in a similar number in all polymorphic populations of western Austria. Five or six lateral plates are included into this complex in 95% of the sticklebacks from this area, typically LP4 to LP8, independent of whether a specimen belongs to the complete or to the low morph. In a few specimens the anteriorly positioned plate (LP3) or the posteriorly following one (LP9) may also be included. We distinguish between a central and a peripheral part of the defensive complex. The central part is characterized by dorsal and ventral elements (see above) and those lateral plates which buttress the basal plates of the first two dorsal spines and the ascending process of the pelvic girdle. In contrast, those lateral plates which are only in contact with the basal plates of these two dorsal spines are ascribed to the peripheral part (Fig. 1a). With few exceptions, three lateral plates (typically LP5 - LP7) belong to the central part of the defensive complex. This is valid for the low plated specimens and also holds true for 91% of all sticklebacks from the Rhine tributaries.

Even if the population we investigated from the Danube tributary can be called monomorphic with respect to the lateral plate development, the specimens differ highly as far as the defensive complex is concerned. Usually (48% of the specimens) 4 plates were included in the defensive complex, 3 plates were found in 21%, 2 in 12%, 1 in 5%. In 12% of the specimens the lateral plates were so reduced that they contact neither the dorsal nor the ventral elements of the defensive complex. These plates have not only lost their function to connect the median bony elements with each other, but this unit has also lost its stabilizing lateral elements and, with them, most of its efficiency. Nothing is left from the function against spine deflection. 98% of the sticklebacks from the

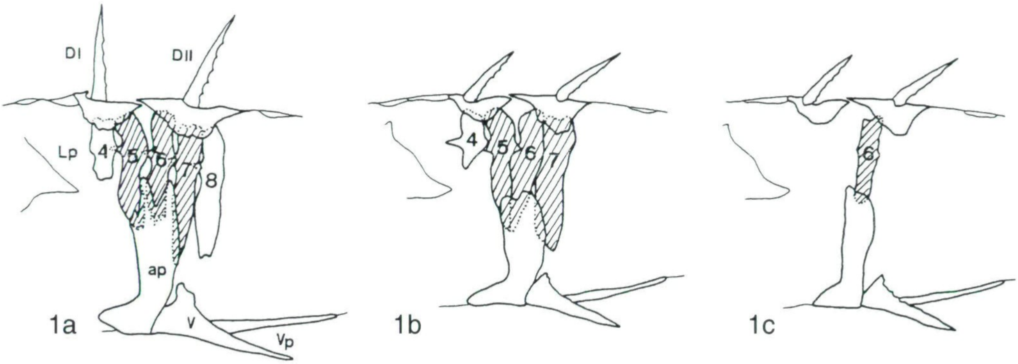


Fig. 1: *Gasterosteus aculeatus*, low plated morph; lateral view (left side) of the defensive complex; (**a**) a specimen from western Austria, (**b**, **c**) two specimens from eastern Austria; hatched - lateral plates of the central part of the defensive complex, those of the peripheral part are white; stippled - covered parts of lateral plates. ap - ascending process of the pelvic girdle; DI, DII - first and second dorsal spines; Lp - lateral plates; V - pelvic spine; Vp - posterior processus of the pelvic girdle.

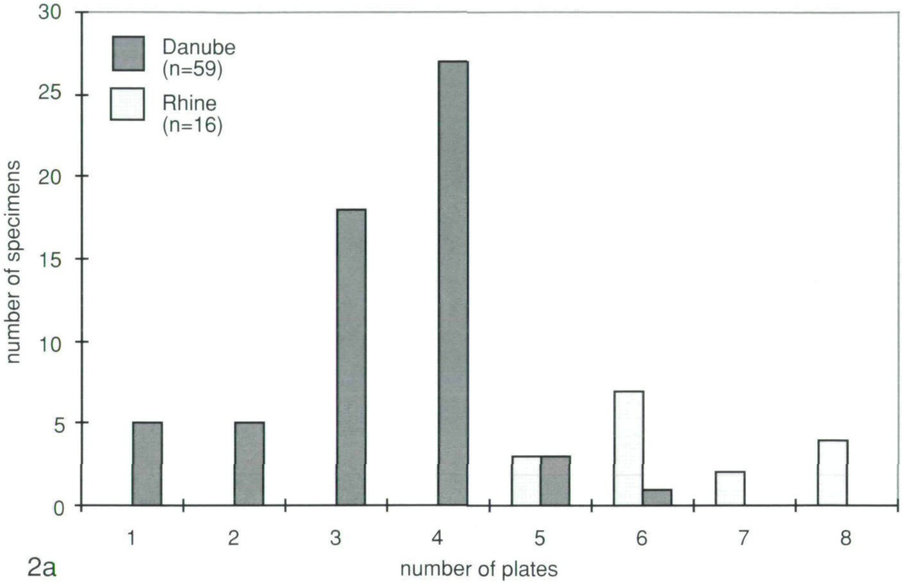
Danube tributary show less then 5 plates in the defensive complex. That means a significant difference to the populations from western Austria, where 75% of the specimens at least own five plates (Figs. 1a, 2b). Therefore populations from western and eastern Austria, respecitively, differ not only in number of lateral plates but also in the degree of development of the defensive complex, which is in general better developed in the specimens from the Rhine. Although the defensive complex is fully functional in 50% of the specimens from the Danube tributary, the remaining specimens have only two or less lateral plates. This relation was never observed in a western Austrian population.

Discussion

The characteristic external bony armour does not protect the threespine stickleback against spatial and trophic competition by other fish species. Even the best developed defensive complex with the longest and strongest spines is not the primary source in predator-avoiding behaviour of this fish (HUNTINGFORD & al. 1994).

Nevertheless, several studies (GROSS 1977, 1978, REIMCHEN 1983, 1994, BAUMGARTNER 1992a, b) have demonstrated that these bony elements usually form a well developed functional unit in all those populations affected by predatory pressure and are reduced, absent or less effectively arranged in environments lacking predators. The elements forming the defensive complex are thus a functional anti-predator unit.

All external bony structures of *G. aculeatus*, i.e. on the head, body or even on the caudal peduncle may protect against serious injury by a predator. This, however, is not the main function of the long series of lateral plates along the body and caudal peduncle in the complete morph. With exceptions, these complete forms are typical for marine and anadromous populations. The lateral plates, which are expanded to a keel on the caudal peduncle, are hydrodynamically advantageous for this small fish, especially when it migrates upstream to its spawning grounds (TAYLOR & MCPHAIL 1985, BAUMGARTNER



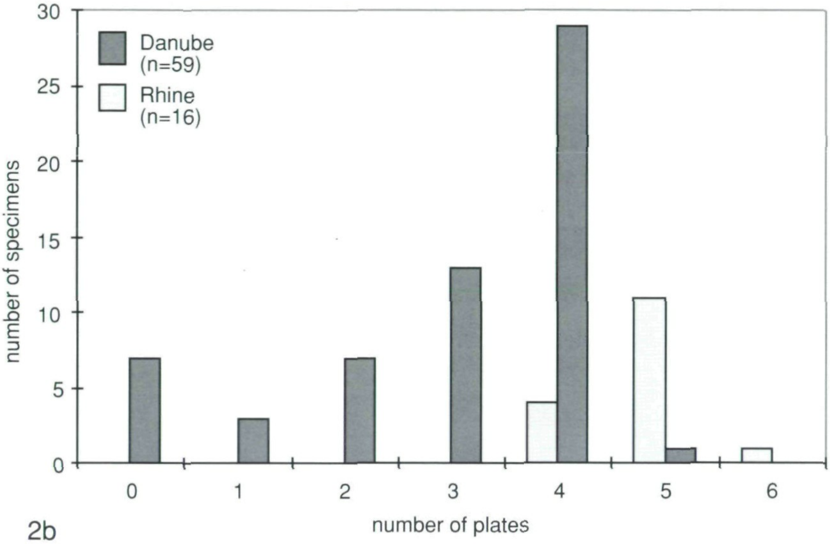
2a

Fig. 2: *Gasterosteus aculeatus*, low plated morph. (a) Total number of lateral plates, (b, see following page) number of lateral plates of the defensive complex in populations of eastern Austria (Danube) and western Austria (Rhine).

1992b). Conversely, the number of lateral plates is distinctly reduced in resident freshwater populations (less than nine plates instead of more than thirty in the complete morph). This condition enables a better burst swimming ability in the low morphs (TAYLOR & MCPHAIL 1986) and better maneuverability in the dense vegetation typical for most freshwater environments in which *G. aculeatus* occurs.

The threespine stickleback is allochthonous in both large Austrian drainage systems, the Danube and Rhine rivers. It was introduced in the second half of the 19th century (AHNELT 1986 and authors summarized therein; AHNELT & al. 1994), and genetic shift is apparently an important factor in the composition of the western and eastern Austrian populations. Polymorphic populations consisting of all three lateral plate morphs seem to trace back to repeated introduction from different populations, possibly anadromous and resident freshwater populations as well (AHNELT & al. 1995). On the other hand, resident populations between the Elbe and the Oder-Neisse rivers are sometimes polymorphic for all three morphs, some of them with a majority of completely plated sticklebacks (PAEPKE 1982, 1996). Potential introductions from such polymorphic freshwater populations cannot be neglected.

While the term polymorphic is widely used for *G. aculeatus* populations composed of several lateral plate morphs like those in western Austria, this does not hold true for the defensive complex in specimens of this region. The number of bony elements forming this functional unit is the same in all morphs (Fig. 3). Differences are minor, individual and independent of morph. The polymorphic character (concerning the external bony elements) of the western Austrian stickleback populations is therefore typified by the occurrence of different lateral plate-morphs only.



2b

In contrast, the population we investigated from the Danube tributary is a monomorphic low plated population. Even if the variability in number of bony elements forming the defensive complex is high, relatively lower number of fewer lateral plates causes reduced effectiveness. This functional unit is lost in a series of specimens with drastically reduced lateral plate number and size, a situation not observed in any western Austrian individual.

What is the explanation for these differences in the occurrence of plate morphs and in the development of the defensive complex between western and eastern Austrian populations? A genetic basis has been demonstrated for the plate morphs of several populations (HAGEN 1973, HAGEN & GILBERTSON 1973, ZIUGANOV 1983, BANBURA & BAKKER 1995). Genetic shift caused by introductions from different populations is therefore the most likely driving force behind the lateral plate morph composition of Austrian stickleback populations. The origin of Austrian sticklebacks remains unknown. Regular occurrence of polymorphic populations along the Rhine and Danube make it very unlikely that they trace back to stocks from South Europe, which are all monomorphic for lows (WOOTTON 1984). An origin in Europe east and south-east of the Vistula river system (Poland) is also unlikely because populations there are nearly 100% monomorphic for completes. On the other hand the resident populations between the Elbe and the Oder-Neisse are sometimes trimorphic. We therefore assume an introduction from such northern Central European populations, most probably from Germany and western Poland. We cannot exclude an introduction of anadromous sticklebacks, but to our knowledge no documentation exists on the fate of their offspring when migration is hindered (i.e. in captivity). Do they transform their behavior from migrating to non-migrating and do they subsequently form resident populations when released in new environments where migration is possible? Another possibility, reported in Europe for Norwegian and Russian populations, is that marine monomorphic completely plated populations transform in freshwater habitats within a few generations into trimorphic populations (ZIUGANOV 1983, 1995, KLEPAKER 1993, 1995).

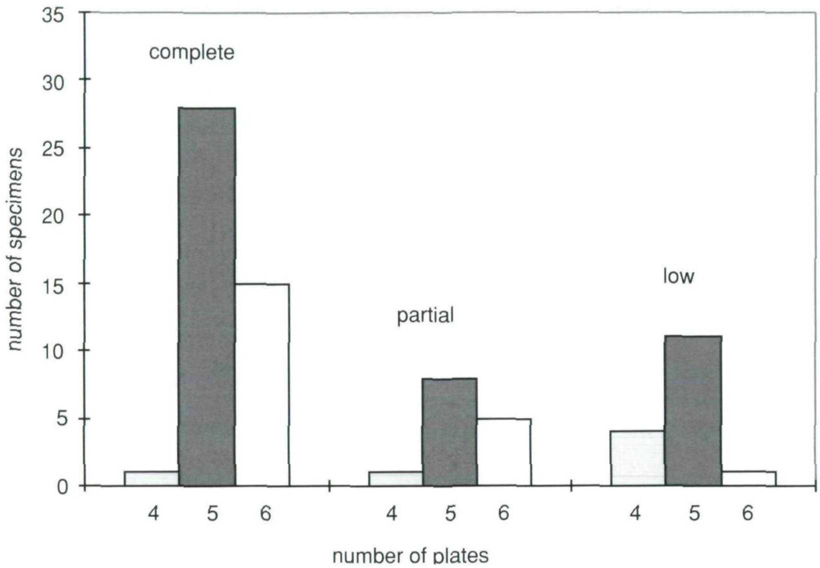


Fig. 3: *Gasterosteus aculeatus*. Total number of lateral plates included into the defensive complex in specimens from western Austria.

Differences in the defensive complex between polymorphic and monomorphic populations or even between low plated specimens from western or eastern Austria are probably not genetic. Comparing reductions of body armour in threespine sticklebacks, BELL & al. (1993) concluded that effects of ancestry and gene flow are very likely insignificant compared to the effects of natural selection. BAUMGARTNER's (1992b) results also suggest that there are few genetic or developmental constraints linking the evolution of the defensive complex to lateral plate morphs. On the contrary, predation is the natural selection mechanism for elements of this complex.

Whether morphological characters such as lateral plate morphs or characteristic defensive complexes are stable within the investigated Austrian populations is unknown. Initial investigations on these typical bony structures were started by one of us (H.A.) in 1993 for specimens from western Austria and in 1994 from eastern Austria (present material). No comparable data are available from periods prior to these investigations.

Changing predator abundance in the environment should lead to changes in the body armour of affected threespine sticklebacks, as demonstrated for many populations (REIMCHEN 1983, 1994, CAMPBELL 1985, BELL & al. 1993, MCPHAIL 1994). On the other hand, the development of this complex is not necessarily linked to lateral plate morphs (BAUMGARTNER 1992b). This also holds true for the low plated sticklebacks we investigated in western and eastern Austria. While the defensive complex is very effectively developed in the former, no stickleback in the Danube tributary reaches such an efficiency. On the contrary, many of these specimens have a distinctly reduced defensive complex, either in the number or size of elements. (An analysis of morphometric and meristic characters will be published elsewhere.) Thus the difference between the well- and the poorly developed defensive complex of the investigated threespine sticklebacks is a distinct indication of a different predatory pressure. While in many Austrian tributaries of the Rhine and in Lake Constanze well-known stickleback-predators (HOOGLAND & al. 1956; GROSS 1977) like pike (*Esox lucius* L., 1758) and perch (*Perca fluviatilis* L., 1758) are common (E. Amann pers. inform.), these species are absent in the environment of the eastern Austrian stickleback population.

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