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# LATERAL PLATE MORPH GENETICS REVISITED: EVIDENCE FOR A FOURTH MORPH IN THREE-SPINED STICKLEBACKS

by

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(With 3 Figures)  
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## Summary

1. The view that four (not three) lateral plate morphs exist in the three-spined stickleback *Gasterosteus aculeatus* is supported in this paper. The morphs are: *trachura* (= completely plated), *semiarmata* (= partially plated), *leiura* (= low plated), and *leiura-with-keel* (= low-plated-with-keel).
2. Two one-locus and four two-locus models of lateral plate morph inheritance are identified and reviewed. A new genetic model for a two-locus system comprising one major gene with three alleles and one dominance modifier gene with two alleles is advocated.
3. Predictions of different models are explicitly examined using the existent data.
4. Results of 10 new crosses that distinguished the form *leiura-with-keel* are presented. The segregation ratios obtained are best explained by the new model.
5. Adaptive value of plate morph differentiation is not clear. Different aspects of selection on the morphs are discussed.

## Introduction

Instead of scales typical of the Teleostei, the sticklebacks (*Gasterosteidae*) have lateral rows of bony plates. In the three-spined stickleback, *Gasterosteus aculeatus*, the number and arrangement of the plates display considerable variability, with three distinct morphs being traditionally distinguished. Following BAKKER & SEVENSTER'S (1988) terminological recommendations these morphs are *trachura* (= completely plated), *semiarmata*

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*mata* (= partially plated) and *leiura* (= low plated). The *trachura* morph has a row of 30-36 plates along each side of the body; in the caudal region the plates form a keel. The *semiarmata* morph has the set of plates divided into anterior and caudal subsets by an unplated region in the middle of each side of the body. The *leiura* morph has only the anterior row of plates with the rest of the body unplated. ZIUGANOV (1983) argued that there exists a fourth morph *leiura*-with-keel that resembles the *semiarmata* form except that there are only very few caudal plates, all of which form a keel.

The discovery of discrete lateral plate morphs has stimulated an effort to investigate the genetics of this variation. Lateral plate genetics has two aspects: plate morphs and plate number within morphs. This latter is assumed to be controlled by a polygenic system (MÜNzing, 1959; HAGEN, 1973). Several discrete genetic models have been constructed to explain morph inheritance (MÜNzing, 1959; HAGEN & GILBERTSON, 1973; AVISE, 1976; ZIUGANOV, 1983; BAÑBURA, 1994a). The models have been based on segregation ratios obtained in laboratory crosses using particular populations, but plate morph inheritance may differ between populations, justifying the construction of several special-case models. However it is possible that one general model can explain segregation ratios in all populations. ZIUGANOV's (1983) model was the first to explain almost all crosses performed so far.

ZIUGANOV (1983) identified a fourth morph of the three-spined stickleback, *leiura*-with-keel. He proposed that the expression of the keel is governed by a locus closely linked but separate from the plate morph locus. BAÑBURA (1994a) argued that a separate keel locus is unlikely because even very strong linkage has to be broken sometimes, but respective recombinant phenotypes have never been recorded. ZIUGANOV's ideas were extended and included in a new model of plate inheritance (BAÑBURA, 1994a) in which the keel is encoded by an allele at the morph locus. BAÑBURA's model successfully predicts the relative proportions of four morphs and seems to offer a worldwide explanation for lateral plate morph segregation.

This paper reviews published plate morph inheritance models, the evidence for and against them, and provides new data that support BAÑBURA's model. Then the evidence for selection on lateral plate morphs is discussed.

### Models of plate morph inheritance.

We identified two one-locus and four two-locus models of lateral plate morph inheritance (Table 1). The one-locus models either lack generality (AVISE, 1976) or are too simplistic (MÜNZING, 1959), but the two-locus models are more promising. Additivity of two morph loci (HAGEN & GILBERTSON, 1973) or epistatic interaction between the morph locus and the modifier locus (ZIUGANOV, 1983; BAÑBURA, 1994a) or both additivity and epistasis (AVISE's (1976) second model) are assumed. The C locus in ZIUGANOV's (1983) and BAÑBURA's (1994a) models modifies the dominance interrelationships between alleles at the major morph locus A which is a two-allele locus in the former model and a three-allele one in the latter, the third allele controlling the expression of *leiura*-with-keel morph. If not modified by the C allele, the order of dominance at the morph locus is: A dominant to a, and a is dominant to  $a_k$ .

Figure 1 illustrates how genotypes at multiple loci produce the plate morphs. It emphasizes an otherwise obscure resemblance between ZIUGANOV and BAÑBURA's models and AVISE's two-locus model. It also becomes evident that AVISE's (1976) model for the Friant population may be regarded as a special case of his two-locus model, with the B allele fixed at B locus.

### Predictions from the models.

The various models of lateral plate morph inheritance predict different segregation ratios which could be used to test them (Table 2). However, testing the models, especially the two-locus ones, using the existent crossing results is problematic (MÜNZING, 1959; HAGEN & GILBERTSON, 1973; SEVENSTER & 't HART, 1974; AVISE, 1976; PAEPKE, 1982, ZIUGANOV, 1983). Unfortunately, the numbers of offspring, especially in most critical crosses, are small so that the estimates of segregation ratios must be interpreted with caution. Some of these low offspring numbers could result from low productivity of interpopulation hybrids, which might not be related to plate morphs themselves (HAGEN & GILBERTSON, 1973; PAEPKE, 1982; ZIUGANOV, 1983). Secondly, a difficulty arises because of the classification of morphs; the *leiura*-with-keel morph has never been distinguished so far and, if present, it might have been classified as *semiarmata* or, occasionally, as *leiura*.

TABLE 1. Genetic models for lateral plate morph inheritance

Description of models	Genotypes	Phenotypes	Reference
I. One-locus models			
A. Two alleles (A and a) with incomplete dominance of A	AA Aa aa	f. <i>trachura</i> f. <i>semiarinata</i> f. <i>leitura</i>	MÜNZING, 1959
B. Two alleles (A and a) with complete dominance of A	A- aa	f. <i>trachura</i> f. <i>leitura</i>	AVISE, 1976
II. Two locus models			
C. Two unlinked loci, each locus with two alleles (A, a and B, b), with additive interaction between them	AAB-, a-BB AAbb, AaBb, aaBB a-bb, aab-	f. <i>trachura</i> f. <i>semiarinata</i> f. <i>leitura</i>	HAGEN & GILBERTSON, 1973
D. Two unlinked loci, each locus with two alleles (a, a and B, b), with additive and epistatic interaction	A-B- A-bb aaB-, aabb	f. <i>trachura</i> f. <i>semiarinata</i> f. <i>leitura</i>	AVISE, 1976
E. Two unlinked loci, each locus with two alleles (A, a and C, c) with epistatic interaction	AAC-, AAcc, Aacc AaC-, AaCc- aaC-, aacc, aa <sub>k</sub> C-, aa <sub>k</sub> cc A <sub>k</sub> a <sub>k</sub> C-, a <sub>k</sub> a <sub>k</sub> cc	f. <i>trachura</i> f. <i>semiarinata</i> f. <i>leitura</i>	ZIUGANOV, 1983
F. Two unlinked loci, one with three alleles (in order of decreasing dominance: A, a, a <sub>k</sub> ) and the other with two alleles (C, c), with epistatic interaction	AAC-, AA <sub>k</sub> cc, Aacc, Aa <sub>k</sub> cc AaC-, Aa <sub>k</sub> C- aaC-, aacc, aa <sub>k</sub> C-, aa <sub>k</sub> cc A <sub>k</sub> a <sub>k</sub> C-, a <sub>k</sub> a <sub>k</sub> cc	f. <i>trachura</i> f. <i>semiarinata</i> f. <i>leitura</i> f. <i>leitura</i> with keel	BAÑBURA, 1994

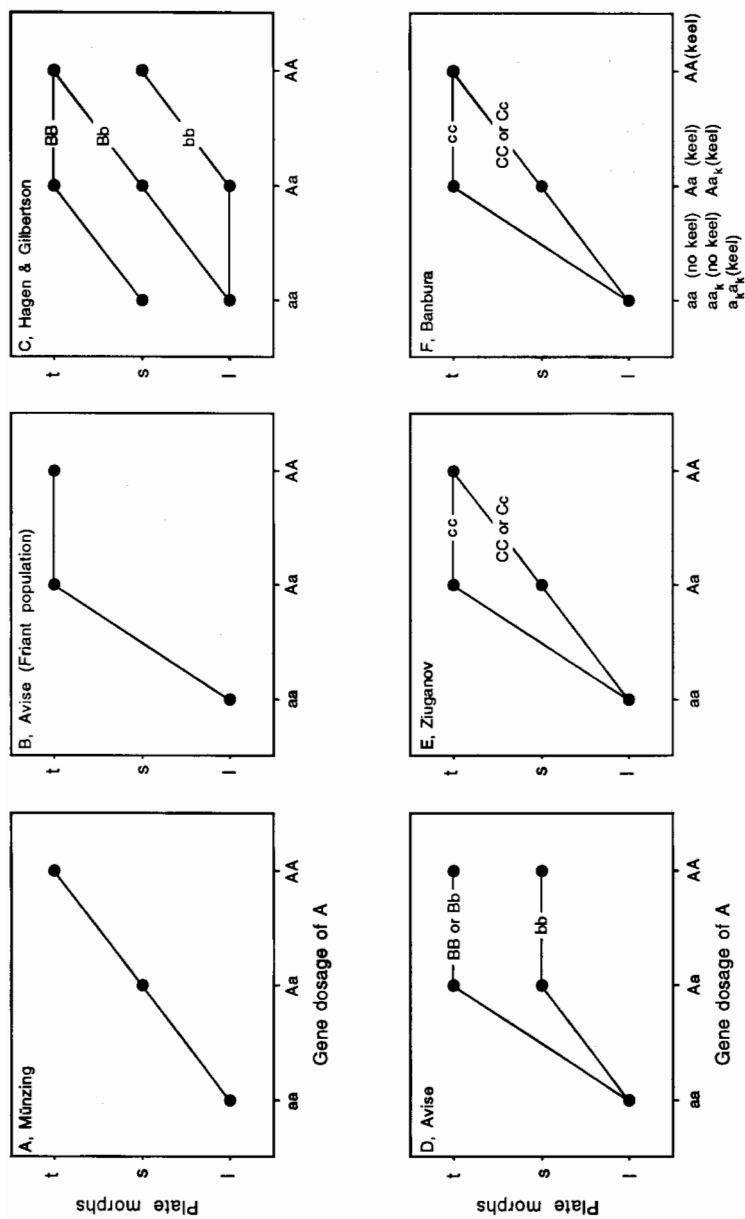


Fig. 1. Phenotype-genotype relationships in the various models of lateral plate morph inheritance (MÜNzing, 1959; HAGEN & GILBERTSON, 1973; AVISE, 1976; ZIUGANOV, 1983; BANBURA, 1994). l = forma *leitura*, s = forma *semarmata*, t = forma *trachura*. Genes at the morph locus A determine the lateral plate morph, those at the B or C locus interact additively (model C), additively and epistatically (models E and F) with alleles at the morph locus.

TABLE 2. All possible crosses between plate morphs and the expected proportions of plate morphs in the progeny according to the different genetic models

Crossing	l:s:t in progeny	Model
I) l×l	1) 1:0:0	M, A, HG, Z, B(1:1+=1:0;0:1;1:1;3:1)
	2) 3:1:0	HG
II) s×s	1) 0:1:0	A, HG
	2) 1:3:0	A
	3) 2:3:3	Z, B(1:1+=1:0;0:1)
	4) 5:6:5	HG
	5) 1:2:1	M, HG, Z, B(1:1+=1:0;0:1)
III) t×t	1) 0:0:1	M, A, HG, Z, B
	2) 0:1:1	Z, B
	3) 0:1:3	A, HG, Z, B
	4) 1:0:3	A, Z, B(1:1+=1:0;0:1)
	5) 4:3:9	A
	6) 2:1:5	A
IV) l×s	1) 1:0:0	HG
	2) 0:0:1	A
	3) 0:1:0	A
	4) 0:1:1	A
	5) 1:0:1	A
	6) 1:1:0	M, A, HG, Z, B(1:1+=1:0;0:1;1:1)
	7) 3:1:0	HG
	8) 4:3:1	HG, Z, B(1:1+=1:0;0:1;1:1)
	9) 2:1:1	A, Z, B(1:1+=1:0;0:1;1:1)
V) l×t	1) 0:1:0	M, HG, Z, B
	2) 0:0:1	A, Z, B
	3) 1:0:1	A, Z, B(1:1+=1:0;0:1;1:1)
	4) 1:1:0	HG, Z, B(1:1+=1:0;0:1;1:1)
	5) 0:1:1	A, HG, Z, B
	6) 0:3:1	Z, B
	7) 2:1:1	A, Z, B(1:1+=1:0;0:1;1:1)
	8) 1:2:1	HG
	9) 4:1:3	A
VI) s×t	1) 0:0:1	A, HG
	2) 1:0:3	A
	3) 0:1:1	M, A, HG, A, Z, B
	4) 0:1:3	HG, Z, B
	5) 0:3:5	Z, B
	6) 1:2:1	Z, B(1:1+=1:0;0:1)
	7) 1:1:2	Z, B(1:1+=1:0;0:1)
	8) 1:3:4	HG
	9) 2:3:3	A

Plate morphs: t = forma *trachura*, s = f. *semiarmata*, l = f. *leiura*, l+ = f. *leiura*-with-keel. Models: M = MÜNZING, 1959; A = AVISE, 1976; HG = HAGEN & GILBERTSON, 1973; Z = ŽIUGANOV, 1983; B = BAÑBURA, 1994. The ratio of l and l+ indicated for the BAÑBURA model.

BELL (1984) examined in detail MÜNZING's (1959) crosses and concluded that his breeding results were in most cases inconsistent with predictions from his model. For the reasons mentioned above, it is impossible to test the two-locus models in the same way. However, some published results of crosses produced morph ratios that are unexpected with some models but explicable in terms of the others. MÜNZING (1959), AVISE (1976) and PAEPKE (1982) repeatedly obtained both *trachura* and *leiura* from individual crosses of *trachura* × *leiura*, which is inconsistent with HAGEN & GILBERTSON's (1973) model but is expected from the remaining two-locus models. These latter models can also account for the production of only *trachura* offspring by a *trachura* × *leiura* cross run by HAGEN & GILBERTSON (1973).

It is still more difficult to evaluate the relative support given by the existing data to the models of AVISE (1976), ZIUGANOV (1983) and BAÑBURA (1994a). HAGEN & GILBERTSON's (1973) cross 23, *semiarmata* × *leiura*, produced only *leiura* morph offspring, which is in fact consistent with their model, but is evidently inconsistent with AVISE and ZIUGANOV's models as well (Table 2). Assuming a possibility of misclassification of the *leiura*-with-keel morph as the *semiarmata* morph, this result would be consistent with BAÑBURA's model.

Actually, this result together with the existence of some dimorphic populations including *semiarmata*-type morphs led BAÑBURA (1994a) to propose that the *a* allele is dominant to the *a<sub>k</sub>* allele in his model. This is in contrast to ZIUGANOV's (1983) hypothesis of a separate keel locus with the allele for the keel being dominant to the one responsible for its absence.

#### Data on new crosses.

Previous studies of three-spined stickleback morphology and genetics fail to distinguish the *leiura* morph with a keel. Here we report on such a study of the lateral plate morph genetics which allows us to distinguish between BAÑBURA's (1994a) model and the alternatives.

#### Methods

##### *Study populations.*

Fish were sampled from three populations. One population is a Dutch anadromous population that was sampled at Den Helder, in 1985 and 1986. This is a polymorphic population



with all four morphs present. The second population is a Dutch freshwater population that was sampled from a trout hatchery 't Smalvert', Emst (near Vaassen) in 1985 and 1986. This population is monomorphic for the form *leiura*. The third population is a freshwater population of plateless sticklebacks with reduced spine number and pelvic girdle. It resides at Loch Fada, Scotland, and was sampled in 1986.

#### *Lateral plate counts.*

Breeding experiments were done in freshwater in the laboratory. Eggs were removed from the father's nest about one hour after fertilization and hatched artificially (BAKKER, 1986). The fish were raised in full-sib groups under simulated summer conditions (16L:8D, 18-20°C) and fed *ad libitum* with various items (live *Tubifex* worms, *Artemia*, *Chironomus* larvae, and frozen *Artemia* and *Mysis*).

Lateral plate counts were done when fish reached at least 35 mm standard length (*i.e.* distance from the tip of the snout to the end of the vertebral column). The number of lateral plates of decapitated fish was counted on both sides of the body using a stereoscopic microscope under low magnification. A preparation needle was used to distinguish successive plates. The plates of the caudal keel, characterized by a lateral process, were not counted because of difficulties in counting them accurately by this method. The presence or absence of a keel was recorded and deviations from this were noted (small keel, keel only on one side of the body, plates missing in keel).

The sum of the left and right plate counts was used in the analysis. Based on the frequency distributions of progeny of many crosses we defined operationally the following four plate morphs: *leiura* ( $\leq 18$  plates, no keel), *leiura*-with-keel ( $\leq 18$  plates, keel present), *semiarmata* ( $19 \leq$  plates  $\leq 38$ , unplated gap(s), keel present), and *trachura* ( $\geq 39$  plates, occasionally one of a few plates missing, keel present). The plate number limits are arbitrary, because an overlap of plate counts between morphs is likely (BAÑBURA, 1994a).

## Results

The frequency distribution of lateral plate counts in the polymorphic Den Helder population is shown, in Fig. 2. The proportions of the plate morphs are 5.7% *leiura* (which agrees with MÜNZING's (1963) score of 8.3% for the same population), 11.4% *leiura*-with-keel, 31.05% *semiarmata* and 51.58% *trachura*. The median plate count for *leiura* and *leiura*-with-keel is the same, 14. Out of 40 *leiura*-with-keel, 6 had a keel on only one side of the body, and 5 had a small keel. In *semiarmata* (N=109), one fish had no keel (plate count 20; possibly a *leiura* morph), one-sided keels were not noticed and 6 individuals had small keels. There were no clear irregularities of the keel in *trachura*. With such a frequent occurrence of *leiura*-with-keel, according to ZIUGANOV's (1983) hypothesis of the keel inheritance one would expect regular *semiarmata* and *trachura* fish without a keel in this population, which is not the case. This is indirect evidence against ZIUGANOV's hypothesis and so evidence in favour of BAÑBURA's (1994a) model.

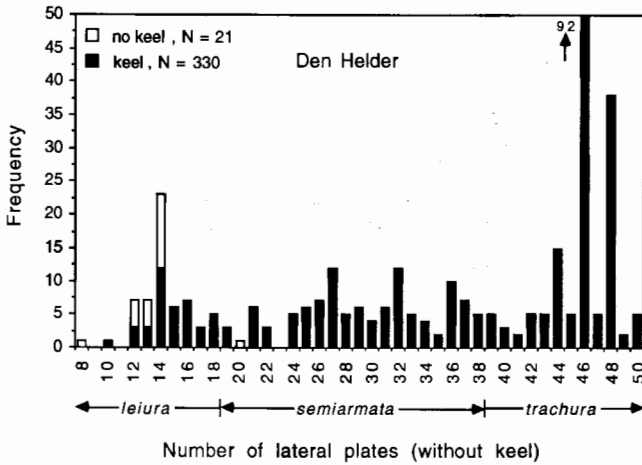


Fig. 2. Frequency distribution of lateral plate counts based on 351 fishes in the polymorphic Den Helder population. Two third (N = 40) of the forma *leiura* ( $\leq 18$  plates) possessed a caudal keel. Indicated are the ranges of plate counts in the *leiura*, *semiarmata*, and *trachura* morphs.

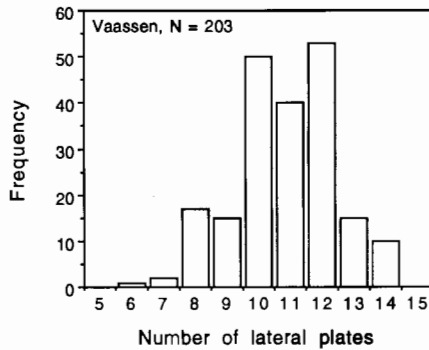


Fig. 3. Frequency distribution of lateral plate counts based on 203 fishes in the monomorphic *leiura* Vaassen population.

All 203 fishes from the monomorphic *leiura* population from Vaassen (Fig. 3) had no keel, with the exception of one fish which possessed one plate without a lateral process on one side in the caudal peduncle. The median plate number in this population was 11. Notice that in both populations, but especially in the Den Helder one, even plate counts are more frequent. These are for the greater part fishes that have identical plate numbers on the left and right sides of the body.

The results of the crosses are presented in Table 3. Each cross can be compared with the segregation ratios given in Table 2. The Roman

TABLE 3. Segregation of lateral plate morphs in crosses of fish from three populations

Parents	Plate morphs of progeny			<i>trachura</i>
	<i>leiura</i> -with-keel	<i>leiura</i>	<i>semiarmata</i>	
a) V/1(<15)×DH/t(44)	- N=0	11(1)/12(3) N=4	30(1) N=1	39(1)/40(1)/43(1)/46(1) N=4
b) V/1(<15)×DH/t(44)	- N=0	12(3)/13(1)/14(2) N=6	- N=0	43(1)/44(1) N=2
c) DH/s(27)×DH/s(32)	16(1) N=1	- N=0	21(1)/24(1)/31(1) N=3	43(1)/46(2) N=3
d) DH/s(26)×DH/s(32)	10(1)/12(1)/14(2)/ 16(2)/17(1)/18(1) N=8	- N=0	22(2)/25(1)/26(3)/27(1)/ 28(4)/29(1)/30(3)/31(5)/ 32(1)/33(1)/34(3)/35(1)/ 36(1)/37(2)/38(1) N=30	39(2)/42(1)/44(1)/ 45(3)/46(13) N=30
e) DH/s(29)×DH/s(28)	12(2)/14(3)/15(2)/ 16(2)/18(1) N=10	12(1)/13(1) N=2	29(2)/30(2)/31(1)/32(1)/ 33(1)/35(2)/38(2) N=11	42(1)/44(2)/45(1)/46(11) N=15
f) DH/1+(14)×DH/ t(48)	- N=0	- N=0	20(1)/26(1)/28(1)/30(1)/ 31(1) N=5	- N=0

Table 3 continued

g) $F_1(V \times DH)/1+(13) \times$ $F_1(V \times DH)/s(23)$	17(1) N=1	7(1)/8(1)/9(3)/10(2)/ 11(1) N=8	22(2)/26(1)/27(1)/28(2)/ 31(1)/34(1) N=8	- N=0
h) $F_1(V \times DH)/1+(13) \times$ $F_1(DH \times V)/1+(12)$	14(1)/15(1)/17(1) N=3	11(1)/12(2) N=3	- N=0	- N=0
i) $DH/t(>38) \times$ $F_1(DH \times LF)/1(10)$	7(1)/8(2)/10(13)/11(5)/ 12(14)/13(8)/14(10)/ 15(7)/16(4)/17(4)/ 18(9) N=77	6(2)/9(1)/9(3)/10(12)/ 11(2)/12(6)/13(2)/14(3)/ 15(1)/17(1) N=33	19(8;1xnk)/20(8;2xnk)/ 21(2)/22(8;1xnk)/ 23(1)/24(3)/26(2) N=32	- N=0
j) $F_1(V \times DH)/1+(13) \times$ $F_1(V \times DH)/1+(14)$	10(1)/12(4)/13(2)/14(2)/ 15(6)/16(7)/17(5)/18(4) N=31	9(2)/10(1)/11(9)/12(9)/ 13(5)/14(2)/15(1)/16(1) N=30	19(3;1xnk)/20(12)/ 21(7)/22(12)/23(4)/ 24(6)/25(2)/26(2)/27(4)/ 28(2)/32(1)/33(1) N=56	- N=0

Indicated for the parents (females first) are the populations (DH = Den Helder, V = Vaassen, LF = Loch Fada), the number of lateral plates in brackets (sum of left and right sides without keel plates), and the plate morphs (t = *trachura*,  $\geq 39$  plates; s = *semiarmata*, 19-38 plates; l = *leitura*,  $\leq 18$  plates; 1+ = *leitura*-with-keel,  $\leq 18$  plates). Indicated for the progeny are the plate counts classified into the four morphs (number of fish in brackets), nk = s without keel.

numbers in this table refer to combinations of parental morphs in Table 2 and the Arabic numbers to specific segregation ratios resulting from a particular combination of parental morphs. Now we comment on the crosses using abbreviations of the genetic models given below Table 2.

*Cross a.* Segregation ratio compatible with V7, 8, or 9. Against M.

*Cross b.* Compatible with V3. Against M and HG.

*Cross c and d.* Compatible with II3. Combined crosses significantly different from II4 and II5 ( $\chi^2 = 9.7$  and  $6.1$ , respectively,  $df = 2$ ,  $p < 0.05$  for both cases). Against M, A, and HG. The fact that all *leiura* had keels is compatible with Z (recombination occurred) and B.

*Cross e.* This result is not explained by any model. At first sight it seems compatible with II3, 4, or 5, so against A. However, the simultaneous segregation of *leiura* and *leiura*-with-keel from *semiarmata* parents is impossible according to Z and B unless one of the parents is actually a *leiura*-with-keel (with extremely high plate count).

*Cross f.* Compatible with V1, thus against A. If the *leiura*-with-keel parent had been a *semiarmata* (as was assumed before the Z model), the segregation ratio would have been impossible according to any model. Thus, this cross supports the recognition of the fourth morph, *leiura*-with-keel.

*Cross g.* Compatible with IV6. If the *leiura*-with-keel had been a *semiarmata*, the segregation ratio would not have fitted any model. So, this is further evidence for existence of the form *leiura*-with-keel. The only *leiura*-with-keel in the progeny seems to be a *semiarmata* with low plate number. If so, then B is more likely than Z (half of *leiura* is expected to have keels, or all *leiura*-with-keels when recombination also occurred in the *semiarmata* parent).

*Cross h.* Compatible with I1. If the *leiura*-with-keel parents had in fact been *semiarmata*, then the segregation ratio would not have fitted any model. Accordingly, this is further evidence for the existence of *leiura*-with-keel. The ratio of *leiura* to *leiura*-with-keel is more compatible with B than with Z (one quarter of *leiura* or none, if recombination occurred more than once, expected).

*Cross i.* Most compatible with V4 (thus against M and A) but *semiarmata* is underrepresented. Because one half of the genes from the father are from the Loch Fada plateless population, it is possible that the range of plate

numbers in each morph is different from our division. This is evidence against Z, because Z would expect all *leiura* either with or without a keel. Note that four *semiarmata* individuals had no keel.

*Cross j.* Illustration of a misclassification of morphs. If both parents had been *leiura*-with-keels, the segregation pattern would have been incompatible with any model. If the *leiura*-with-keel parents had been *semiarmata*, the segregation ratio would have fitted only A, thus being against all other models. If one of the parents was, however, *semiarmata*, the outcome would be compatible with IV6. So, this is indirect evidence for the existence of the form *leiura*-with-keel. Note that one of the *semiarmata* had no keel, but it could be a *leiura*.

In summary, the segregation ratios in the ten crosses are best explained by BAÑBURA's (1994) model. Five of the crosses are against M (a, b, c, d, i), five against A (c, d, e, f, i), three against HG (b, c, d). Six crosses are evidence for the existence of the *leiura*-with-keel morph (c, d, f, g, h, j). All crosses are explained by Z and B, but in three cases the ratios between the *leiura* and the *leiura*-with-keel morphs are better explained by B (g, h, i). The simultaneous segregation of the *leiura* and *leiura*-with-keel in cross e is not explained by the Z and B models, nor is the presence of *semiarmata* without a keel in cross i.

## Discussion

It is difficult to test different models of lateral plate morph inheritance because large progeny numbers are needed to discriminate statistically between different segregation ratios. A further difficulty is that the range of plate number within a given plate morph is not fixed. HAGEN (1973) showed high heritabilities for plate numbers in the *leiura* morph in a monomorphic population. The same is likely to be true of the other morphs. This means that when crosses are made, the range of plate numbers within the morphs may shift, making a classification less accurate. Some examples of this are given in Table 3. The polygenic systems that probably determine plate numbers within morphs act also on the plate numbers of the keel (see description of Fig. 2). Crosses of individuals belonging to different populations often produce fish that have gaps of one or more plates instead of continuous rows of plates.

We are convinced that the existent models will not be the last word to be said on plate morph inheritance. The evidence for ZIUGANOV's (1983) and BAÑBURA's (1994a) models is good, and so is the evidence for the fourth morph *leiura*-with-keel. Although some details are not explained by them, there is now good evidence for a general model of plate morph inheritance. Differences between populations are well explained by differences in allele frequencies and/or fixation of particular alleles. Though there are some results in favour of BAÑBURA's model, the evidence is still weak and further studies are certainly needed.

Whatever the genetic mechanism controlling the expression of lateral plate morphs in the three-spined stickleback is, the question of the ultimate significance of morph differentiation still remains to be explained. Once originated a polymorphic system can evolve in various directions – it can change, disappear, or be maintained at a particular level by some factors. The worldwide and local scale distribution of the stickleback morphs displays a more or less regular pattern (*e.g.* HEUTS, 1947a; MÜNZING, 1963; WOOTTON, 1976, 1984; HAGEN & MOODIE, 1982; BAUMGARTNER & BELL, 1984; BELL, 1984; BAÑBURA, 1994b), which suggests that some equally regular causes should exist. However, caution is necessary in interpreting some results because the *leiura*-with-keel morph has almost never been distinguished.

Variation of the predation regime, climate, and water chemistry have been proposed as global-scale selection factors (GROSS, 1978; HAGEN & MOODIE, 1982; GILES, 1983a; WOOTTON, 1984). Relatively rapid changes in morph composition observed in freshwater populations of the three-spined stickleback recently isolated from the sea (FRANCIS *et al.*, 1985; KLEPAKER, 1993, M.A. BELL, pers. comm.) suggest that some factors correlated with the transition from sea to freshwater play a role in this respect, perhaps intermorph variation in osmoregulatory properties (HEUTS, 1947b; GUDERLEY, 1994).

HEUTS (1947b) demonstrated an association between lateral plate morphology and salinity tolerance and suggested that there is genetic linkage between these properties. His results show that the *leiura* morph eggs survive better at low salinity and *trachura* at high salinity, this association being modified by temperature. The extent to which these relations shape local- and global-scale spatial distribution of plate morphs is not clear. If these relations only resulted from genetic linkage, they would most cer-

tainly be more or less frequently recombined and indeed the low plated morph can breed in salt water (*e.g.* BELL, 1979) and the complete morph can do very well in fresh waters (*e.g.* BAUMGARTNER & BELL, 1984; BAÑBURA, 1994b).

An association between stream gradients and morph frequencies was observed by several authors (*e.g.* HEUTS, 1947b; HAGEN, 1967; PAEPKE, 1982); perhaps the most consistent pattern was reported by BAUMGARTNER & BELL (1984). Such results support the view that physical characteristics of habitats can influence the plate morph distribution. However, this association may also be indicative of biotic community-level factors, like predation, which are known to vary along river continuum (*e.g.* ZALEWSKI *et al.*, 1990).

Precise predation-related selection mechanisms remain unknown, however. It is only anterior plates which are known to buttress the basal plates supporting dorsal spines and to protect the body from injuries from attacks of predatory fish (REIMCHEN, 1983, 1992, 1994). As most of the anterior plates are common to all morphs, it is not clear if their anti-predator function could be involved in the evolution of distinct morphs. It seems clear that fish and bird predation influence evolution of anterior plates of *leiura* in a completely different way, this being a potentially effective disruptive selection factor (REIMCHEN, 1988, 1992, 1994, this volume). The direction of inquiry initiated by REIMCHEN (1983, 1992, 1994, this volume) seems promising. The role of plates as components of the body armour, changing manipulation efficiencies of various predators, in anti-predatory behaviour and in swimming performance should certainly be further explored experimentally.

Another potentially significant factor is parasitism. For example *Schistocephalus solidus* is known to severely affect stickleback physiology and to cause a considerable distension of the body (GILES, 1983b; WOOTTON, 1984). It is conceivable that infection by this worm may affect fitnesses of different morphs in a different way. Indeed, at least in some studies, the intensity of *Schistocephalus solidus* infections of sticklebacks displayed a non-random relation to plate morphology, although this relation was not everywhere the same (GILBERTSON, 1980 cited in BELL, 1984; MACLEAN, 1980). The heavily infected Friant population (AVISE, 1976) consisted almost entirely of *leiura* and *trachura* morphs. It is possible that when infected, different morphs experience different risk of predation, as *Schis-*



*tocephalus* is known to influence the anti-predator behaviour of the three-spined stickleback (e.g. GILES, 1983b; MILINSKI, 1985; LO BUE & BELL, 1993).

There is some evidence for a relation between variation in reproductive success and lateral plate number in *leiura* morphs (MOODIE, 1972; KYNARD, 1979; BELL, 1984 for review). Unfortunately, nothing is known about variation in reproduction among plate morphs. Such variation could be influenced by both natural selection through the ecological factors mentioned before and by sexual selection.

MILINSKI, BAKKER and coworkers (e.g. MILINSKI & BAKKER, 1990; BAKKER & MILINSKI, 1991; BAKKER & MUNDWILDER, 1994) studied breeding coloration of three-spined sticklebacks as a sexually selected trait. However, mate selection has been studied in this fish mostly in the context of interpopulation anadromous-freshwater life-style differentiation and related variability (e.g. HAGEN, 1967; HAY & MCPHAIL, 1975; MCPHAIL & HAY, 1983; RIDGWAY & MCPHAIL, 1984; BLOUW & HAGEN, 1990; see MCPHAIL, 1994 for review). Studies of isolating mechanisms between anadromous *trachurus* and stream *leiurus* forms confound effects of plate morphology with those of membership in separate biological species, because assortative mating may result from numerous factors other than plate phenotypes. It is, however, conceivable that plate phenotypes may constitute one of the cues used for discriminating between mates belonging to different populations. The ability to discriminate between potential mates is a precondition for sexual selection of any kind to work (WILLIAMS, 1992; ANDERSSON, 1994).

It is not known whether plate morphs or plate numbers undergo assortative, disassortative or random mating or any form of sexual selection. Assortative mating and sexual selection (see O'DONALD, 1980 for the differences) are capable of causing either phenotypic differentiation or stabilization of existing polymorphism, depending on initial conditions (O'DONALD, 1980; LANDE, 1981; ARNOLD, 1983; SPIESS, 1989; ANDERSSON, 1994). These mechanisms could potentially play some role in the evolution of plate morphs. They seem to be important in some other polymorphic systems with obscure adaptive meaning, as in the two-spot ladybird *Adalia bipunctata* (MAJERUS, 1989; MAJERUS & KEARNS, 1989) and the Arctic skua *Stercorarius parasiticus* (O'DONALD, 1983).

Another still unexploited way to investigate the functional meaning of the three-spined stickleback plate morphs is the application of formal comparative methods (*sensu* HARVEY & PAGEL, 1991), which gave interesting results concerning behaviour (MCLENNAN *et al.*, 1988). Some other Gasterosteids are known to have lateral plate morphs analogous to those of the three-spined stickleback (BELL, 1984) which makes possible looking for a common evolutionary explanation.

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