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Plate Morphs of *Gasterosteus aculeatus* Linnaeus (Pisces: Gasterosteidae): Comments on Terminology

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On the basis of the number and arrangement of the lateral plates of the threespine stickleback *Gasterosteus aculeatus*, three morphs are commonly distinguished: *leiurus* (low plated), *semiarmatus* (partially plated), and *trachurus* (completely plated). However, these terms came to be used not only in a morphological sense, but in an ecological and evolutionary sense as well. This causes considerable confusion in the literature concerning plate morphs of *G. aculeatus*. This paper gives a history of the confusion that has enveloped the terms *leiurus*, *semiarmatus*, and *trachurus*, and proposals to resolve this terminological confusion.

IN the stickleback genus *Gasterosteus* (family Gasterosteidae) the typical teleost scales have evolved to form a distinct row of bony plates along each flank of the body. In the threespine stickleback (*Gasterosteus aculeatus* L.), three major morphological forms or morphs are distinguished on the basis of the number and arrangement of the lateral plates. In the 19th

century these plate morphs of *G. aculeatus* were considered distinct species. Bertin (1925) reassembled these taxa in the original species described by Linnaeus and distinguished a number of forms within this species, based on the number and arrangement of lateral plates: form "*trachura*" (completely plated: a series of plates running the entire length of the body, of which the most caudal ones form a keel that projects laterally); form "*semiarmata*" (partially plated: an anterior row of plates, an unplated region, and a caudal row of plates which form a keel); form "*gymnura*" (low plated: only an anterior row of plates), and form "*hologymnura*" (plateless). The names of these morphs were derived from the species names that had been given to them by Cuvier (1829). To avoid confusion with the former species names, Bertin used the feminine ending "a." This emphasized that the names refer to the forms only, not to the generic name *Gasterosteus* (masculine), with which their gender should agree if the forms were species or subspecies (Article 31b of the International Code of Zoological Nomenclature). Heuts (1947a) used "forma" instead of "form," which is more common and indicates even more clearly that it has nothing to do with races or subspecies. Forma or morph denotes a special variant of a species, and various formae may occur within one population.

The term "forma *hologymnura*" has fallen out of use. The distribution of the rather rare plateless threespine sticklebacks is restricted. So far, they have been reported in isolated, freshwater populations from the southwest portions of North America and Europe (Bell, 1984; Wootton, 1984), from the Queen Charlotte Islands, Canada (Moodie and Reimchen, 1976), and from the Outer Hebrides, Scotland (Campbell, 1979, 1985). The zero plated fish are extreme variants of the forma *leiura*. Confusingly enough, the forma which is now called *leiura* was referred to by Bertin as *gymnura*.

The large majority of *G. aculeatus* belongs to the other three plate morphs. Apart from an occasional author (Heuts, 1947a), Bertin's proposal to use the feminine ending "a" in referring to the plate morphs has not been followed. Most authors use the terms *trachurus, semiarmatus,* and *leiurus,* either as a substantive or accompanied by the term form or morph, when referring to the plate morphs. But, unfortunately, the terms *trachurus* and *leiurus* are also frequently applied in an ecological sense (see below). This dual usage causes considerable confusion in the literature concerning plate morphs of *G. aculeatus.*

On ecological grounds one can distinguish two kinds of populations of *G. aculeatus*: some are resident in freshwater throughout the year, whereas others are anadromous, migrating to the sea in autumn and then migrating back into rivers, salt marshes, or tidal pools in the spring to breed. Münzing (1959) introduced the term "stationäre Süsswasserform" (landlocked freshwater form) for fish that belong to the former populations, and "Wanderform" (anadromous form) for fish of the latter populations. Other names that are frequently used are "landlocked" or "freshwater" form and "marine" form. In view of Bertin's term form, Münzing's choice of the term "form" for the two lifestyles of *G. aculeatus* does not seem to have been very fortunate, but perhaps unavoidable. The term form indicates a group of conspecifics having something in common (ecologically, morphologically, physiologically, or whatever), which distinguishes them from the rest of the species. This is of such general usage in zoology, that it is quite acceptable to use the term form for the two alternative lifestyles of *G. aculeatus.* We will use the term form in this connotation from now on. To avoid confusion, we will reserve the terms morph and forma for the morphological forms of *G. aculeatus.*

Populations consisting of one or the other form have been given a wide variety of names. Besides the ones for the ecological forms mentioned above, one may encounter terms such as "permanent freshwater," "resident freshwater," "inland," or "resident" populations; and "marine anadromous," "anadromous migrating," "coastal," or "migrating" populations. Sometimes populations which complete their life cycle in marine water, although they migrate to shallow marine water to breed, are distinguished from the anadromous populations, and are called "marine" populations (Bell, 1984).

Fortunately, most of these terms are sufficiently unequivocal and thus their use can hardly cause any confusion. But, this is certainly not the case for the use of the terms *trachurus* and *leiurus,* at worst followed by the term form, to describe the anadromous and landlocked form, respectively. This misuse of the terms *trachurus* and *leiurus* was the consequence of incorrectly adopting the terms that Münzing (1959, 1962a, 1963) used to characterize the European populations of *G. aculeatus* with respect to both the plate morphs and the ecological forms. The Eu-

ropean landlocked populations of *G. aculeatus* with which Münzing was dealing were monomorphic for the *leiurus* morph and hence he called them *leiurus* populations. In the European anadromous populations, he distinguished between *trachurus* populations (monomorphic for the *trachurus* morph) and mixed populations (polymorphic with all three morphs, i.e., *leiurus, semiarmatus,* and *trachurus,* present in various proportions).

Anadromous populations on the west and east coast of North America are often monomorphic for the *trachurus* morph (Bell, 1984; Wootton, 1984), and these monomorphic populations were correctly named *trachurus* populations. After Münzing, the North American landlocked populations were called *leiurus.* Unfortunately, Münzing's terminology was not followed properly. First, Münzing (1959) made a clear distinction between (ecological) form, population (consisting of fish of a particular form), and (lateral plate) morph (which he actually called type or phenotype). He referred to populations with either the names of the forms or the names of the morphs. However, he never referred to the forms with the names of the morphs, as Hagen (1967) proposed: "Following Münzing and others the marine form is referred to as *trachurus,* and the freshwater form is called *leiurus.*" Unfortunately, with Hagen's terminology one must always decide whether reference is being made to the ecological form or the morphological form. Secondly, with respect to plate morphs, Münzing distinguished three kinds of populations. In the first place, their names (*leiurus,* mixed, and *trachurus*) were indicative for the make-up of the populations with respect to plate morphs; and in the second place, also for the ecological form. Hagen confused things when he proposed the use of the names *leiurus* and *trachurus* morph for the two ecological forms, thus to call all populations of the anadromous form *trachurus* and the landlocked form *leiurus.* Hagen (1967) went even further by suggesting that *leiurus* and *trachurus* represent species that hybridize only locally. In a general way, this claim is questionable, and the new terminological problems it introduces are not relevant to the present discussion.

Even with Hagen's terminology nothing would have gone wrong, if most North American landlocked populations consisted only of the *leiurus* morph and most anadromous populations of the *trachurus* morph. For most North American anadromous populations, this happened to be true, although exceptions have been found (Hagen and Moodie, 1982; Bell, 1984). However, the generalizations made on the terminology of the two ecological forms of *G. aculeatus* appeared untenable on account of the existence of numerous landlocked populations which are not monomorphic for the *leiurus* morph (Miller and Hubbs, 1969; Hagen and Gilbertson, 1972; Hagen and Moodie, 1982; Baumgartner and Bell, 1984).

Instead of abandoning the misuse of the terms *leiurus* and *trachurus* for landlocked and anadromous populations respectively, Hagen and Gilbertson (1972) introduced new terms for the three plate morphs in landlocked populations of *G. aculeatus*: low plated, partially plated, and completely plated morphs; or in short, lows, partials, and completes. Recently, Hagen and Moodie (1982) proposed to generalize the use of the terms low plated, partially plated, and completely plated morph for the plate morphs in both landlocked and anadromous populations, and to generalize the misuse of the terms *leiurus* and *trachurus* for landlocked and anadromous populations, respectively.

In further contrast to European authors, American and Canadian authors have avoided the use of the term *semiarmatus.* This term did not fit in with their vocabulary, because the terms *leiurus* and *trachurus* had already been given to the two known ecological forms. However, Hagen and Moodie (1982) advanced another, and in our opinion an incorrect, argument for the disuse of the term *semiarmatus*: "*Semiarmatus* is a name that has been applied historically to partially plated hybrids between *leiurus* and *trachurus.* But as we have seen, the partial morph often occurs where hybridization is not involved. To call these '*semiarmatus*' is historically incorrect and misleading. If the term is to be used it should refer to known hybrids." We would rather call their statement historically incorrect and misleading, because the term *semiarmatus* had been introduced by Bertin (1925) for the partially plated morph (form *semiarmata*) on purely morphological grounds. At Bertin's time nothing was known about the genetics of plate morphs. In fact, he interpreted the morphs as environmentally induced modifications.

After preliminary investigations of Heuts (1947b), the genetics of plate morphs in *G. aculeatus* was studied in detail by Münzing (1959). He defined the *semiarmatus* morph as the hybrid between the *leiurus* and *trachurus* morph. But with Münzing's genetic characterization of *semi-*

armatus, the history of *semiarmatus* did not start, as suggested by Hagen and Moodie (1982). Admittedly, Münzing's generalization had apparently been premature due to the presence of the *semiarmatus* morph in populations in which one or both parental morphs (viz., *leiurus* and *trachurus*) are absent. In studying a population that was monomorphic for the *semiarmatus* morph, Münzing himself was faced with this contradiction. He concluded that the *semiarmatus* morph in that population had to be genetically different from the one in a trimorphic population (Münzing, 1962b). Ziuganov (1983) recently shed new light on this issue by claiming that the number of lateral plates (exclusive of the ones forming the keel) and the presence or absence of a caudal keel are two genetically different, independent characters. This means that those fish which are classified as *semiarmatus* by the presence of a keel, but which also possess as few anterior plates as the *leiurus* morph, are, genetically speaking, "*leiurus* with a keel." This might explain the absence of segregation in monomorphic populations for the *semiarmatus* morph. These facts should not, however, cause one to avoid use of the term *semiarmatus* (as suggested by Hagen and Moodie, 1982), but rather to readopt its original (morphological) meaning.

How might this terminological confusion be resolved? We propose the following: 1) the use of the terms *leiurus* and *trachurus* to indicate the two alternative lifestyles of *G. aculeatus*, should be abolished altogether. The two lifestyles, at least so far as is known at present, are population characteristics, and it is therefore more appropriate to speak of two kinds of populations, each with a different life history mode and not necessarily correlated with a morphological condition. 2) As suggested by Bell (1984) and Wootton (1984), these two kinds of populations with a different life history mode should be called anadromous and freshwater populations. It will be evident that reference to such populations on purely morphological grounds (i.e., as *trachurus* and *leiurus*, respectively) is fundamentally wrong and has been the major source for the terminological confusion with respect to the lateral plate morphs in *G. aculeatus*. Therefore, in no case should the names of the plate morphs be used for these two kinds of populations. 3) Concerning the nomenclature of the lateral plate morphs, Bell (1984) and Wootton (1984) proposed to abolish all terms that have been used in the past in more than one sense, and use the terms low, partial, and complete to describe the three plate morphs (following Hagen and Gilbertson, 1972; Hagen and Moodie, 1982). However, some authors still use the old terms *leiurus*, *semiarmatus*, and *trachurus* when referring to the plate morphs (Paepke, 1982, 1983). Further, it also seems important to preserve the continuity with the old literature concerning plate morphs of *G. aculeatus*. It seems therefore necessary also to reinstate Bertin's (1925) terms "*leiura*," "*semiarmata*," and "*trachura*" for the three major lateral plate morphs of *G. aculeatus*. Originally these terms were defined on morphological characteristics and ever since no additional meanings have been attached to them. In any case, the derived terms *leiurus*, *semiarmatus*, and *trachurus* should be abolished altogether.

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