NOTE

Eur. J. Entomol. **95**: 307–310, 1998
ISSN 1210–5759

Evolutionary origin of squamiform microsculpture on the forewing-holding devices (frenae) in Heteroptera

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Heteroptera, Enicocephalomorpha, Dipsocoromorpha, Schizopteridae, *Rectilamina*, morphology, microsculpture, frenae, microtrichia, acanthae

Abstract. Frenae are forewing-holding ridges situated in the Heteroptera parallel to the lateral sides of mesoscutellum, and covered by a squamiform, overlapping, glabrous microsculpture. The situation found in *Rectilamina* sp. (Dipsocoromorpha: Schizopteridae: Hypselosomatinae) suggests that each single squamiform element is homologous to a strongly modified microtrichium, and that, at least in this case, there is no basic difference between microtrichium and acanthus.

Introduction

The order Heteroptera is notorious for the universal presence of several kinds of coaptations fixing in adults the resting macropterous forerewings to various parts of the thorax (in many cases to the abdomen as well), and mutually together. Coaptation of anal (= posterior claval) margins of forewings with the lateral sides of the mesoscutellum is a universal feature of adults. The thoracic parts of frenae are covered by a conspicuous squamiform, glabrous microsculpture whose elements overlap in a fishscale-like manner. The origin of this microsculpture has, to the best of my knowledge, never been considered.

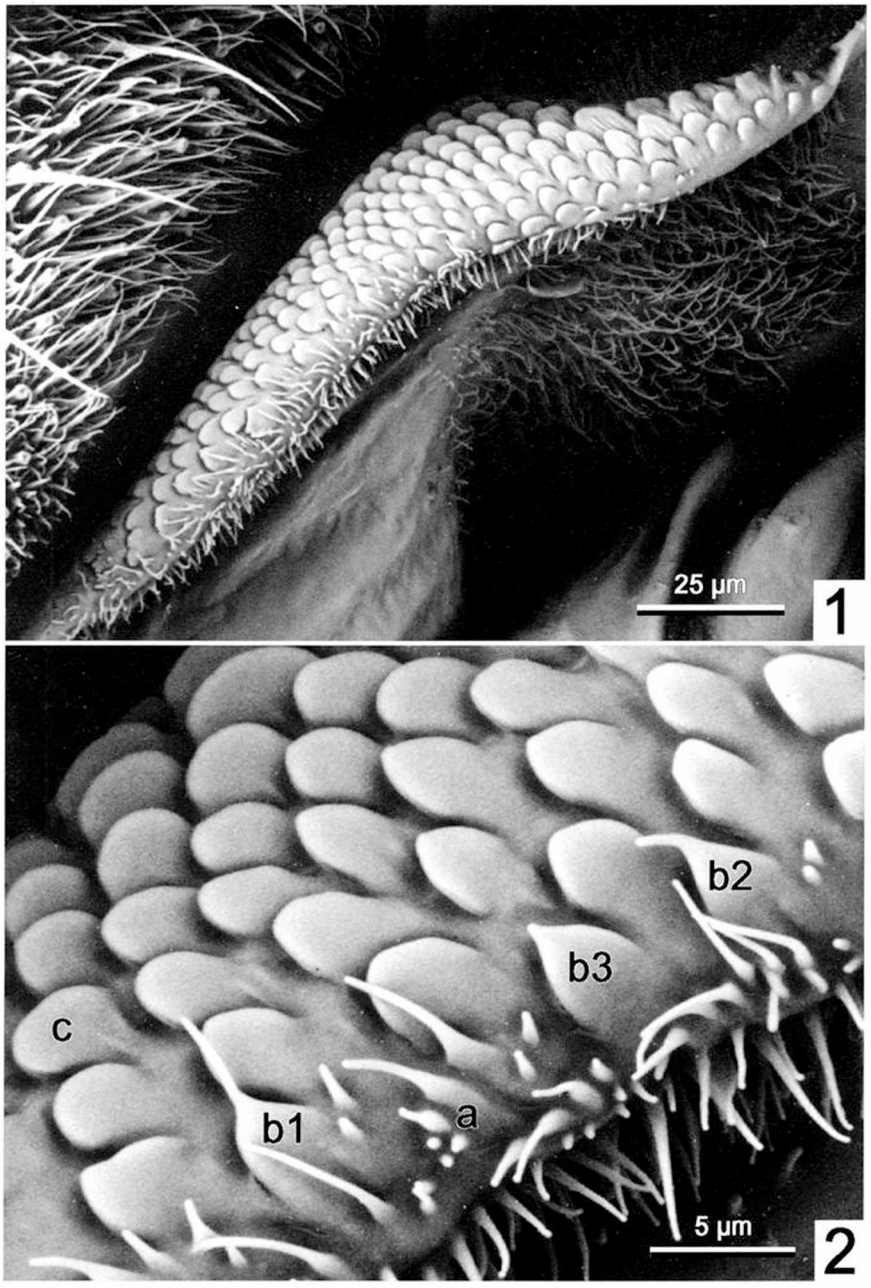
The SEM micrographs included in this paper are based on alcohol preserved specimen which were sonicated, critically point-dried, gold-coated, and examined and photographed by a scanning electron microscope.

Topography and terminology

The lateral sides of the heteropteran mesoscutellum are fringed by shallow grooves (*tergal wing grooves*: Kramer, 1950 in the "Auchenorrhyncha"; Parsons, 1963 in the Heteroptera (Saldidae); Matsuda, 1970, generally in the Hemiptera; *sillon alaire tergal*: Matsuda, 1979 in the Heteroptera) which are laterally paralleled by low convex folds called *frenae* (Figs 1, 2)*.

The general opinion of heteropterists is that both tergal wing grooves and frenae are of mesoscutellar origin, but Matsuda (1970, 1979) considered them to represent the posterolateral mesoscutal sutures (sulci). However, Parsons (1963) suggested with caution that both the grooves and frenae may be actually derived from mesopostnotum – I agree with her opinion.

* The latter term has been in general use since the time of Fieber (1860), although actually coined some twenty years earlier by Kirby (fide Fieber, the original reference has not been found). The word *frena* (pl. *frenae*) is a femininum while the correct and original Latin spelling and gender are frenum, pl. frena, neuter. C.W. Schaefer points out that – according to a classical quotation from Vergil – the original gender might have been masculine. However, I do not attempt to change the established usage.



Figs. 1–2. *Rectilamina* sp. (cf. *borealis*), macropterous male, frena, dorsal view, right side. 1 – general view. Note from left to right: part of the mesoscutellum (covered by trichoid macrotrichia, truncate TP sensilla, and microtrichia), wing groove (appearing dark), frenum, and mesopostnotum (covered with microtrichia, anteriorly, or glabrous, posteriorly). 2 – part of frena showing transition zone from hair-like to squamiform microtrichia (acanthae?). Letters a, b1–3, c indicate the transitional series from multimicrotrichial to acanthal equipment. Only the type c occurs in all other Heteroptera examined.

Microsculpture of frenae and its origins

In all the heteropteran species examined (representing all the established infraorders/suborders – Štys & Kerzhner, 1975) the surface of the frenae is formed by a squamiform microsculpture – overlapping and projecting rows of glabrous, suboval to subacuminate elements arranged in a fishescale-like pattern (as in Fig. 2 sub c), and it is probable that each of them corresponds to one hypodermal cell. I know of only two exceptions to this situation, the first interesting but irrelevant to the present inquiry, and the second essential.

(1) This type of microsculpture is in some species of Aenictopecheidae (jointly with the Enicocephalidae forming the Enicocephalomorpha, sister group to the rest of the true bugs – the Euheteroptera) limited to auriculiform frenal projections situated laterad of the mesoscutellum and hidden beneath the forewing bases. The structure was regarded by Wygodzinsky & Schmidt (1991, e.g., their Figs 30E, F) to be parts of dorsally shifted openings of metathoracic scent glands. In fact, the structure is a wing-holding device, and has nothing in common with scent gland openings which are situated ventrally near the thoracoabdominal junction.

(2) Though the situation in all the Dipsocoromorpha (a first branching clade of the Euheteroptera) examined is modal, the SEM study of frenae in *Rectilamina* sp. from New South Wales, Australia (cf. *R. borealis* Hill, 1984 from W Australia – Schizopteridae: Hypselosomatinae) is different (Figs 1, 2). The microsculptural elements of the frenal cuticle are formed in the lateromesal direction by (a) irregularly shaped, rounded polygonal elements provided with numerous microtrichia each, (b) transitional elements with (b1) two (basal and apical) to (b2) one (apical) large microtrichia, or, with (b3) one apical microtrichial projection (no macrotrichia are ever present), and (c) the simple projecting squamiform glabrous elements. The transitional series a-b1-b2-b3-c is distinct, and the microtrichial equipment (a) is identical to that covering most of the body.

The situation described and illustrated for *Rectilamina* sp. cf. *borealis* allows for the following hypotheses (A, B) and suggests necessity of further observations (C).

A. It is probable that the individual projecting squamiform elements of frenae represent hypertrophied and rounded single microtrichia, thus arising from the usual non-specialized microsculptural units.

B. The situation described suggests that there is no clear distinction between microtrichia in the conventional sense (multiple cuticular projections of one hypodermal cell) and acanthae (single cuticular projections of one hypodermal cell), a situation envisaged even by Richards & Richards (1979), the proponents of this structural dichotomy. For other remarks on acanthae see Boudreaux (1979).

C. Other aptational microsculptures should be examined and assessed in anagenetic and cladogenetic contexts; this applies in the Heteroptera not only to other wing-holding devices which may exhibit a microsculpture similar to that of the frenae, but particularly to microsculptures of the evaporatoria associated with openings of adult "metathoracic" scent glands which in the plesiomorphic situations (Enicocephalomorpha, most Dipsocoromorpha) are clearly based on microtrichial preadaptations.

ACKNOWLEDGEMENTS. The study has been supported by a Research Fellowship granted me by the Australian Museum in Sydney as well as by Grant No. 205/95/1138 provided by the Grant Agency of the Czech Republic. My thanks are due to G. Cassis and L. Hill for advice and material, to S. Lindsay for taking SEM photomicrographs, and to anonymous reviewers for comments though I have not followed them in all cases.

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Received August 15, 1997; accepted October 14, 1997