COMMENTS ON THE TAXONOMY OF THE THREE-SPINED STICKLEBACK, *GASTEROSTEUS ACULEATUS* LINNAEUS[1]

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ABSTRACT

On the basis of 5491 specimens from 61 habitats in all parts of Poland, the author infers that the present accepted division of the three-spined stickleback into *trachura*, homozygote living in salt waters and coastal waters, and *leiura*, homozygote living in fresh continental waters, with *semiarmata* separated off as the hybrid of both adaptive types living in the borderline between both homozygotes, has not found confirmation in the analysed material. Members of trachura in Poland have their habitats in the whole area of this species. The semiarmata and leiura types appear in small numbers either together with, or independently of, the members of trachura, and are confined to the coastal waters of the Baltic Sea east of the mouth of the Vistula, and to the Odra and Vistula rivers not farther south than 51 degrees north latitude.

Despite many published works dealing with the taxonomy of the three-spined stickleback, *Gasterosteus aculeatus*, the problem of geographic variation in this species has not yet been solved. Investigations into the taxonomy of the three-spined stickleback are still far from being satisfactory and the suggestions of many modern zoologists concerning the biology and the taxonomy of this species are at once revealing and contradictory. Discussion concerning the taxonomy of this stickleback, which began nearly 200 years ago, has maintained a continuing interest among naturalists.

Bloch (1801) was the first to report on differences in the lateral armorature of this species, and he presented illustrations of the more conspicuous specimens. In Germany, he found stickleback that did not always meet the definition of this species presented by Linnaeus (1758): "Gasterosteus aculeatus spinis dorsalibus tribus . . . corpus ad caudam utrinque carinatum . . . ."

In 1817, Cuvier divided the three-spined stickleback into two species, and in 1829 the same author, in collaboration with Valenciennes, selected a few more, which at the beginning of the present century were already represented by over 40 synonymous names relating to *Gasterosteus aculeatus*.

Admittedly, already before 1925 some authors assumed a more or less critical attitude toward the pluralistic school, but a turning point in the taxonomy of the species was the publication of Bertin's monograph in 1925. His one-species theory of the three-spined stickleback in the Palearctic Realm was a long stride forward, but his division of this species into forms and his assumption that the number of plates increases wedgewise in proportion to the salinity of the water were destined to be short lived.

The results of Tagliani's investigations (1926) were published a year after Bertin's. He assumed a most extreme and a most ill-advised attitude in this matter. He insisted on there being only one species of the three-spined stickleback in the whole Holarctic, without subspecies, races, or forms, and the apparent differences in armouring he called anomalies, as he considered the number of plates to be independent of sex, temperature, latitude, or the amount of salt in water.

Hubbs' attempt (1929) at assigning the American stickleback to a distinct genus, *Gladiunculus*, was undoubtedly too daring, whereas Putnam's decision, in 1866–1867, to describe it as *Gasterosteus wheatlandi* Putnam is questioned by no one (Berg, 1949; Bigelow and Schroeder, 1953; Jordan and Everman, 1927; McAllister, 1960a, 1960b, 1960c; Münzing 1959; Penczak 1962b; and others).

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Also, Leiner's suggestion (1934) to include the nine-spined stickleback, *Pungitius pungitius* (Linnaeus), in the genus *Gasterosteus* Linnaeus was not one that could be accepted. The serological investigations on both species (Penczak, 1961a) have been a further justification of the decision of modern taxonomists who classified the three- and nine-spined sticklebacks in two different genera.

Although the specific unity of the three-spined stickleback, as it was described by Linnaeus, is today unchallengeble, mutability in this species is so apparent that it allows for describing certain populations of limited range as separate subspecies (Berg, 1949: *G. aculeatus algerensis* Sauvage—the Palearctic Realm; *G. aculeatus williamsoni* Girard—the Nearctic Realm; Miller, 1960: *G. aculeatus williamsoni*

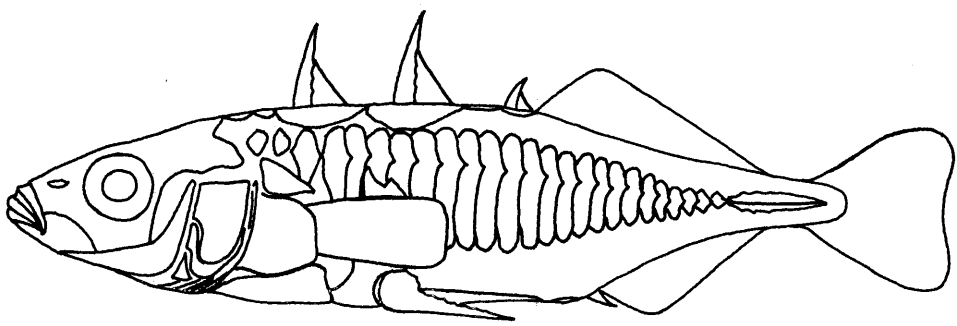

FIGURE 1. The trachura homozygote of *Gasterosteus aculeatus* L.

Girard—the Nearctic Realm; Penczak, 1964a: *G. aculeatus islandicus* Sauvage—the Palearctic Realm).

Under the influence of Heuts (1947a, 1947b), many zoologists became persuaded that the problem of mutability in this species had finally been solved. Heuts found that the stickleback from northwestern Europe included two clear-cut adaptive types. The armouring of one of the types could be identified with that of trachura, and the one of the other type was characteristic of leiura (fig. 1 and 2).

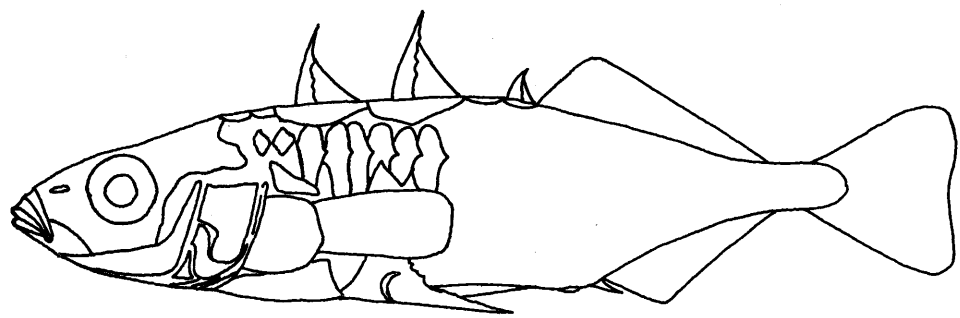

FIGURE 2. The leiura homozygote of *Gasterosteus aculeatus* L.

He indicated that the first type inhabits salt waters and the coastal waters of the North Sea, while the other type is confined to fresh continental waters and isolated coastal lakes. Moreover, on the borderline between the two homozygotes, there are heterozygous sticklebacks, which are partially armoured and have a caudal keel (semiarmata—fig. 3). These observations were further corroborated by the same author in his genetic studies (Heuts, 1947b), by the investigations of Münzing relating to the territory of Germany (Münzing, 1959), and by taxonomic investigations in other areas (Bigelow and Schroeder, 1953; Greenbank and Nelson, 1959).

Münzing (1959), who explored the estuary of the Elbe and its surroundings, found a regular Mendelian ratio of the two homozygotes and their hybrids, which may be observed when cross-breeding homozygotes with the dominant and recessive types. In relation to that, he suggested a new division of this species into two groups: the "Wanderform," whose mixed populations consist of: 55 per cent trachura, 40 per cent semiarmata, and 5 per cent leiura, and who inhabit the lowest part of the Elbe and its immediate branches; and the "Stationäre" group, whose populations consist exclusively of leiura, and who are limited to fresh waters and cannot mix with members of the other group. A similar distribution of stickleback and a similar percentage of populational forms in the "Wanderform" group were found by this author in the coastal waters off Holland (Münzing, 1962a).

The fact that no such regularities are found in the area of the Baltic Sea, and particularly in its eastern parts, was explained by Münzing (1961) as due to the prolonged glaciation of this area, which, after the ice-sheet had finally receded, was exclusively populated by armoured sticklebacks either from the North Sea or from the White Sea. According to Münzing, the first members of leiura migrated to the coastal waters of northwestern Europe in the post-glacial period (ca. 3000 B.C.), e.i., when the British Islands had already separated from the Continent and the temperature of the water reached its maximum. The semiarmata stickleback appeared here as the result of the subsequent hybridization of trachura and leiura.

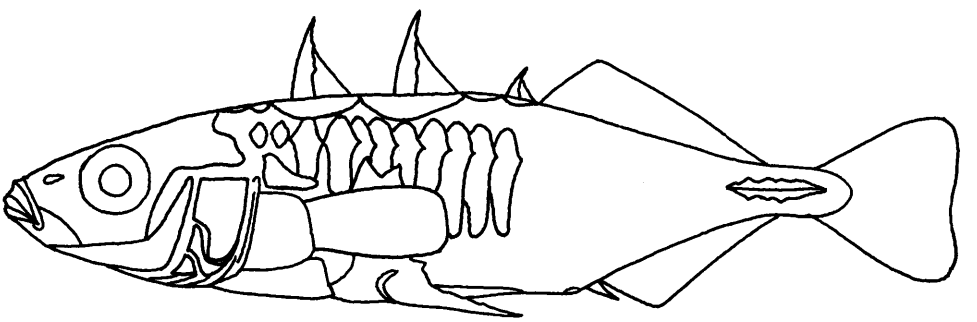

FIGURE 3. The semiarmata heterozygote of *Gasterosteus aculeatus* L.

Before discussing the observed mutability in, and the distribution of, this species in Poland, reference must be made to Lindsey's work (1962). This author has reported that an apparent correlation exists between the parents and their progeny in respect to the number of the lateral plates, which may account for the different numbers of plates exhibited by hybrids of both homozygotes. He has also found a proportional interrelationship between the phenotypic number of plates and the low temperature of water.

In recent work, I have retained the term trachura for the armoured type, the term leiura for the poorly armoured type, and the term semiarmata for the hybrids of both types (Penczak, 1965).

The terms trachura, leiura, and semiarmata have been employed only as temporary conventional symbols, having nothing to do with zoological nomenclature, because the definitions of the interspecific taxons so far used, namely "forme" (Bertin, 1925), "morpha" (Berg, 1949), and "race" (Heuts, 1956), are irrelevant to the cases of mutability in question, and moreover, they are not recognized in the International Code of Zoological Nomenclature published in 1961 and edited by XV International Congress of Zoology.

Similar difficulties were encountered in the case of sticklebacks with different numbers of spines. Two-, four-, and five-spined sticklebacks might be ascribed

to separate genera, species, subspecies, races, morphs, or forms. The question whether to reject those taxons of sticklebacks with more than three spines has been finally decided by the works of Lindsey (1962) and Penczak (1963a). Lindsey obtained two-, three-, and four-spined sticklebacks from the spawn of three-spined parents, and Penczak invariably obtained three-spined progeny by cross-breeding specimens with a greater number of spines.

The changing views in the zoological nomenclature on the taxonomy of this species and the interpretation of the observed cases of mutability indicate that the investigators still have scarce and fragmentary evidence. Hence, greater attention should be concentrated on investigating the morphological differentiation of the species in new areas, and the choice of new taxa should be a secondary consideration.

Although the division into trachura and leiura, with seminarmata separated off as the hybrids of both adaptative types, seems to be the most logical, one may assess even today that it is not a final solution, for it does not cover the whole of the species as it was defined by Linnaeus. New facts from new areas indicate that the commonly accepted genetic basis upon which to set apart the two adaptative types and to define their requirements of habitat (". . . one type occupies fresh water habitats and the other type salt water habitats." Heuts, 1947b) is not wholly correct in relation to the newly investigated areas. Of particular interest has been the discovery of homogenous populations of the semiarmata type in Romania (Bascescu and Mayer, 1956) and in Turkey (Münzing, 1962b) (Only

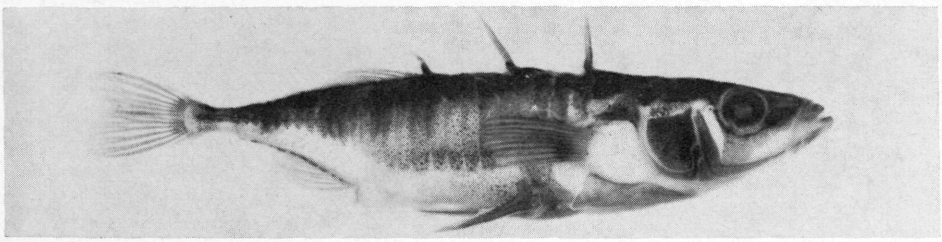

FIGURE 4. The trachura type of *Gasterosteus aculeatus* L. from the Ner River (near Łódz), the east tributary stream of the Warta River belonging to the Odra River basin, Poland.

two specimens of semiarmata were caught in Poland in 1927, in the vicinity of Toruń in a dystrophic marsh—Penczak 1963b). Such populations, according to Heuts (1947a, 1947b) and Münzing (1959), should be hybrids of the armoured and the slightly armoured homozygotes, and which should never appear separately, as upon a further cross-breeding they would also produce homozygous specimens.

Equally interesting and unlike the situation in western Europe is the distribution of the differently armoured sticklebacks in Poland.

The characteristics of the morphological differentiation of this species in Poland have been determined by a study of 5491 specimens from 61 habitats in all parts of Poland (Münzing, 1961; Penczak, 1960a, 1962a, 1962c, 1963b; Piesik, 1937).

Members of trachura (fig. 4) in Poland have their habitats in the whole area of this species. Each test contained, if not all, at least 90 per cent of trachura.

The semiarmata and leiura types, except the two above-mentioned specimens of semiarmata caught at Kluczyki near Toruń, appear in small numbers either together with, or independently of, the members of trachura. The habitats of the incompletely armoured sticklebacks (leiura and semiarmata) are confined to the coastal waters of the Baltic Sea east of the mouth of the Vistula, and to the

Odra and Vistula rivers not farther south than 51° North Latitude. One specimen of semiarmata together with specimens of Trachura was caught west of the Vistula, in Swiecajty Lake, a branch of the Mamry Lake, in the watershed of Pregola river.

In relation to Münzing's post-glacial interpretation of the exclusive habitation of trachura in the region of the Baltic Sea, I would also like to add some more facts. In my opinion, Münzing's suggestion as to the route by which the species came from the White Sea or the North Sea to the southeast Baltic countries was not the only way. Moreover, in the east branches of the Vistula as well as in the Russian part of the Black Sea watershed, the species appeared later than stated by Münzing (1961). It seems to me that mixed populations of this species penetrated into this country also from Germany, along both the coasts and the continental waters. Here, it was the sticklebacks with dominant features ("The trachura gene (TT) proved to be largely dominant over the leiura gene (tt) . . ."—Münzing, 1963) that took the lead in the populating of the new areas and, by the end of the 19th and beginning of the 20th century, they had inhabited all the eastern parts of Poland and the areas of Byelorussia and the Ukraine, in consonance with the physiographic investigations of these areas (Beling, 1914; Grochmalicki, 1920; Berg, 1949; Grote, Vogt, and Hofer, 1909; Heckel and Kner, 1858; Kessler, 1877; and Schmiedeknecht, 1906). The incompletely armoured type appeared in those areas later, at first in small numbers and in association with the armoured variety. The above suggestions are supported by the following facts:

(1) Piesik (1937), who examined 304 three-spined sticklebacks from the Fishing Farm "Wilczak" near Bydgoszcz, found no specimens with an incomplete armouring. About 30 years later, when examining 238 three-spined sticklebacks from the same locality, I found that about 10 per cent were leiura and semiarmata (Penczak, 1960a).

(2) No specimens of leiura and semiarmata could be found in the east branches of the Vistula, in the Dnepre, or the Dnestre rivers.

(3) The first reports on the appearance of trachura in the watersheds of the Prypec, Dnepre, and Dnestre rivers date from the first half of the present century (Beling, 1914; Berg, 1949; Grochmalicki, 1920; and Grote, Vogt, and Hofer, 1909).

In relation to the supposed influence of the salt content of the water on the morphological differentiation of the three-spined stickleback, I have observed differences between the specimens inhabiting fresh waters in Poland and those from the coastal waters of the Baltic Sea in the structure of the pelvis and in body proportions. Short and underdeveloped wings of the pelvis have been found only in specimens from the Baltic Sea and the White Seas, and from a salt-water habitat near Bergen, Norway (Penczak, 1960b). In addition, the caudal peduncle of the specimens from the Baltic Sea is a little shortened.

In addition, it should be pointed out that small gaps in the armouring of the body amounting to a few plates are not due, as was formerly thought, to mechanical injury; in regeneration investigations, Penczak (1961b) showed that amputated plates regenerate quickly. Heuts (1947b), Münzing (1959), and Lindsey (1962) have suggested that the number of missing plates in a given type is dependent on hereditary factors, particulary on the number of plates of the mother.

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