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A new model of lateral plate morph inheritance in the threespine stickleback, *Gasterosteus aculeatus*

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Abstract The threespine stickleback, *Gasterosteus aculeatus*, is polymorphic for the arrangement of lateral bony plates. It is confirmed in this paper that four morphs (not three) should be distinguished in this species: low plated, low plated with a keel, partially plated and completely plated. A new model is proposed to explain the inheritance of these morphs which involves one major gene with three alleles displaying a dominance hierarchy with A (completely plated) dominant to a (low plated) which is dominant to a_k (low plated with keel). The dominance of the A allele is modified to semidominance by a dominant allele C at a second locus. This scheme explains all the results of relevant breeding experiments published so far. Field data also fulfill predictions derived from this model.

Key words Lateral plates · Morphs · Inheritance *Gasterosteus aculeatus*

Introduction

The threespine stickleback, *Gasterosteus aculeatus*, is a common Holarctic fish in both freshwater and saltwater environments (Wootton 1976, 1984). Variation in its morphology and ecology has been the subject of extensive studies, starting with those of Bertin (1925), and has been summarized by Bell (1984) and Wootton (1984). Particular attention has focused on variation in the arrangement of lateral bony plates (see Coad 1981), to the extent that the different morphs and life style forms which had been given special taxonomic status (Penczak 1966) now have only historic value.

Terminology concerning lateral plate morphs in a systematic and ecological context has been clarified by Bakker and Sevenster (1988) whose suggestions will be followed in this paper (see also Bańbura 1993). Traditionally, three morphs have been distinguished based on the arrangement of lateral plates (Fig. 1). The completely plated (complete) morph (= *trachura*) has a row of plates along either side of the body while on the caudal region the plates form a keel and the entire set consists of 30–36 plates on each side (Bell 1984). The partially-plated (partial) morph (= *semiarmata*) has two sets of plates (abdominal and caudal) separated by an unplated region, with part of the caudal set forming a keel. In the low plated-morph (= *leiura*) only abdominal plates are present with no keel and in some populations plateless individuals occur as an extreme variant (Bell 1984). During the development of young complete-morph individuals, stages resembling first the low morph and then the partial morph appear (Bell 1981; Bańbura 1989).

The genetic nature of this morphological variation has been investigated in several studies (Heuts 1947a; Münzing 1959; Hagen and Gilbertson 1973; Avise 1976; Ziuganov 1983), resulting in four explicit models which have been used to explain the results of the crossing programmes conducted by these authors. In this paper I analyze some inconsistencies of these older models and present a new model which provides a closer fit to the existing data. I also suggest possible consequences of this model for studies of natural populations of *G. aculeatus*.

Previous models of lateral plate morph inheritance

Münzing (1959) suggested that the three-plate morphs represent three different genotypes with respect to a locus with two semidominant alleles a/A (Fig. 2). He thought that the phenotypic expression of these genotypes might result from a modifying effect of some other genes.

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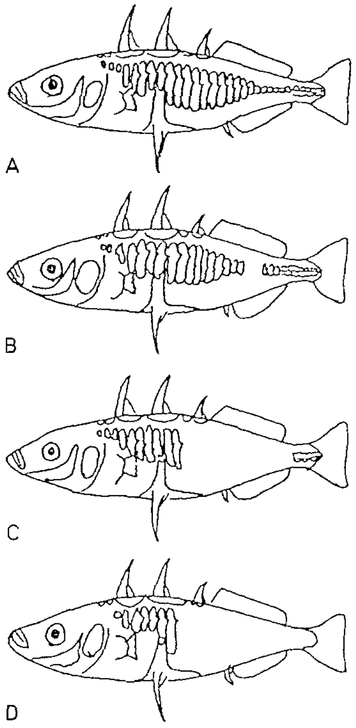


Fig. 1A–D Traditionally-distinguished lateral plate arrangement morphs of the threespine stickleback, *G. aculeatus*. **A** complete morph; **B**, **C** partial morph with two extreme plate number variants shown; **D** low morph

Fig. 2 Munzing's (1959) one-locus model of lateral plate morph inheritance

Hagen and Gilbertson (1973) proposed that the expression of plate morphs is governed by two alleles at either of two loci acting additively (Fig. 3).

A third model was put forward by Avise (1976) in order to explain an unusual plate morphology observed in a Californian population of *G. aculeatus*. In this population only the low and complete morphs occur, i.e., the partial morph has been lost. To explain this he proposed a one-locus two-allele model of inheritance with complete dominance (Fig. 4).

A fourth model was proposed by Ziuganov (1983), who assumed that there is only one major plate-morph locus with two alleles whose dominance relationships are modified by a second two-allele locus *c/C* such that allele *C* causes allele *A* to become semidominant (Fig. 5). This model is the most general one and explains some of the inconsistencies in the results of Münzing (1959) and Hagen and Gilbertson (1973), as well as the dimorphic Californian population of Avise (1976). However, Ziuganov's (1983) model also has its problems since it does not account for the results of 3/30 low × low crosses conducted by Hagen and Gilbertson (1973), which gave 43 lows and 8 partials in their progeny and the three partial × partial crosses conducted by these authors which gave only partial progeny.

Ziuganov (1983) suggested an alternative explanation for the latter problem. He thought that the partials used in these crosses were low morphs with a keel (*leiurus* with a keel). His supposition was that there is another locus involved in the formation of the keel plates, with its dominant allele being strongly linked to allele *A*. Accordingly, the keel would be expressed only in the *AA* and *Aa* genotypes but not in the *aa* homozygotes in which only the recessive no-keel-allele is present. This linkage might sometimes be broken and, as a consequence, other recombinant forms would result. Thus the form low with a keel could segregate as would a partial without a keel and a complete without a keel. However, the latter two have never been recorded.

Fig. 3 Hagen and Gilbertson's (1973) two-locus model of lateral plate morph inheritance

	AA	Aa	aa
BB	AABB Complete	AaBB Complete	aaBB Partial
Bb	AABb Complete	AaBb Partial	aaBb Low
bb	AAbb Partial	Aabb Low	aabb Low

The new model

The most important result of Ziuganov's (1983) study is the hypothesis that there is a separate low morph with a keel. This fact is in accord with the existence of monomorphic partial populations (Münzing 1962; Kynard and Curry 1976). However, the genetic explanation of the stickleback morph variation offered by Ziuganov (1983) can be developed further.

I suggest that there is a single major gene with three allelic variants controlling the expression of lateral plate arrangement forms. I call these alleles *A* (complete), *a* (low) and a_k (low with keel). They display a straightforward order of dominance with *A* dominant to *a* which is dominant to a_k. The top dominant *A* becomes semidominant when allele *C* at the modifier locus *c/C* is present (Fig. 6). Consequently, the allelic genotypes of the gene $A/a/a_k$ control four lateral plate morphs: low, low with a keel, partial and complete. The variable number of plates within every morph is due to a polygenic system (Hagen 1973).

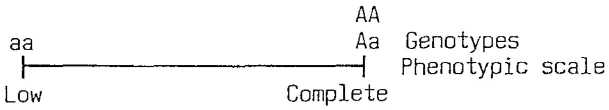


Fig. 4 Avise's (1976) one-locus complete dominance model of lateral plate morph inheritance

Implications of the proposed model

In this section I discuss consequences of, and predictions derived from, the new model in comparison with its predecessors. An advantage of the present model is its capacity to explain all results of the crosses conducted so far (including the results from Table 1) in a single theoretical framework with no need to apply hypotheses *ad hoc*. In particular, it is consistent with the results of the partial × partial and low × low crosses which produced only partials, and lows and partials, respectively (Hagen and Gilbertson 1973). In both these cases partials are in fact lows with keels. With the proposed inheritance model it is no

Fig. 5 Ziuganov's (1983) one-major locus one-modifier locus model of lateral plate morph inheritance

	AA	Aa	aa
CC	AACC Complete	AaCC Partial	aaCC Low
Cc	AACc Complete	AaCc Partial	aaCc Low
cc	AAcc Complete	Aacc Complete	aacc Low

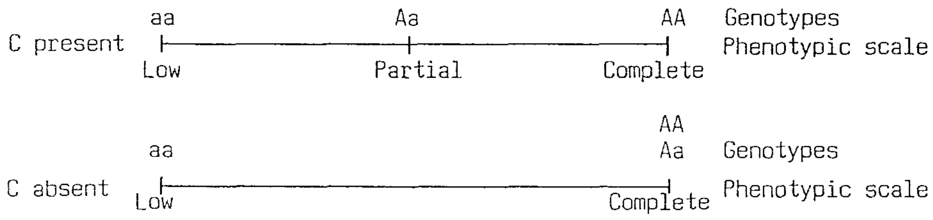
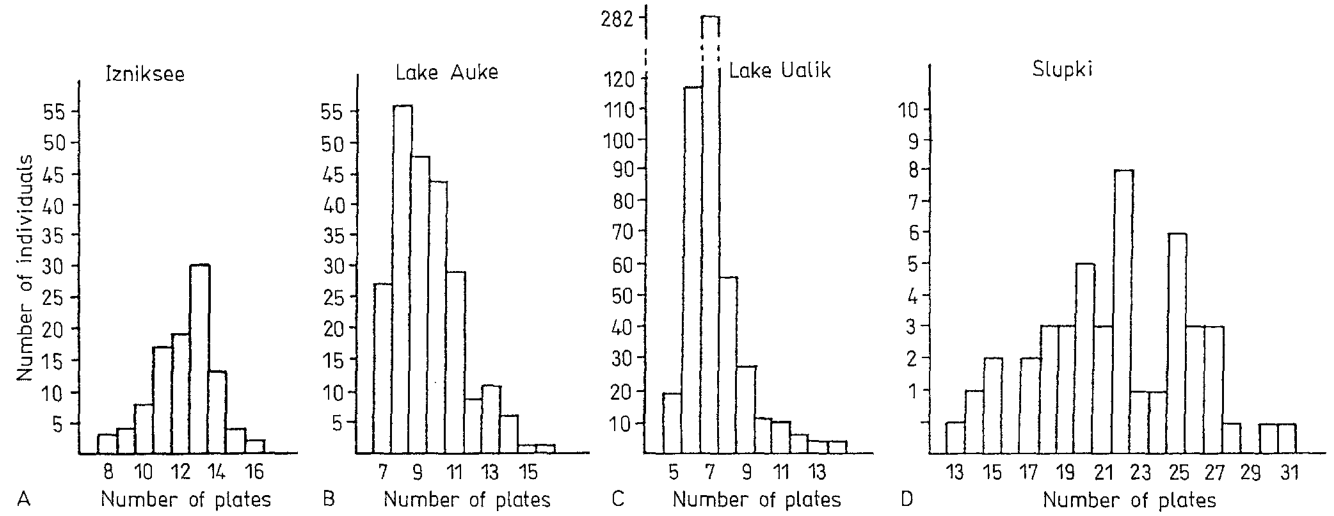


Fig. 6 A new one-major locus one-modifier locus model of lateral plate morph inheritance: genotypes and corresponding phenotypes

	AA	Aa	Aa_k	aa	aa_k	a_ka_k
CC	AACC Complete	AaCC Partial	Aa_kCC Partial	aaCC Low	aa_kCC Low	a_ka_kCC Low with keel
Cc	AACc Complete	AaCc Partial	Aa_kCc Partial	aaCc Low	aa_kCc Low	a_ka_kCc Low with keel
cc	AAcc Complete	Aacc Complete	Aa_kcc Complete	aacc Low	aa_kcc Low	a_ka_kcc Low with keel



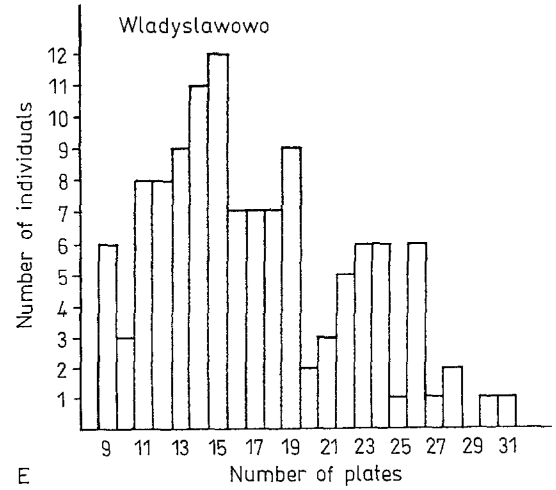


Fig. 7A–E Frequency distributions of the number of lateral plates of the partial-type morphs in different populations of *G. aculeatus*. **A, B** monomorphic populations, Izniksee (data from Munzing 1962) and Lake Auke (data from Kynard and Curry 1976); **C** dimorphic population with the low morph present, Lake Ualik (data from Hagen and Gilbertson 1972); **D** dimorphic population with the complete morph present, Slupki, Baltic Sea (Bańbura, unpublished data); **E** polymorphic population, Wladyslawowo, Baltic Sea (Bańbura, unpublished data)

Table 1 Results of crosses run by Munzing (1959) and Hagen and Gilbertson (1973) inconsistent with their models of lateral plate morph inheritance. Symbols: L, low plate morph; P, partial plate morph; C, complete plate morph

Model	Cross	Progeny
Münzing	P×C	1L:2P:1C
	L×C	2P:1C
	L×C	C
	L×C	1C:1L
Hagen and Gilbertson	L×C	C

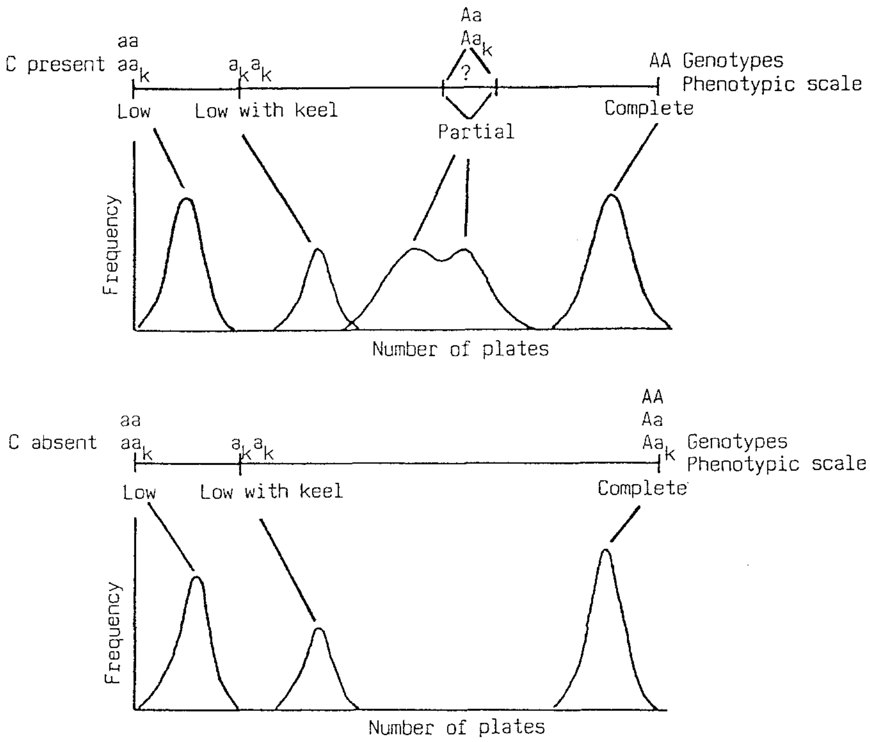
longer necessary to assume different genetic control in different parts of the threespine stickleback distribution.

Results of crosses made by Paepke (1983) agree qualitatively with this model but cannot be used to test it precisely because the author conducted group crosses with the implicit assumption that there always is a one genotype – one phenotype relation, which is evidently not true in his study populations. Hence, some of his results are actually mixed compositions.

The critical point in evaluating various models of the inheritance of plate polymorphism in threespine sticklebacks is the nature of the partial morph. Bell (1984) suggested that the number of lateral plates within this morph is more variable than in the other morphs. However, nobody has explicitly analysed the shapes of their distributions. The distributions turn out to slightly vary from a strict unimodal distribution in populations where the range of plate number variation is greatest (Fig. 7). A common statistical view suggests that these distributions are actually mixtures of simpler ones and, consequently, that uncontrolled discretely-distributed variables could be involved (Bradley 1977). In the case considered in the present paper, the uncontrolled variable in question is evidently the existence of separate genotypes regulating the development of two distinct morphs which have previously been grouped under a single partial morph (= *semiarmata*).

The new model predicts that what has been called the partial morph [with the exception of Ziuganov (1983)] is in fact made up of three different genotypes. It is evident that there exists a low morph with a keel and it is possible that the two heterozygous genotypes (Aa and Aa_k) may code for slightly different distributions of plate number with two modal values and widely-overlapping ranges (Fig. 8). The distribution of plate number in partial morphs

Fig. 8 A new model: diagrams of genotypes and phenotypes and hypothetical frequency distributions of the number of plates



may also overlap with the distribution of the number of plates in the low with a keel morph. As a consequence, the proposition of Ziuganov (1983) that morph determination should be based on lateral plate number rather than their arrangement is also doubtful. Ziuganov (1983) defines the low morph (with and without a keel as well) as having 2–10 plates and the partial morph as having 10–20 plates with an unplated region in the middle of the body.

Predictions concerning the shapes of frequency distributions of plate number in the partial morph will vary in relation to the genetic composition of a particular population. When the recessive allele c is fixed and the allele a_k is absent, there are no partials as, probably, in the case of the Californian population described by Avise (1976). When the allele a_k is fixed, only the low morph with a keel is present with a narrow unimodal plate number distribution (Fig. 7 A, B) (Münzing 1962; Kynard and Curry 1976). The same is true of pseudo-partials belonging to populations without allele A, i.e., the complete morph (Fig. 7 C) (Hagen and Gilbertson 1972). In populations with alleles A and a_k present, two different plate number modes, excluding completes, would be expected (Fig. 7 D) (Bańbura, unpublished data). Depending on the presence of allele a_k, two or three plate number modes of the non-complete-non-low forms may be expected in mixed populations (Fig. 7 E) (Bańbura, unpublished data), and this expectation seems to be confirmed by the data from several European populations (Bertin 1925; Heuts 1947 b; Münzing 1959; Paepke 1983; Bańbura, unpublished data). These predictions should be tested using field data and a precise breeding programme.

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