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Cuticular microstructure in some genera of Hydrophilidae (Coleoptera) and their phylogenetic significance

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Abstract

Several species of the genera *Georissus*, *Hydrochus*, *Epimetopus*, *Helophorus*, *Berosus*, *Hemiosus* and *Derallus* have been examined under scanning electronmicroscope. The different types of sculpture and of trichobothria, the distribution of these, the modifications of meso- and metasternum, the femoral vestiture, the microtrichia on the inner face of the elytra, the stridulatory apparatus, the sensilla on the apical segment of the maxillary palpus have been examined for each case, illustrated with SEM photographs and used for a tentative scheme of phylogenetic relationships. Slit-like sunken sensilla have been found on the apical palpite in *Georissus*, *Hydrochus* and *Epimetopus*, and also in *Helophorus (Empleurus)*; this appears to be associated with a non-swimming mode of life. The genera *Georissus* and *Hydrochus*, which have been the subject of discussion as to their clasification, share as well a remarkable type of elytral internal microtrichia. Some evidence of secretion in *Hydrochus* may be related to the crust that covers these beetles in the field. Some considerations on the colouring have been added. Most modified conditions can be related to the acquisition of swimming and to hydrodynamic efficiency.

Key-words: Hydrophilidae; trichobothria; adaptations to aquatic life.

Resumé

Plusieurs espèces des genres *Georissus*, *Hydrochus*, *Epimetopus*, *Helophorus*, *Berosus*, *Hemiosus* et *Derallus* ont eté examinées au microscope electronique à balayage. Les differents types de sculpture et de trichobothries, la distribution de ces dernières, les modifications du méso- et du métasternum, la vestiture fémorale, les microtriches de la face interne de l'élytre, l'appareil stidulatoire, les sensilla du segment apical du palpe maxillaire ont eté examinés pour chaque cas, illustrés avec des photos au microscope electronique et employés pour un schéma provisoire de relations phylogénétiques. Des sensilla enfoncés, en forme de fente, ont eté trouvés sur le palpite apical chez *Georissus*, *Hydrochus* et *Epimetopus*, et aussi chez *Helophorus (Empleurus)*; ceci paraît associé à un mode de vie non aquatique. Les genres *Georissus* et *Hydrochus*, qui ont eté le sujet de discussions à propos de leur classification, partagent aussi un type particulier de microtriches élytraux internes. Une certaine evidence de sécretions chez *Hydrochus* pourrait être en relation avec la croûte que recouvre ces coléoptères dans la nature. Quelques considérations sur la coloration ont été ajoutées. La plupart des conditions modifiées peuvent être correlées avec l'adoption de la natation et avec l'efficacité hydrodynamique.

Mots-clé: Hydrophilidae; trichobothries; adaptations à la vie aquatique.

Resumen

Se han examinado bajo microscopio electrónico de barrido varias especies de los géneros *Georissus*, *Hydrochus*, *Epimetopus*, *Helophorus*, *Berosus*, *Hemiosus* y *Derallus*. Los diferentes tipos de escultura y de tricobotrias, la distribución de estas últimas, las modificaciones del meso- y metasterno, la vestitura femoral, las microtriquias de la cara interna del élitro, el aparato estridulador y los sensilos del segmento apical del palpo maxilar han sido examinados para cada caso, ilustrados con microfotografías y usados para un esquema tentativo de afinidades filogenéticas. Se han encontrado sensilos hundidos, en forma de hendidura, sobre el palpito apical, en *Georissus*, *Hydrochus* y *Epimetopus* así como en *Helophorus (Empleurus)*; esto parece asociado con una modalidad de vida no nadadora. Los géneros *Georissus* e *Hydrochus*, que han sido tema de discusión con respecto a su clasificación, comparten también un tipo especial de microtriquias elitrales internas. Cierta evidencia de secreciones en *Hydrochus* podría relacionarse con la costra que cubre a estos coleópteros en su estado natural. Se han agregado algunas consideraciones sobre la coloración. La mayoría de las condiciones modificadas pueden relacionarse con la adopción de la natación y con la eficiencia hidrodinámica.

Palabras clave: Hydrophilidae; tricobotrias; adaptaciones a la vida acuática.

1. Introduction

The family Hydrophilidae has been based on large free-swimming beetles, which have a smooth, diffusely melanic dorsum, a hydrodynamic shape and legs modified for swimming. The position within the family (or super-family) of several non-aquatic or aquatic but non-swimming beetles has been a subject for long and inconclusive discussion.

In this paper I propose as a working hypothesis that the ancestral Hydrophiloid stock was composed of small, stocky beetles living in damp places, which had prominent pronotal disk and humeral humps, a coarse sculpture with hair-bearing dorsal granules, ten elytral striae plus a basal one between first and second, raised odd-numbered elytral interstriae, a sparse ventral pilosity, decumbent spines on the ventral face of the femora, sturdy tibiae with rows of strong spines and short maxillary palpi, the distal segment of which was ensiform and bore slit-like sunken sensilla at its base. All these characters are found in several other families of Coleoptera and may be considered as primitive. The coloration was possibly as follows: head, pronotal disk and scutellum melanic with a metallic sheen, pronotal sides and elytra testaceous, the latter with melanic spots; sternites melanic; appendages testaceous; apex of distal palpites melanic; perhaps apical melanization of some segments of legs. It is possible, too, that these colours were covered by a crust of mud or similar matter, and that there was some type of secretion that held this in place.

The adoption of aquatic habits by some Hydrophilidae led to an adaptation of the antennae for air captation, the maxillary palpi assuming the functions of the antennae under the water. The sternal pilosity gave rise to the hydrofuge pubescence, so characteristic of the Hydrophilidae. This stage is represented by the *Hydrochus* that live underwater clinging to the vegetation, and by most species of *Helophorus*. Real swimming appears to have arisen twice in the history of the Hydrophilidae, once with the Berosinae and once with the Hydrophilinae. Swimming requires not only the adaptation of the legs (which does not affect their basical structure), but also a remodelling of the dorsum and of the meso- and metasternum; furthermore (and I believe that this had not been pointed out before), the hydrofuge pubescence must extend to the femoral bases, which modifies the shape of the ventral bubble.

This paper is based mainly on the examination under Scanning Electronmicroscope (SEM) of material of the following taxa:

Georyssus laesicollis GERMAR and *G. crenulatus* (ROSSI, 1794)

Hydrochus LEACH: two undetermined species from South America

Epimetopus trogoides (SHARP, 1875)

Helophorus (Empleurus) porculus BEDEL, 1881

Helophorus (Meghelophorus) aquaticus (L., 1758)

Helophorus (Atracthelophorus) brevipalpis BEDEL, 1881 and *H. (A.) arvernicus* MULSANT, 1846

Hemiosus mulvianus ORCHYMONT, 1940

Berosus zimmermanni KNISCH, 1921, *B. auriceps* BOHEMAN, 1859, *B. patruelis* BERG, 1887, *B. pedregalensis* JENSEN-HAARUP, 1910, *B. batesi* OLIVA in litt., *B. coptogonus* JENSEN-HAARUP, 1910, *B. obscurifrons* KNISCH, 1921, *B. truncatipennis* CASTELNAU, 1840.

Derallus angustus SHARP, 1882, *D. ambitus* ORCHYMONT, 1940, *D. altus* (LECONTE, 1855)

Some observations made under light microscope, and sometimes concerning taxa not examined under SEM, have been added to complete interpretation.

2. Patterns of colouring

In most genera of Hydrophilidae there is a considerable intraspecific variation of colour. To a certain degree, this is due simply to the age of the specimens. Newly emerged imagines are poorly sclerotized and do not show melanine deposition (teneral specimens). In a latter stage, non-pigmented areas darken with the tanning of cuticular protein and melanine is deposited in its less polymerized form (reddish). A screen of melanine is necessary to bring out the metallic sheen. Mature imagines are, according to genus or to species, deep black, greenish black, brown with black spots (and often with green metallic sheen) or bright metallic green or bronze. Aged specimens are frequently very dark, so that testaceous areas appear almost black, and metallic-shining ones are darkly green. Finally, I have observed a tendency to earlier or more intense darkening of those parts where the cuticle is thickened; for instance, sternal carinae are often darker than the rest of the sternite in subteneral specimens. It is sometimes difficult to determine how far this is due to melanine deposition rather than to a more energetic tanning.

2.1. The Helophorinae

Within the genus *Helophorus*, the species of the subgenus *Empleurus* (not aquatic) differ from the rest in not having any metallic sheen. The dorsum of head, the pronotal disk and several spots on the elytra are black (fig.1); the rest of the dorsum is testaceous. In some specimens of *H.(E.) rufipes* the elytral spots form two definite transversal bands (fig.1) (cf. Epimetopinae, 2.3).

One curious species, *Helophorus (Cyphelophorus) tuberculatus*, has the elytra deep black. This species, associated with peat bogs, is not aquatic although it has a row of hairs (swimming hairs?) on the dorsal face of meso- and metatarsi.

All species of the subgenera *Atracthelophorus* and *Meghelophorus* that have been examined have a metallic sheen on the head, the pronotal disk, the scutellum and (frequently) a narrow basal band on the elytra; these parts are deeply melanic in mature specimens. The pronotal edges and the elytra are testaceous; the latter bear small black spots, usually without any sheen. The legs are usually testaceous, with apical darkening of the femora and of the distal segment of the tarsi. The maxillary palpi are testaceous, in some cases with a small apical darkening.

I have considered the pattern with metallic sheen and small elytral spots as the primitive one, for, as it will be seen further on, it is found in other groups that have specialized along different lines.

2.2. The Berosinae

It is interesting that several species of the Neotropical genus *Hemiosus* retain the colour pattern found in most *Helophorus*, save that the basal, pubescent part of the femora is usually deeply melanic (fig 2). In many species of *Hemiosus* the metallic area of the pronotum is reduced, often divided by a medial testaceous line; sometimes the metallic sheen is absent. When the pronotum is extensively melanic (and metallic-shining), the elytral spots are often much expanded and with some metallic sheen, or at least an iridescence showing at the bottom of the punctures.

Many species of *Berosus* have the same colour pattern as the *Hemiosus* with small melanic spots. The well-defined elytral spots have a shape-breaking effect in species that live in clear water over sandy or pebbly bottom. A tendency to lose the metallic sheen, and eventually the melanization, of various parts of the dorsum can be observed in several groups of species. In most species-complexes (as defined by the male genitalia, cf. OLIVA, 1989) there are at least some species without any metallic sheen, and with melanine restricted to the posterior part of the frons, a pair of small paramedial spots on the pronotal disk and small elytral spots (fig. 3). At least some species with this colouring are associated with clear water on muddy bottom (personal observation). Intermediate cases may show a dissapearance of the metallic sheen on the pronotum (more rarely on the scutellum as well), while the head remains entirely melanic; in two species, the clypeus is testaceous, the frons melanic with a metallic sheen. In a few cases loss of metallic sheen goes with diffuse melanization of the dorsum. The urosternites are melanic in most species; the meso- and metasternum may be melanic or testaceous. The femora may be melanic on the pubescent part as in *Hemiosus* (the most frequent case), or entirely testaceous, or testaceous with a diffuse basal melanization. In at least two cases, deply melanic tarsi and tibial apices are added to femoral melanization. Maxillary palpi are testaceous with an apical darkening; in a few species this dark area is consistently more extense than in allied species (v.g. *B. coptogonus* as compared to allied *B. pallipes* BRULLE, 1835).

The genera *Derallus*, *Regimbartia* and *Allocotocerus* (= *Globaria* auctorum), which probably belong into a separate tribe, have a deeply and extensively melanic dorsum (fig. 4), often whith some metallic iridescence. In subteneral specimens it can sometimes be seen that the head and scutellum have a metallic sheen, while the pronotum and the elytra are a very dark brown. This was observed, indeed, in the typical series of *Derallus perpunctatus* Oliva, 1983, an Amazonian species that presents several primitive traits. This species, with its convex pronotum, prominent humeral humps and coarse dorsal sculpture, ressembles a minute *Berosus*. It can be supposed that a line of very small beetles, evolved from a *Hemiosus*-like stock with spotted elytra, acquired a uniform blackish colouring because this was more adaptative that "shape-breaking". This could be explained by the small size and a preference for water with floating débris, in at least some *Derallus* (personal observation). However, too little is known of species living in tropical or subtropical latitudes.

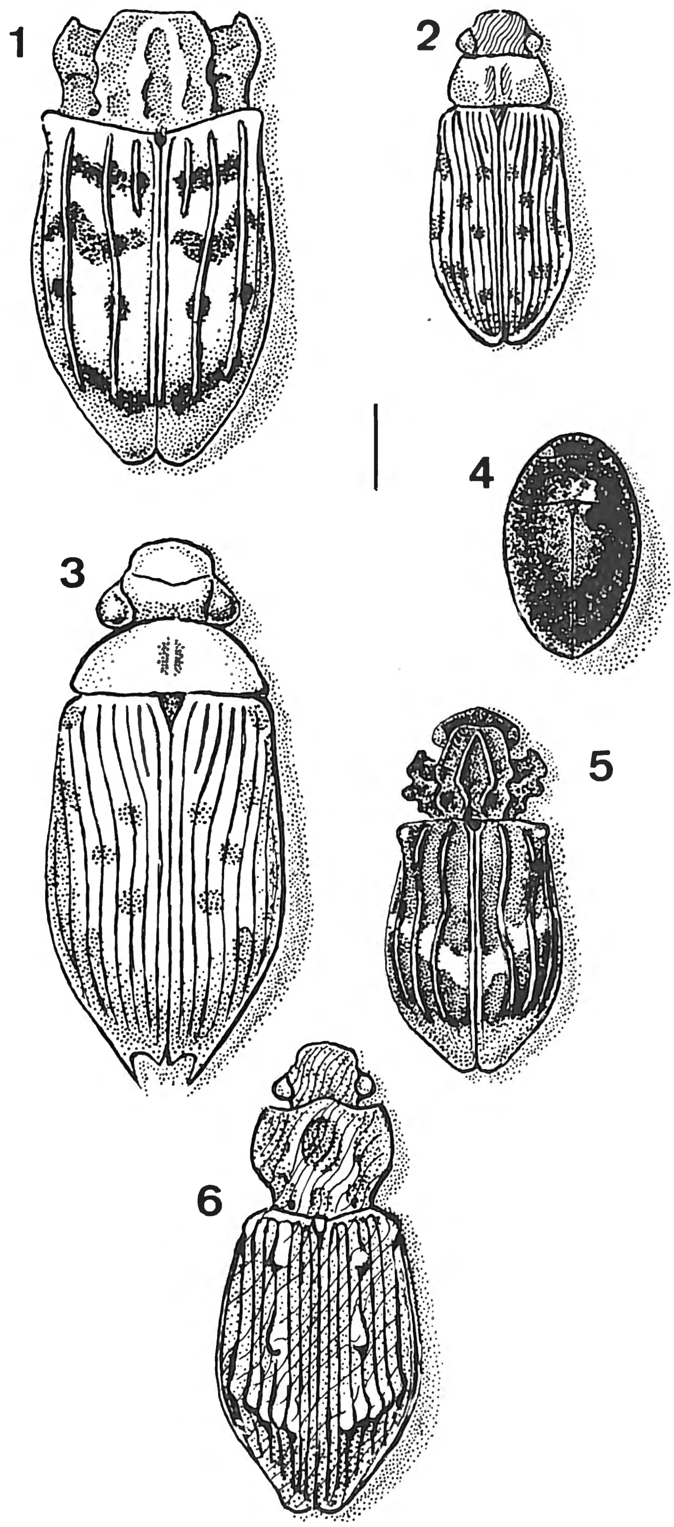


Plate I:
Fig. 1-6. – habitus views (schematic). – Fig. 1: *Helophorus (Empleurus) rufipes*. – Fig. 2: *Hemiosus dejeani*. – Fig. 3: *Berosus decolor*. – Fig. 4: *Derallus ambitus*. – Fig. 5: *Epimetopus trogoides* (very extensively melanic specimen). – Fig. 6: *Hydrochus scabratus*

2.3. *The Epimetopinae*

Beetles of this subfamily are usually covered with a muddy crust, which masks their colour. I have not so far been able to examine any of the Afrotropical *Eumetopus*, but among the Neotropical *Epimetopus* the prevailing pattern is practically the same as in the *Helophorus (Empleurus)* (see fig. 1, 5), save that the elytral spots extend into bands. Some minute species appear to have no bands, but I have seen only subteneral material. One species has a diffuse melanization of the whole dorsum.

2.4. *The genus* Georissus

These small to minute beetles usually show a deep melanization of the whole dorsum; some tropical species from the Old World have bright metallic colours. Practically all the known species are found covered by a layer of mud or sand; at least one species covers itself with grains of sand actively (BAMEUL, 1991). It is clear that colour cannot play an important role for this genus.

2.5. *The genus* Hydrochus

Covered, when living, with a crust of vegetable matter, these aquatic but non-swimming beetles have often been described as differing greatly from the usual Hydrophilidae pattern because of their bright metallic colours. Actually, in most species the metallic sheen is less strong on the elytra, which in several cases show small but distinct melanic spots following to a certain degree the pattern in *Helophorus* or in *Hemiosus*. A few species are diffusely dark, with a metallic iridiscence that is often absent from the elytra, more rarely from the pronotum as well. The small South-American species *Hydrochus richteri* BRUCH, 1915 (which is much broader than the rest, to the extent of approaching the shape of the more elongate Berosinae) has nearly the same colour pattern as a *Hemiosus*: head and scutellum melanic with metallic sheen, pronotum and elytra testaceous. In most species of *Hydrochus* the legs are testaceous with apical darkening of the femora and of the distal segment of the tarsi, as in most *Helophorus*.

3. The pronotal relief

A raised pronotal disk with depressions, and pronotal sides expanded to some degree, are found in several families of Coleoptera. This has been here assumed to be the primitive condition for the Hydrophiloid stock. In most species of Hydrophilidae the pronotum is either flat or smoothly convex, probably as an adaptation to aquatic life. A similar tendency is found in several (nonaquatic) families that include some groups with the primitive type of pronotal relief, so it is to be presumed that there are several types of selective pressure in favour of a smooth pronotum. However, a few riparian genera of Hydrophilidae show a remarkable developement of the pronotal disk.

3.1. *The primitive relief*

It has been taken as a working hypothesis that the *Helophorus (Empleurus)* have kept the ancestral relief. *Helophorus (Empleurus) porculus* has been taken as material for SEM observation and as a basis for conjecture on the evolution of the Hydrophilid stock (fig. 7). In this species the disk is moderately raised, marked by three longitudinal grooves (one medial, two submedial) and limited by a pair of submarginal grooves. The sides of the pronotum are only weakly expanded, and bear a pair of marginal grooves. At the base of each submarginal groove there is a deep roundish pit, also a primitive feature to be found in other families (fig.7). The rhomboidal shape of the submedial grooves should be compared with the relief in *Epimetopus*. The surfaces between grooves are covered with granules that bear hairs of moderate length (see part 4); the grooves bear small, well-spaced granules, which do not appear to bear hairs. Observation of the species *H.(E.) rufipes* under light microscope shows that the pronotal grooves are irregularly widened, forming rather chains of roundish depressions (fig. 1); it is interesting to compare this with *Hydrochus scabratus* (fig. 6).

3.2. *Adaptations leading to swimming forms*

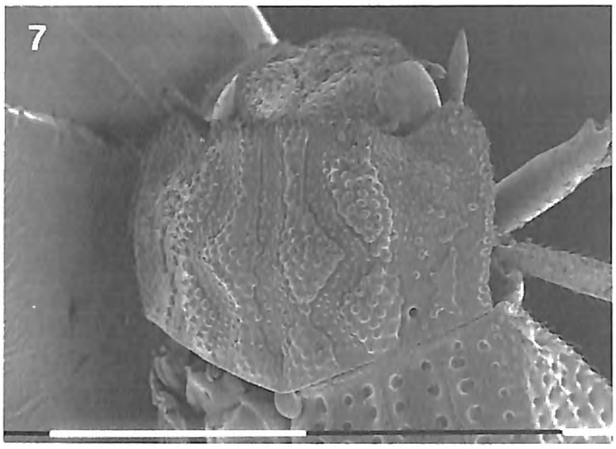
In most species of *Helophorus* the pronotum is only weakly convex, without a distinct raising of the disk; the rhomboidal shape of the submedial groove is not always marked (fig. 15). The roundish pits at the base of the submarginal grooves are usually evident. Trichobothria are present at the sides of the pronotum (fig. 16).

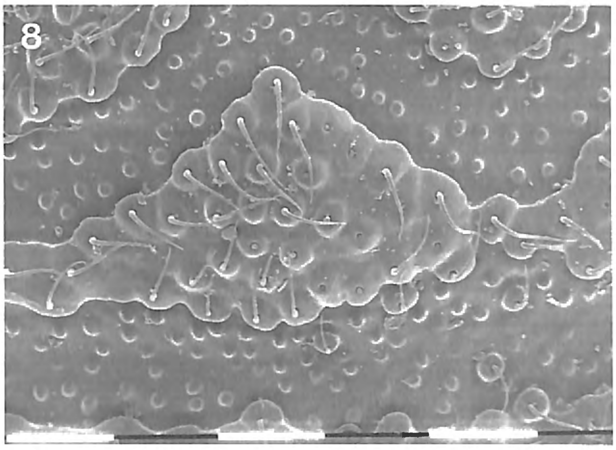
In all the Berosinae, the pronotum is strongly but smoothly convex (fig. 2, 3, 71), with a sculpture of punctures (see IV), which usually leaves a narrow, unpunctured medial line. Trichobothria are disposed in a pair of oblique, submarginal rows; because of this, I suggest that the pronotum of the Berosinae developes at the expense of parts that in the Helophorine go to make up the sides.

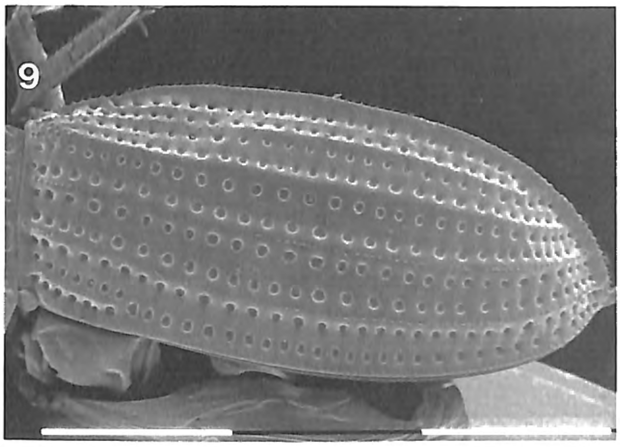
3.3. *Adaptations to riparian life*

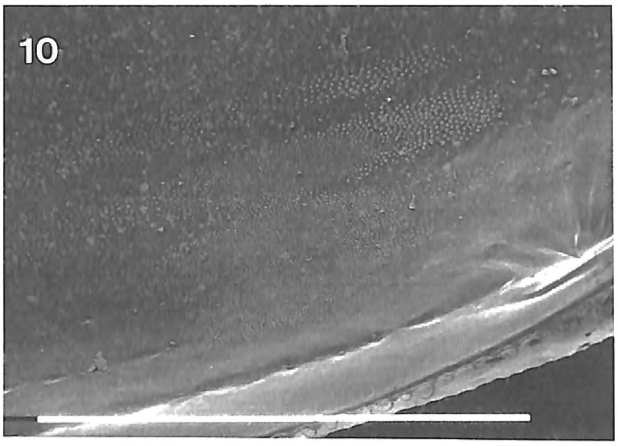
Very little is known about the habits of *Georissus* and of the Epimetopinae, but the sturdy legs with rows of strong tibial spines and the character of the dorsum suggest burrowing; the european *G. crenulatus* is found on sandy or clayish soil near water (HANSEN, 1987). The common feature between the two groups of beetles mentioned is a developement of the pronotal disk that overshadows the head (fig. 79, 95, 101). In *Georissus* the pronotal relief is quite modified with respect to the primitive type, and varies greatly from one species to another (fig. 95, 101; cf. *Hydrochus*, fig. 103).

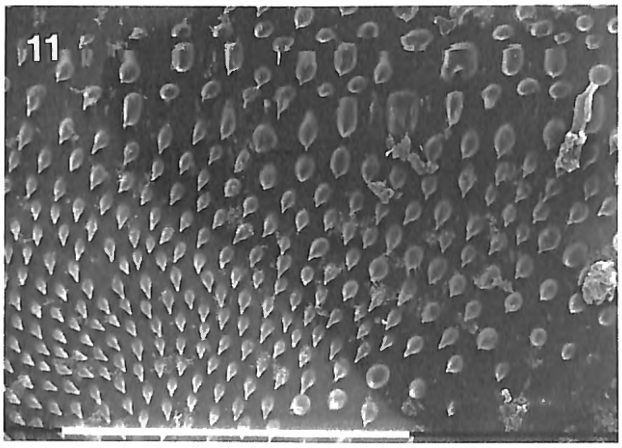
The disk is strongly produced forwards in the Epimetopinae. The Neotropical species *Epimetopus trogoides* has been used for this study (fig. 79). The raised, produced disk bears a rhomboidal ridge

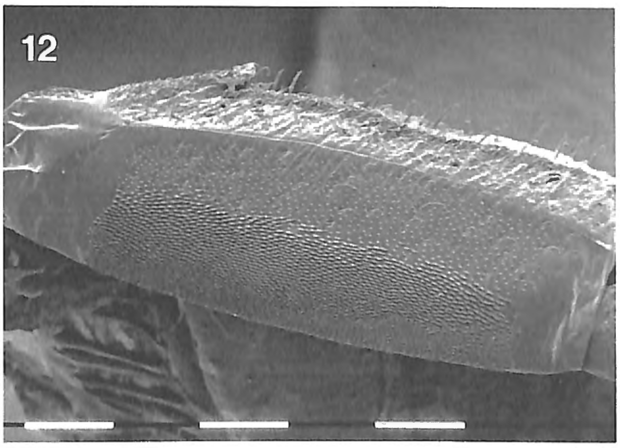


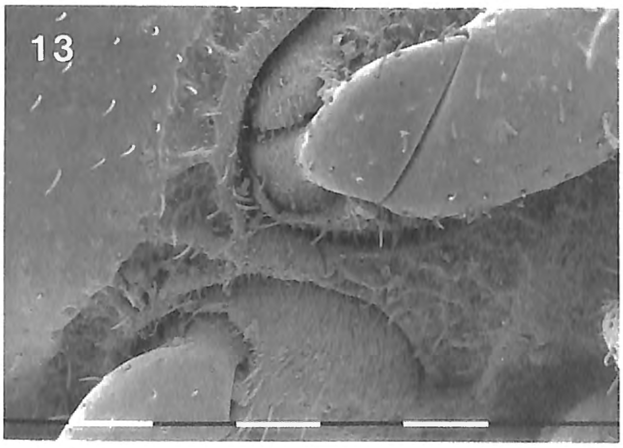












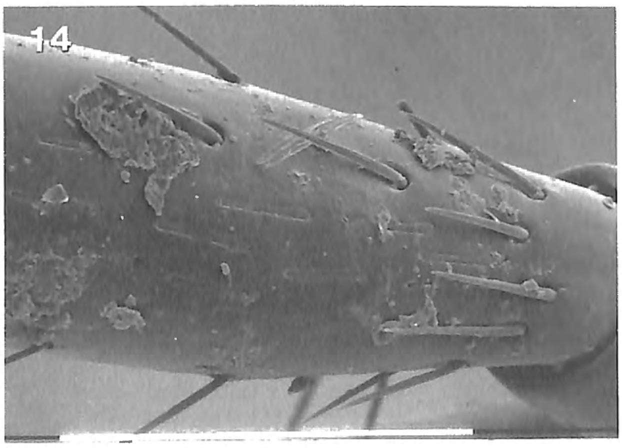
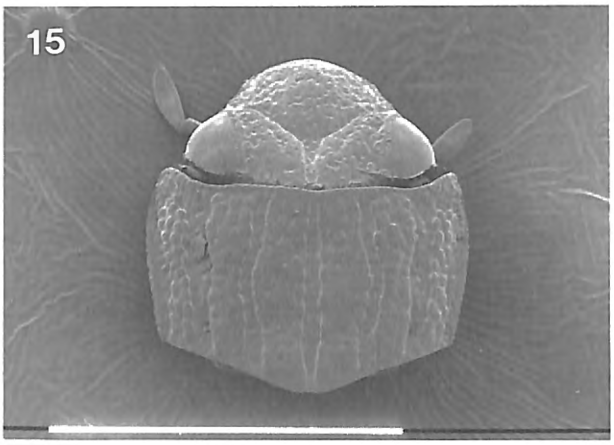
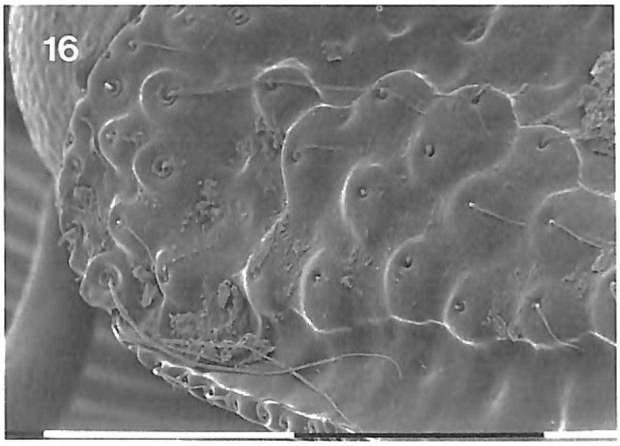
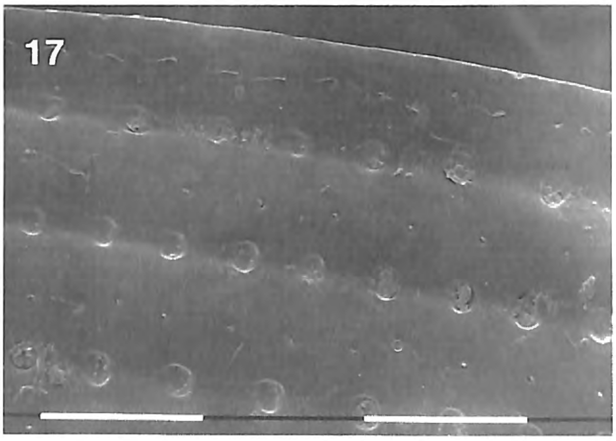
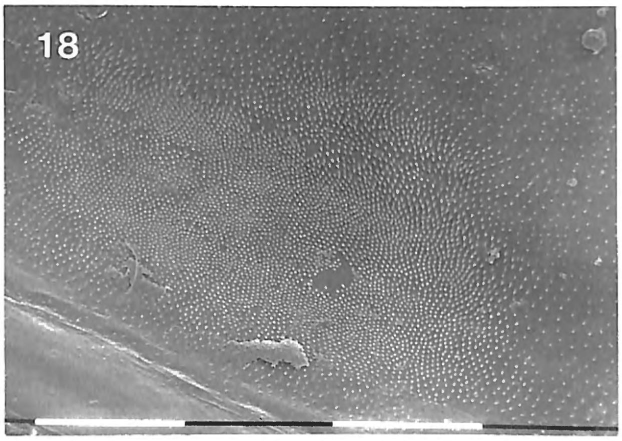


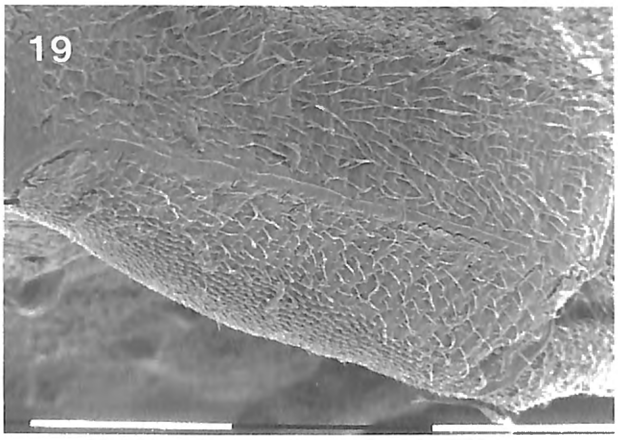
Plate II:
Fig. 7-14: *Helophorus (Empleurus) porculus.* – Fig.7: pronotum, 44.4 X. – Fig. 8: detail of submedial groove, 178 X. – Fig. 9: elytron, outer face, 32.8 X. – Fig.10: elytron, inner face, 85 X. – Fig. 11: detail of microtrichia, 600 X. – Fig. 12: laterosternite of first apparent urite, 150 X. – Fig. 13: mesosternal process and intercoxal bridge formed in part by the mesosternum, in part by the metasternum, 150 X. – Fig. 14: apical segment of maxillary palpus, with sunken sensilla, 710 X.

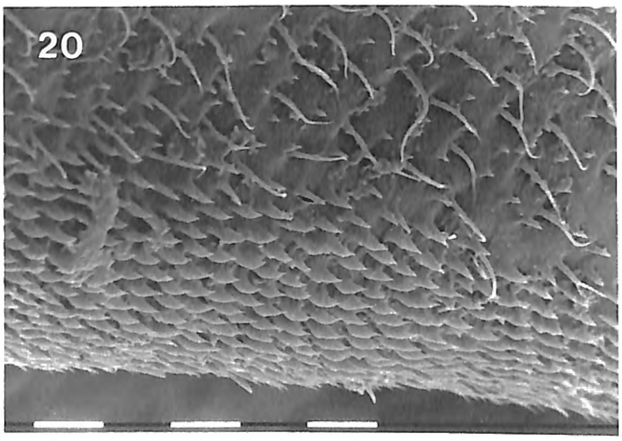


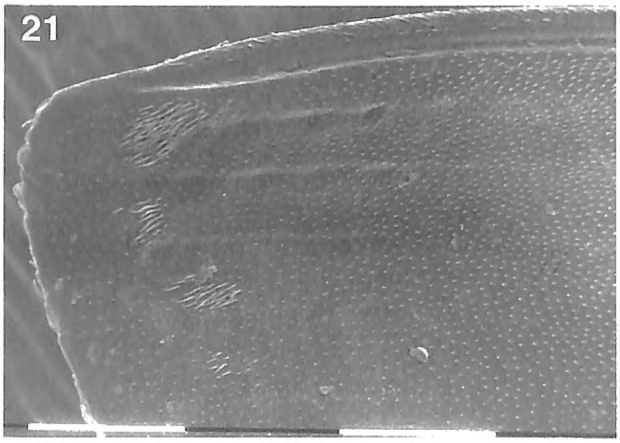












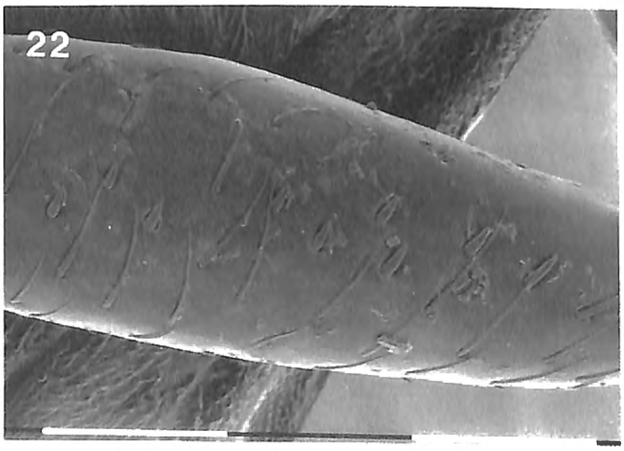


Plate III:
Fig. 15-22: *Helophorus (Atracthelophorus) brevitarsis*. – Fig. 15: head and pronotum, 63 X. – Fig. 16: anterolateral angle of pronotum, 442 X. – Fig.17: elytron, outer face, 281 X. – Fig. 18: elytron, inner face, 263 X. – Fig. 19: laterosternite of first apparent urite, 356 X. – Fig. 20: detail, 1,200 X. – Fig. 21: elytron, inner face, apical microtrichia, 274 X. – Fig. 22: metafemur, ventral face with spines and long hairs, 326 X.

delimitating a medial depression. Another ridge delimitates the disk, sharply in front, less so in the posterior part. The depressions between the ridges bear granules with sunken sensilla (see 4). The sides are expanded. The shape of the rhomboidal ridge should be compared with the submedial groove of *Helophorus (Empleurus) porculus* and the produced disk with that of *H.(E.) rufipes* BOSCH (fig.1).

3.4. The genus Hydrochus

Most species have a very elongate body shape, with a moderately convex pronotum, the disk of which is weakly – or hardly – raised (fig. 103). In the Neartic species *H. scabratus* MULSANT, however, a broad and angular shape is accompanied by a moderately raised pronotal disk, on which there are two medial depressions (fig. 6; cf. *Helophorus (Empleurus) rufipes* (fig.1). The tendency to a flat pronotum in *Hydrochus* appears to culminate in the Neotropical *H. metallipes* KNISCH, in which the flat pronotum bears a pair of very small depressions.

4. Dorsal sculpture and sensilla

The dorsal sculpture is basically composed of three kinds of elements: 1) hairs borne on granules or inserted in punctures; 2) trichobothria; 3) micropores, which have not been discussed, as they do not appear to be associated with sensory structures.

4.1. The riparian genera

In the riparian genera *Georissus* and *Epimetopus* the hairs are borne on granules (fig. 82, 98), save on the elytral striae that are sculptured, as in all Hydrophilidae, with punctures that bear each a short, excentrically inserted hair (fig. 96, 97). In *Georissus* the hairs are short, thick, with very small, cribate basal plates; from their appearance they could be either sensorial or secretory (fig. 98). At least one species of *Georissus* has been observed sticking grains of sand moistened with buccal secretions on to its dorsum (BAMEUL, 1991); all the species are usually found covered with a crust. Hairs on granules probably rise clear of this crust.

In *Epimetopus* the granules have a deep hollow, inside which are partially sunken the short, conical hairs with a large basal torus (fig. 82); it seems evident that these are sensilla. As in *Georissus*, they appear to be outside the crust. On the odd-numbered elytral interstriae, the granules form ridges (fig. 81). Isolate granules are found between strial punctures (fig. 83).

In both riparian genera, sunken punctures are found on the internal margin of eyes, anterior margin of clypeus and on different areas of the pronotum (fig. 80). It is not clear how far these correspond to the trichobothria in other genera (described further on), since the energetic cleaning techniques used to remove the crust for observation also remove hairs.

4.2. The condition in aquatic Hydrophilidae

On the other genera of Hydrophilidae examined, trichobothria with a large basal torus have been found on the inner margin of eyes (fig. 23), on marginal or submarginal areas of the pronotum and on the odd-numbered elytral interstriae, mixed with ordinary hairs (fig. 29, 65).

In the Helophorinae, the head and pronotum bear granules (flattened in many species) with curved hairs of moderate length that do not appear to have any basal structure; similar hairs are found on elytral interstriae, but inserted into punctures (fig. 8, 16, 17).

In the Berosinae, only punctures are found on the dorsum. The pronotal trichobothria are set, not on the anterolateral angle, but on an oblique submarginal line behind each eye. Some of the "ordinary hairs" have basal structures that suggest a sensorial function.

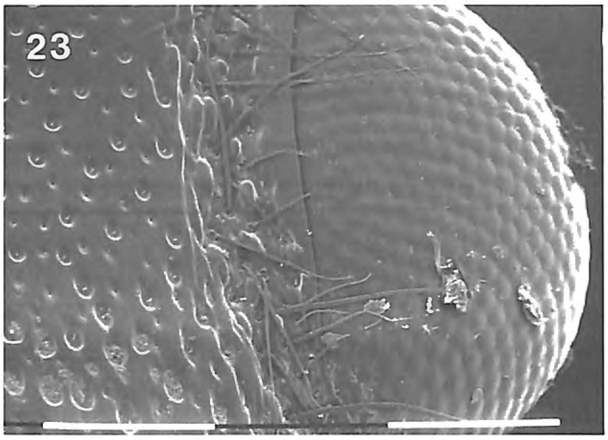
In *Hemiosus mulvianus* the elytral hairs ressemble those of the Helophorinae (fig. 29). On the head and the pronotum the punctures bear short thick hairs with a small fenestrate basal plate (fig. 25). The trichobothria have a thick basal torus and a basal plate with two concentrical rows of fenestrae (fig. 26). Between the ommatidia there are sensilla like those of the ordinary punctures (fig. 24).

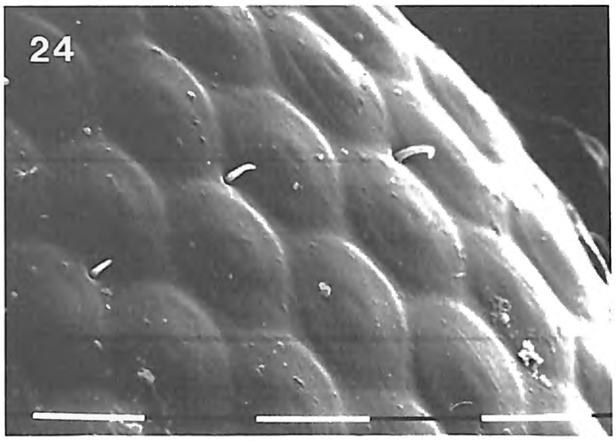
Several species of *Berosus* have been examined, to show a good diversity of sculpture, which in this genus varies greatly from one species to another. In *B. zimmermanni* (fig. 34, 35), which has a hypertrophied sculpture, the basal torus of the trichobothria is thick and prominent. Some plain punctures with "helophorine" hairs are interspersed with the hypertrophied pronotal punctures that bear short, slightly excentric clavate sensilla; a marginal row of "helophorine" hairs is present (fig. 35). In the smooth-sculptured *B. truncatipennis* the punctures are quite modified: there is a short thick sensillum inserted into a depression of a wide, concave plate (almost funnel-shaped), around which there appears to be a narrow fenestrate structure (fig.56). Some punctures on all the elytral interstriae bear decumbent spine-shaped hairs (fig. 57, 58). The pronotal ground is distinctly reticulate. Although in the Staphylinidae microreticulation is considered a primitive character (DRUGMAND, personal communication), I think that in *Berosus* it is a secondary acquisition, since it has not been observed in less specialized species (fig. 55).

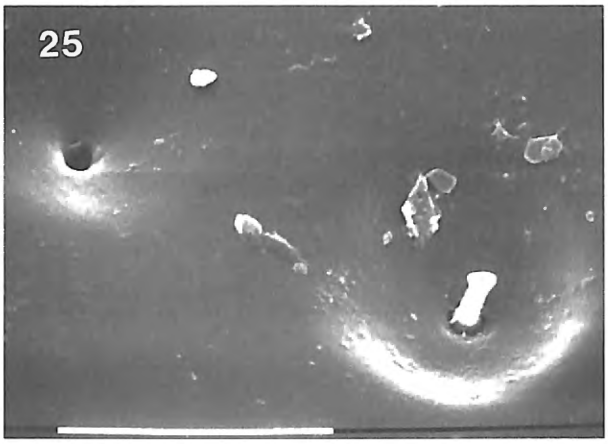
A remarkable modification of the strial and some of the pronotal punctures was found in the genus *Derallus*. There is a short spatulate sensillum, flanked by one, two or even three accessory punctures, according to species (fig. 65, 66, 72, 77).

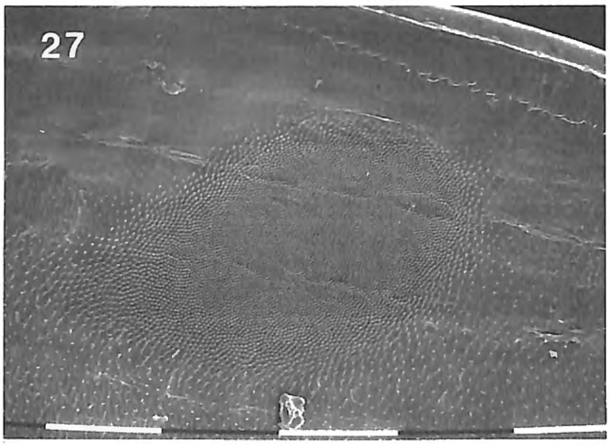
4.3. The genus Hydrochus

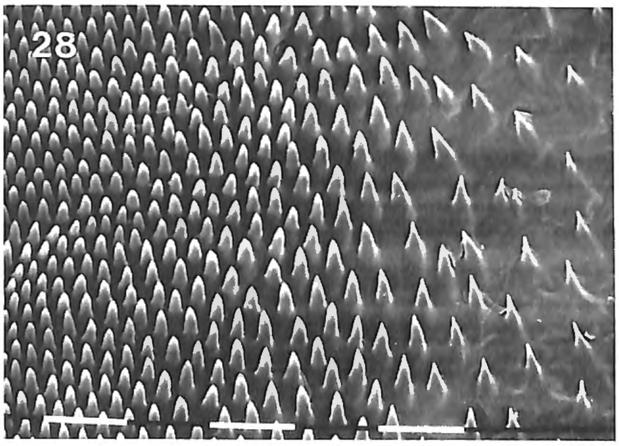
Most species of *Hydrochus* have a remarkably coarse sculpture. In some species, as the Neartic *H. squamifer* LECONTE, the head and pronotum are covered with granules; it is fairly safe to assume that they correspond

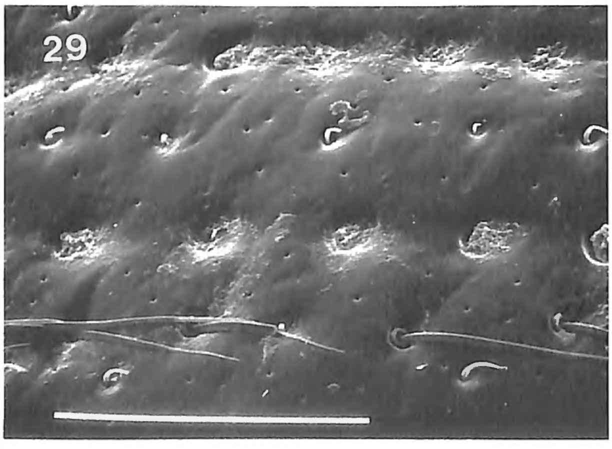












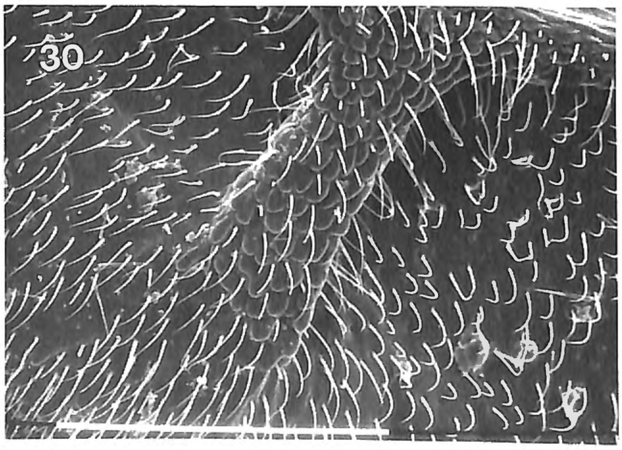
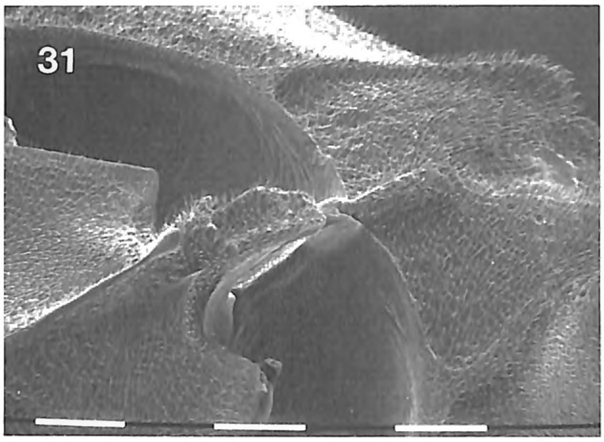
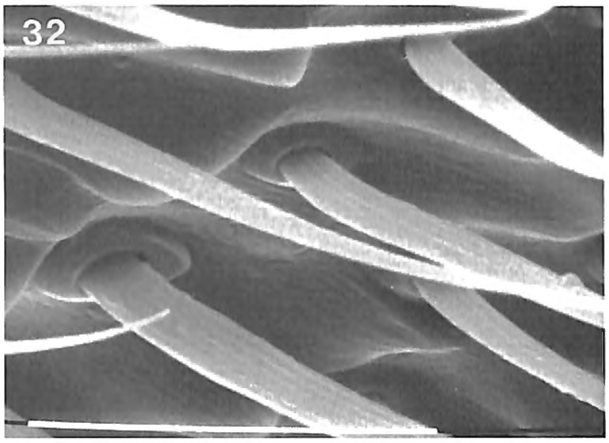
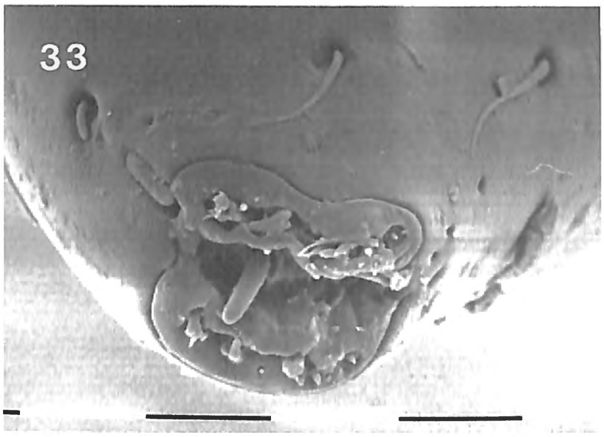
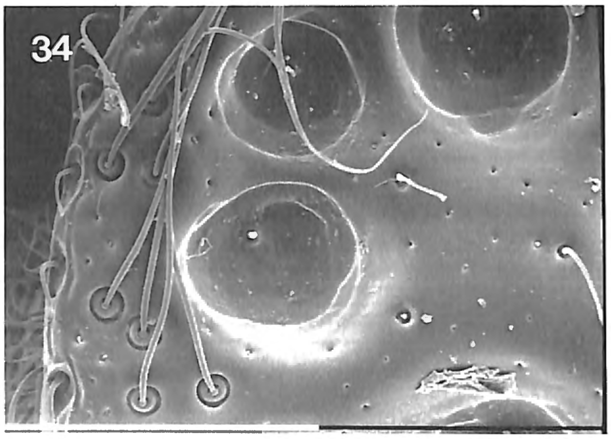


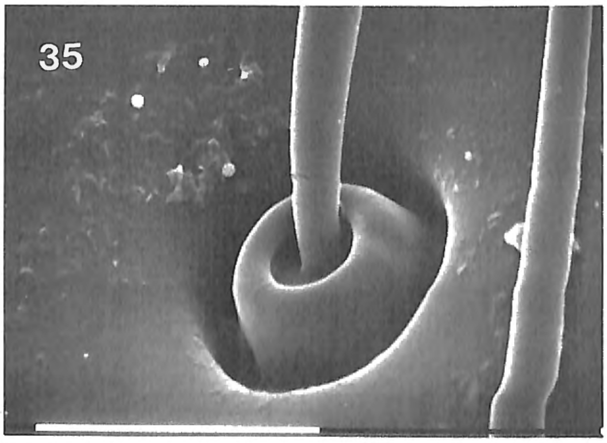
Plate IV:
Fig. 23-30: *Hemiosus mulvianus*. – Fig. 23: inner margin of eye, with trichobothria, 312 X. – Fig. 24: Sensilla between ommatidia, 2,020 X. – Fig. 25: punctures on frons, 5,000 X. – Fig. 26: trichobothria near eye, with torus and fenestrate basal plate, 4,400 X. – Fig. 27: Elytron, inner face with plectron, 212 X. – Fig. 28: Detail of plectron, 1,490 X. – Fig. 29: elytron, outer face, 573 X (notice trichobothria on odd-numbered interstriae only). – Fig. 30: lateral carina of first urosternite, 600 X.

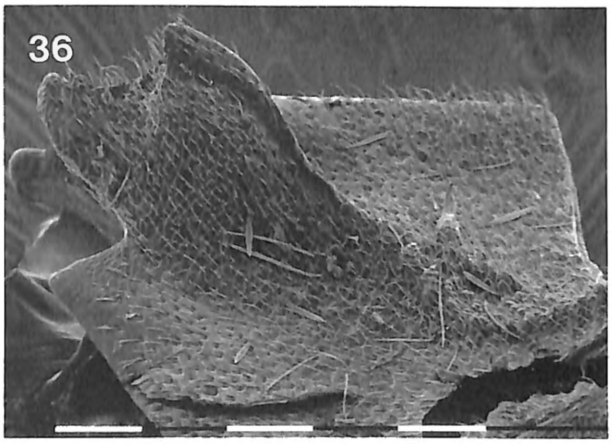


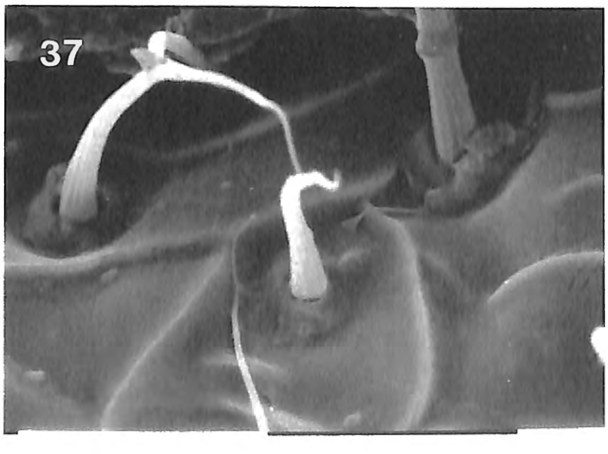












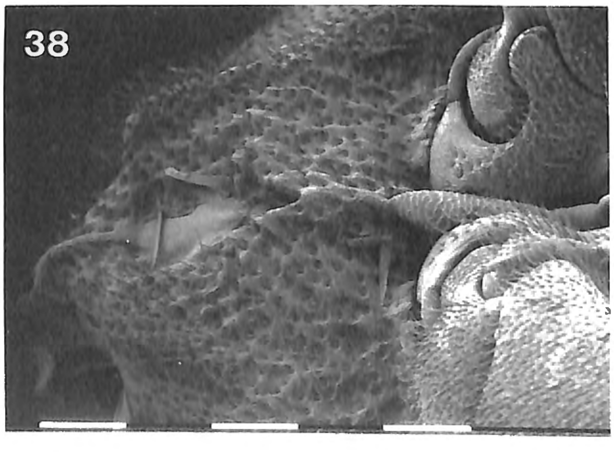
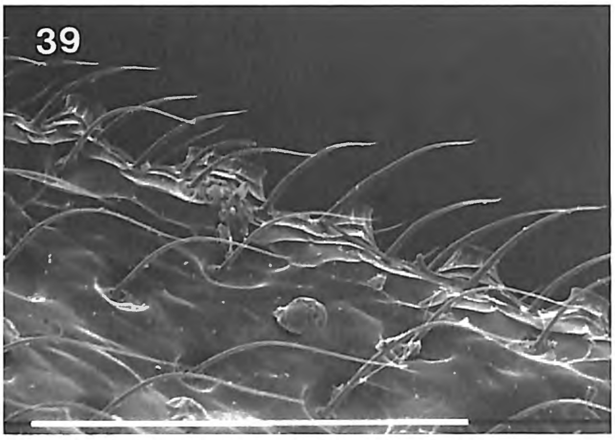
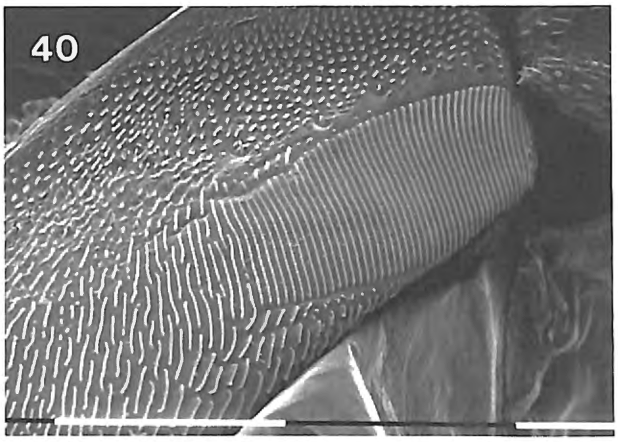
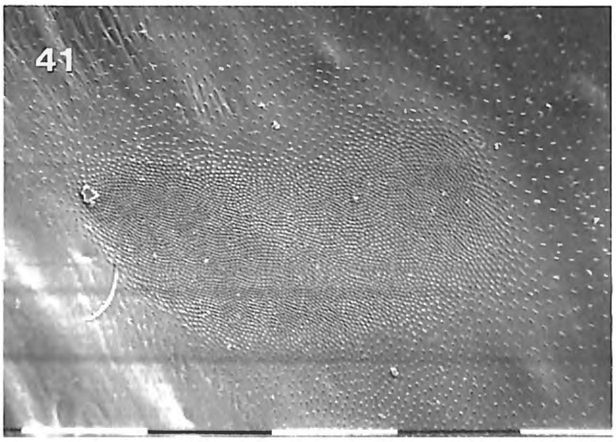
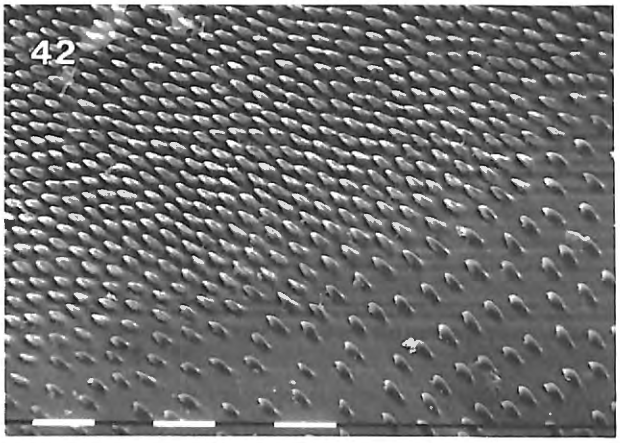


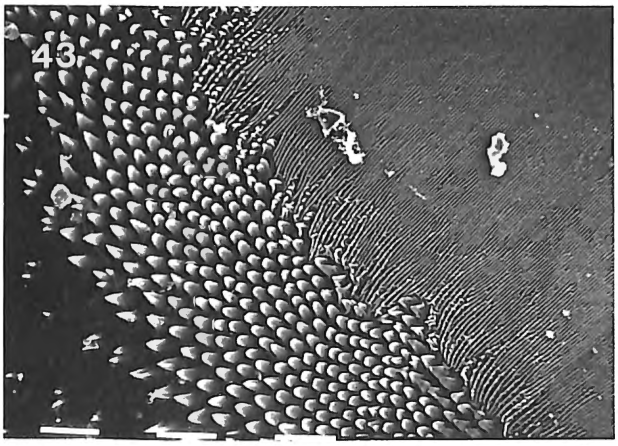
Plate V:
Fig. 31-33. *Hemiosus mulvianus*. – Fig. 31: mesosternal process, 163 X. – Fig. 32: detail of trichobothria, 7,400 X. – Fig. 33: maxillary palpus with apical complex of sensilla, 2,300 X. – Fig. 34-38: *Berosus zimmermanni*. – Fig. 34: pronotum: lateral edge, trichobothria, two types of punctures and micropores, 573 X. – Fig. 35: trichobothria near eye, 5,000 X. – Fig. 36: mesosternal process, 150 X. – Fig. 37: detail of trichobothria, 4,400 X. – Fig. 38: metasternal process, 150 X.

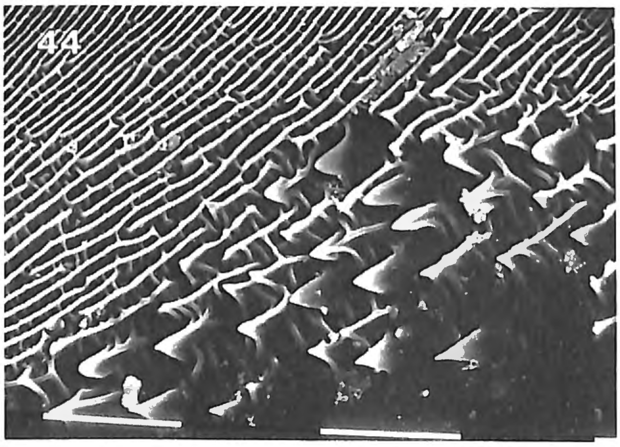


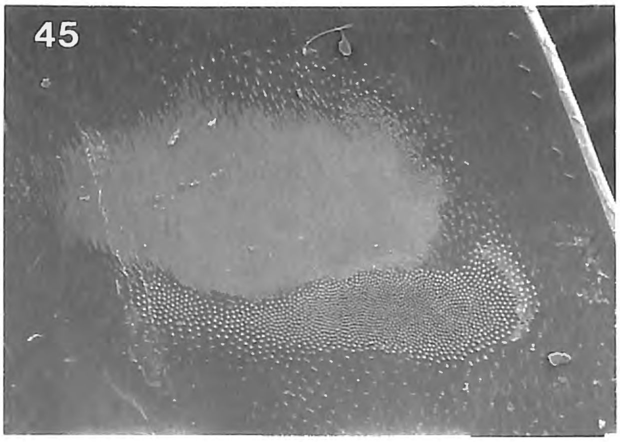












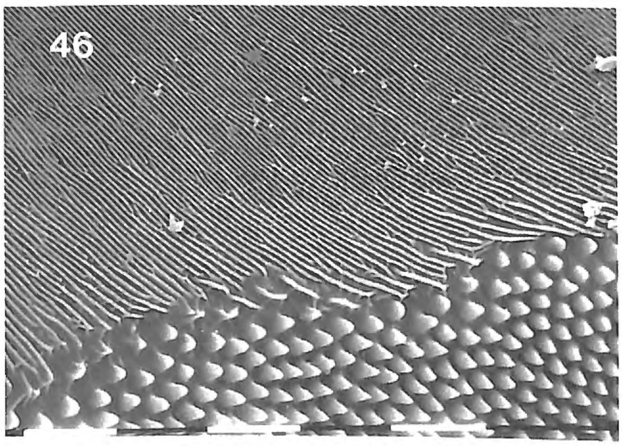


Plate VI:
Fig. 39-42: *B. zimmermanni.* – Fig. 39: lateral edge of urosternite showing crenulation, 775 X. – Fig. 40: pars stridens on first urite, 406 X. – Fig. 41: Elytron, inner face with plectron, 221 X. – Fig. 42: detail, 1,050 X. – Fig. 43-44: *Berosus patruelis*: elytron, inner face, details of plectron formed by elements of two types, 1,050 X and 2,500 X. – Fig. 45-46: *B. batesi.* – Fig. 45: plectron formed of two parts, 231 X. – Fig. 46: detail, 1, 550 X.

with those observed in the Helophorinae. In the Neotropical species observed under SEM there are no granules (fig.103). Curved, moderately long hairs, set in small plain punctures, are interspersed with large, very deep punctures with irregular concentrical ridges on their walls, into which inserts a short, thick, acuminate hair (fig. 104, 106, 107). The long hairs appear to be hollow, from what can be seen of the broken ones (fig. 106). The elytral striae bear deep punctures, the interstriae "helophorine" ones (in contrast to the findings in the Berosinae) (fig. 108). The trichobothria are disposed in much the same pattern as in the Berosinae and have a basal torus raised into a short, thin-walled cylinder (fig.105).

5. Microtrichia on the internal face of the elytra

The inner surface of the elytron is covered with microtrichia, which are small, conical and sparse unless otherwise specified.

5.1. The Helophorinae

The microtrichia thicken into an irregular external patch in which the elements are larger than on the rest of the elytron (fig. 10, 11, 18). The position of this patch corresponds approximately with that of the plectron of the stridulatory apparatus in other subfamilies of Hydrophilidae. In these cases, the pars stridens is formed by a "file" on the laterosternite of the third (first apparent) urite (fig. 40). In the Helophorine that have been examined there is a patch of very regular thick microtrichia on the laterosternite, but not a distinct file (fig. 12, 19, 20). So far as I know, no stridulation has been recorded in this subfamily.

Four apical patches of hair-shaped microtrichia have been found in *H. brevitarsis* in addition to the lateral patch described (fig. 21).

5.2. The Berosinae

In this subfamily, the well-defined external patch acts as a plectron, as explained. In *Hemiosus mulvianus* it is oblong in shape, composed of dense subconical microtrichia (fig. 27, 28). In several species of *Berosus* two distinct patches, with different size and density of elements, are found. An extreme case of this are the closely allied species *B. pedregalensis*, *B. patruelis* and *B. batesi*. In these, the anterior part of the plectron is formed of fine ridges (therefore appearing iridescent under light microscope); the posterior part is formed of very thick and dense subconical microtrichia (fig. 43, 44, 45, 46, 47, 49, 50).

In several species of *Derallus* a roundish plectron, composed of dense subconical microtrichia, has been observed (fig. 73, 74).

5.3. The Epimetopinae

In *Epimetopus trogoides* there is a roundish plectron (fig. 84), formed by oblong elements. Some rows of fine cones near the edge (fig. 85) suggest that those elements are formed by the coalescence of small microtrichia of the ordinary type. A band of dense, blade-shaped microtrichia on the epipleuron of the first urite represents the pars stridens (fig. 86).

In front of the plectron there is a sharply raised, curved ridge, and in front of the presumed pars stridens an abruptly raised process; this appears to be some sort of elytral locking structure.

5.4. Hydrochus *and* Georissus

These genera have in common a remarkable type of microtrichia (fig. 100, 102, 111, 112), and a ridge near the outer elytral margin (fig. 99, 102, 109, 110), which is probably an elytral locking structure (HANSEN, 1992). In *Georissus* the microtrichia are rather like row of cones; some rows of separate cones appear at the edge of the patch, which is apical. The ridge is quite long. In *Hydrochus* (fig. 111, 112) the microtrichia are a little more modified and they appear on a larger area; the ridge is short, but very strongly raised, with the free edge turned outwards (fig. 110). The double row of pits (fig. 111, 112), should be remarked; no similar structure has been found in any other genus studied here. They do not appear to go through the elytron, and their function remains unknown.

6. The shape of meso- and metasternum

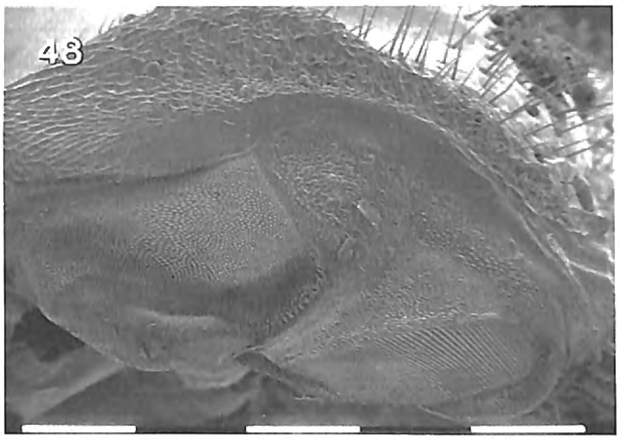
6.1. The Helophorinae

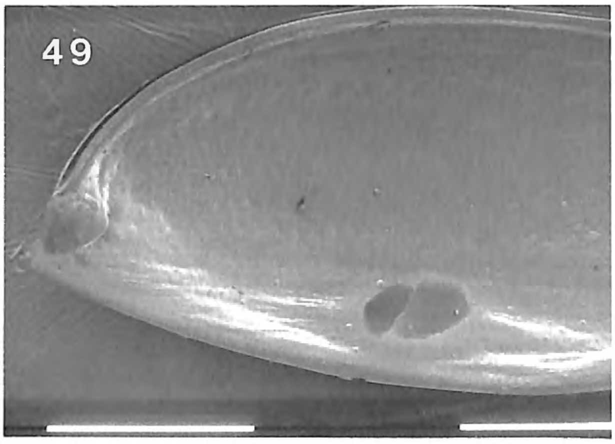
The mesosternum has a weak crescent-shaped process, with trichobothria on the concave edge and behind on the intercoxal bridge (fig. 13). The metasternum is quite smooth and flat, without any process.

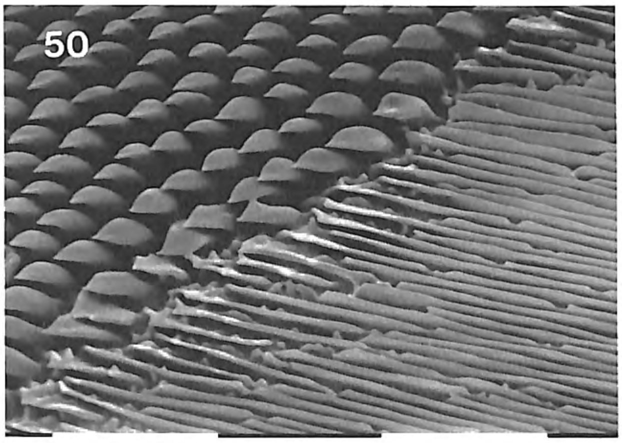
6.2. The Berosinae

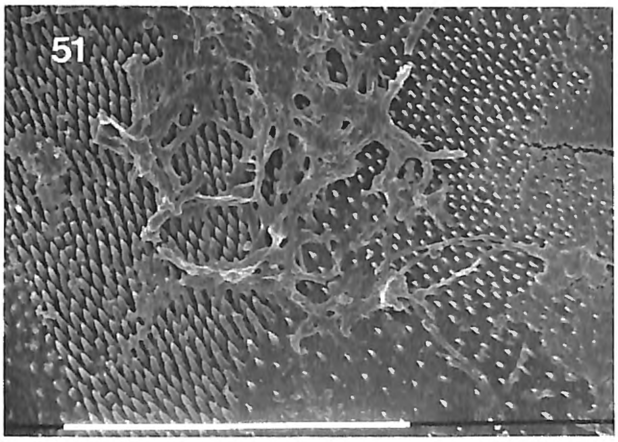
There is always a strongly raised mesosternal process, with the free (ventral) face or edge carrying trichobothria (fig. 31, 32). In most *Derallus* (fig. 67, 68, 75, 76), most *Hemiosus* (fig. 31) and some *Berosus* (fig. 36) there is a distinct hollow, which I think to be homologous to the helophorine crescent. Behind this, the sternite is raised on the middle line. A smooth ridge runs along the anterior edge of the mesosternal process, and in most cases culminates in a tooth, called "anterior tooth" when describing the process (fig. 36, 53).

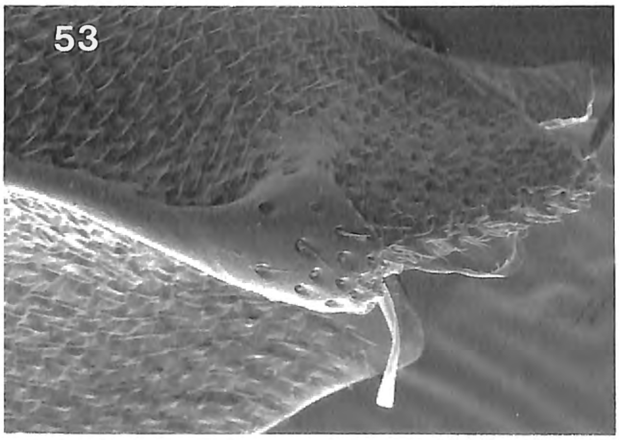
The metasternum bears a weak process, the shape of which is more or less determined by the metafemora when they are directed forwards; it has a carina at least on the anterior part, including the intercoxal bridge (fig. 38, 61, 67). In *Derallus* and *Regimbartia* the process is keeled











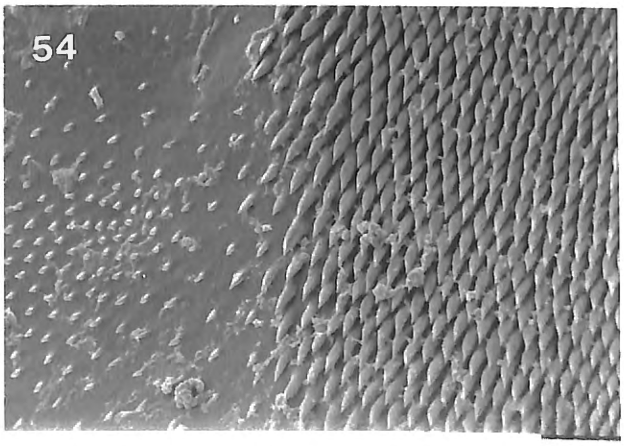
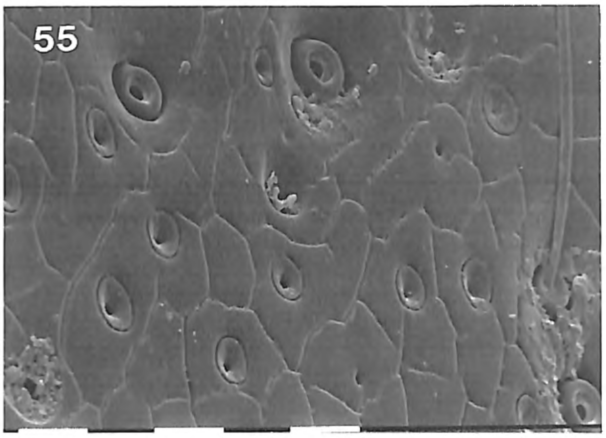
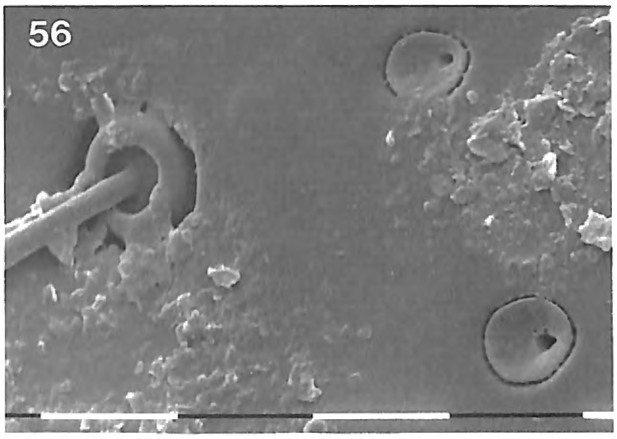
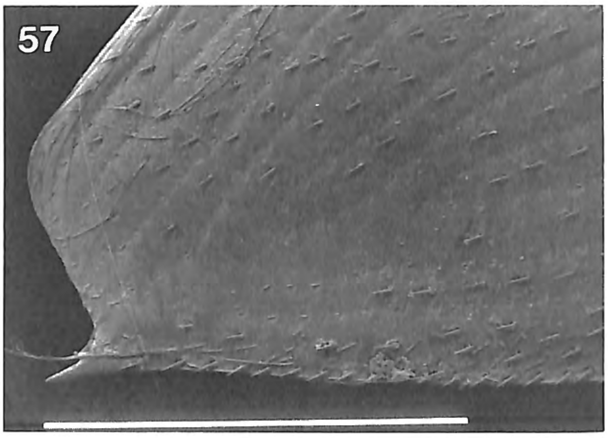
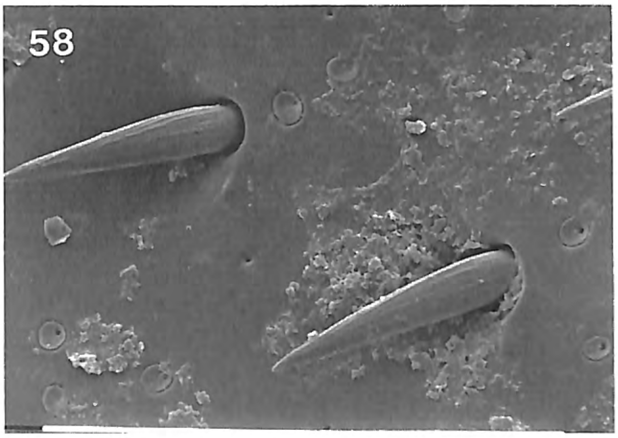


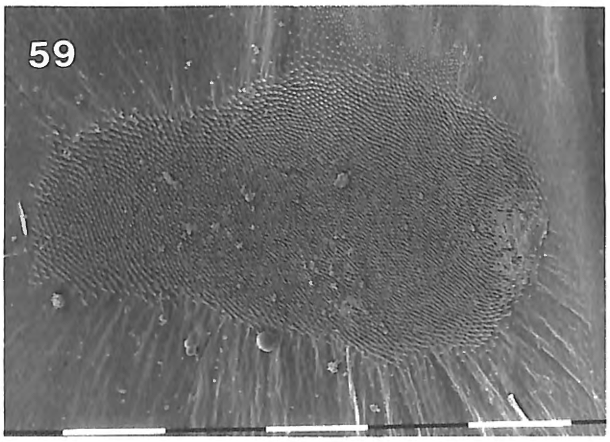
Plate VII:
Fig. 47: *Berosus batesi*: pars stridens, 300 X. – Fig. 48-50: *B. pedregalensis*. – Fig. 48: pars stridens, 194 X. – Fig. 49: elytron, inner face with plectron formed of two parts, 358 X. – Fig. 50: detail of plectron, 2,840 X. – Fig. 51: *B. vilipendus*: detail of plectron, 600 X. – Fig. 52-53: *B. auriceps*: Fig. 52: first urite (laterosternite) with pars stridens, 150 X. – Fig. 53: mesosternal process, 194 X. – Fig. 54: *B. obscurifrons*: detail of plectron, 925 X.

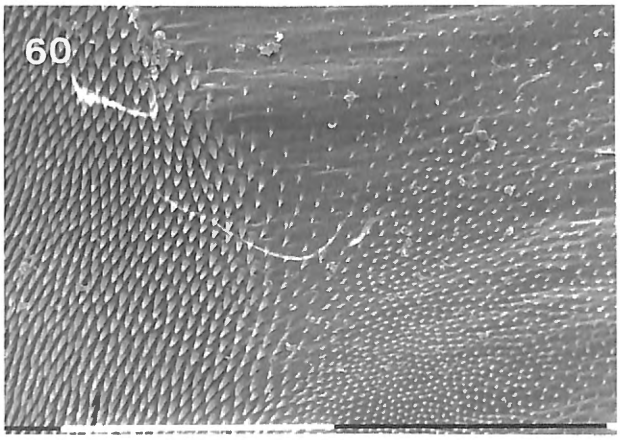


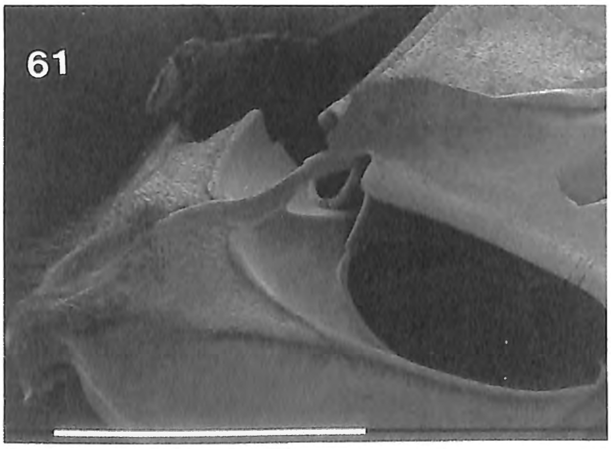












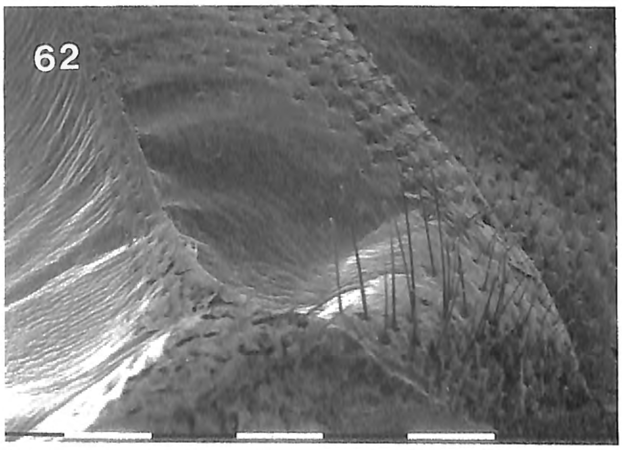
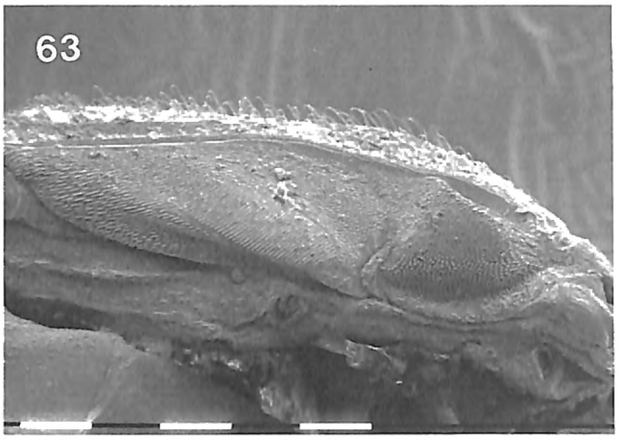
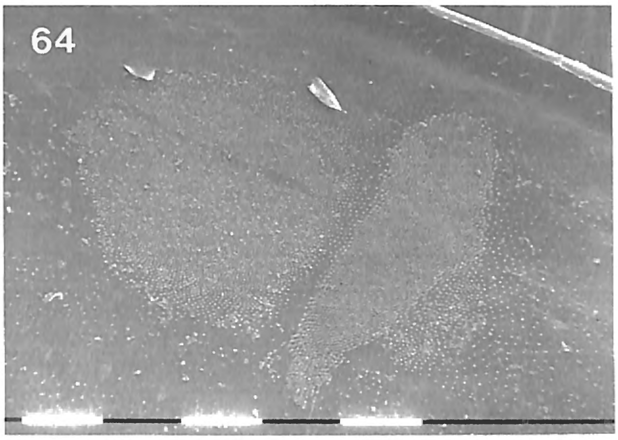
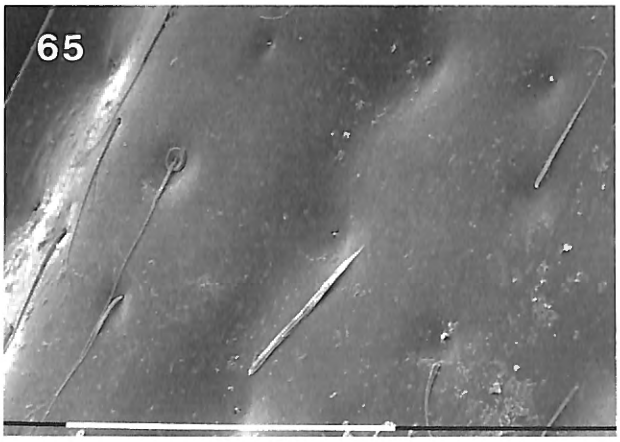
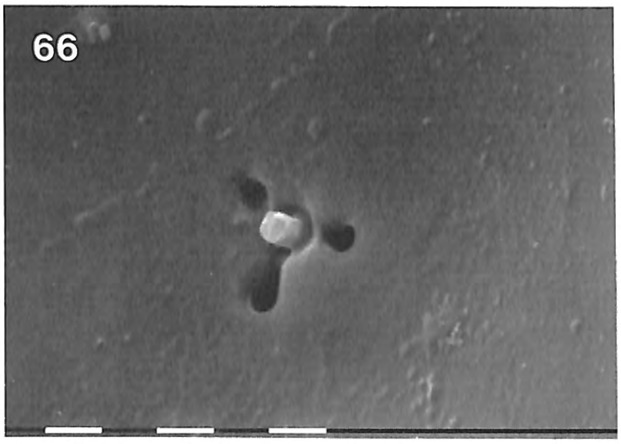


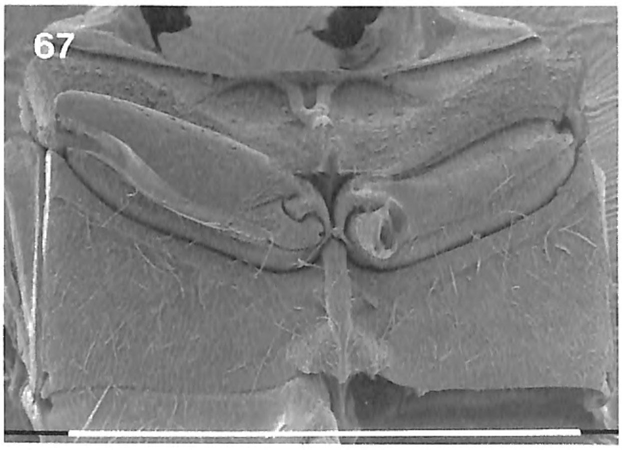
Plate VIII:
Fig. 55-62: *B. truncatipennis*. – Fig. 55: pronotal sculpture, 1,200 X. – Fig. 56: elytron, outer face: trichobothria and two punctures, 2,400 X. – Fig. 47: apex of elytron, outer face, 65 X. – Fig. 58: detail of spine-like hairs, 925 X. – Fig. 59: plectron, 178 X. – Fig. 60: detail, 482 X. – Fig. 61: mesosternum and metasternum, 55 X. – Fig. 62: lateral depression on first urosternite, with marginal trichobothria, 150 X.

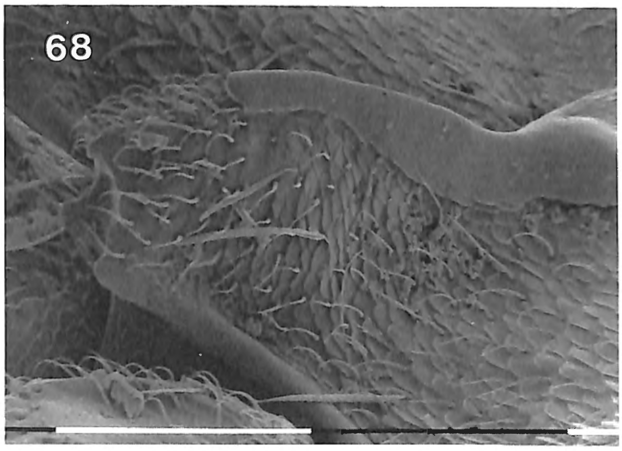


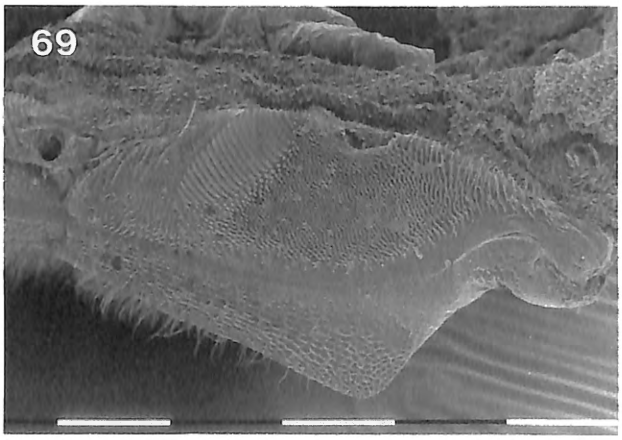












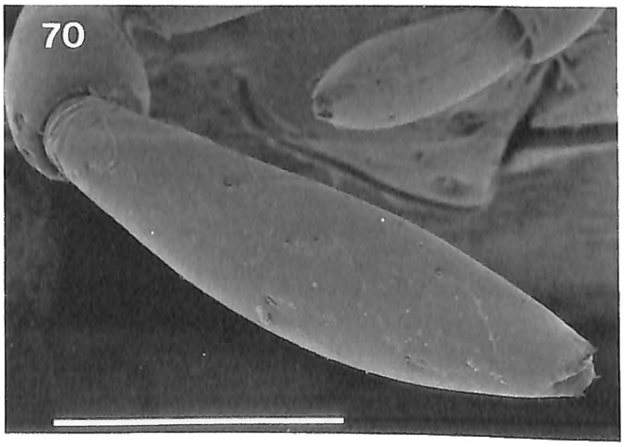


Plate IX:
Fig. 63-64: *B. coptogonus*. – Fig. 63: first urite with pars stridens, 120 X. – Fig. 64: plectron, 137 X. – Fig. 65-70: *Derallus angustus*. – Fig. 65: elytron, outer face, 600 X (notice trichobothria on 11th interstria). – Fig. 66: detail of puncture on stria, 10,000 X. – Fig. 67: meso- and metasternum, 93 X. – Fig. 68: mesosternal process, lateral view, 462 X. – Fig. 69: laterosternite of first urite, with plectron, 203 X. – Fig. 70: fourth maxillary palpite, with apical complex of sensilla (no sunken sensilla on outer face), 526 X.

in all its length (fig. 67), while in *Allocotocerus* there is an interrupted carina. In *Hemiosus* and *Berosus*, on the contrary, there is a deep depression in the medial part; this may provide mechanical reinforcement for energetic swimming. The posterior angle is strongly raised, in some species forming a raised lamina. The primitive type of metasternal process may have been like that of *Allocotocerus* which could have originated the other two types, one associated to smooth subglobular shapes, the other to angular shapes with prominent humeral humps. In many species of *Berosus*, and in those species of *Regimbartia* that have been examined under light microscope, the mesosternal process is laminar (fig. 61). Some species of *Derallus* have an almost laminar process, but there is usually some indication of the hollow behind the anterior tooth. In all the species of *Hemiosus* known to present date the mesosternal process has a flattened ventral face that comprises the whole length of the process, ending in a narrow angle between the mesocoxae. This is a diagnostic character for the genus, as in all species of *Berosus* the mesosternal process is laminar at least in its posterior part. The distribution of the trichobothria suggests that the primitive condition was much as in the Helophorinae, and that a sharp rising of all the surface bearing trichobothria produced the Berosinae process.

The examined species of *Allocotocerus* have a small mesosternal process with a hollow, triangular ventral face.

6.3. The Epimetopinae

A very small, hood-shaped process (fig. 87, 88) could be homologous with the helophorine crescent, although no trichobothria have been observed under SEM. The metasternum bears smooth granules that contrast with the reticulate sternite; there are indications of a weak process.

6.4. The genus Hydrochus

The sternal structure is peculiar to this genus, with depressions that appear filled with granulate matter, and the rest of the surface densely pubescent. The granules appear to be some secretion, probably related to the crust that covers these beetles (cf. SEM photographs of Gerridae in HAUSER, 1985). There is a thick pubescent process without distinct carinae and a weak metasternal process (fig. 114).

6.5. The genus Georissus

The sternal configuration of the studied species appears quite different from that of other Hydrophilidae. There is a small, but sharply raised mesosternal process (fig. 93), but more information is needed for interpretation, which is made more difficult by the presence of large granules in all the sternites. This may be a primitive character retained, as in *Epimetopus*, together with the riparian habits.

7. The visible urosternites

Nearly all the Hydrophilidae have five apparent urosternites (corresponding to segments III to VII). Segment VIII is usually well sclerotized, but internal; the IX reduced and modified. Segment VIII may be protruded under certain conditions (killing by vapours of certain esthers, or by plunging in alcohol that has been insufficiently diluted). This artifact can be easily detected as the protruded segment is smooth and unlike the others in texture.

7.1. The Helophorinae

The five urosternites are smooth, the fifth rounded. In many species the posterior edge of the fifth is crenulate, either in its whole length, or only at the apex.

7.2. The Epimetopinae

The urosternites are as in the Helophorinae, but the basal one very short; the edges are smooth in all observed species.

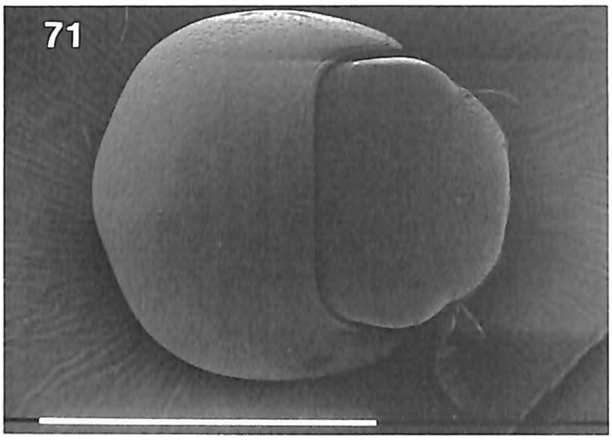
7.3. The Berosinae

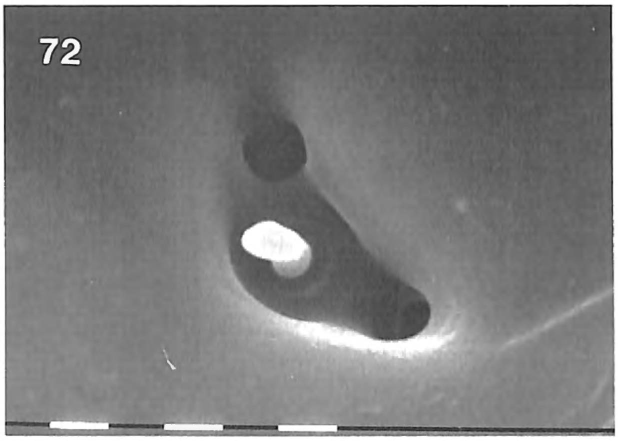
In this subfamily the fifth apparent urosternite has a broad,shallow apical notch. In *Regimbartia* and *Allocotocerus* this sternite is invaginated (but well sclerotized); these are among the few exceptions having four apparent urosternites, the fourth rounded, in some species of *Regimbartia* with a small apical carina.

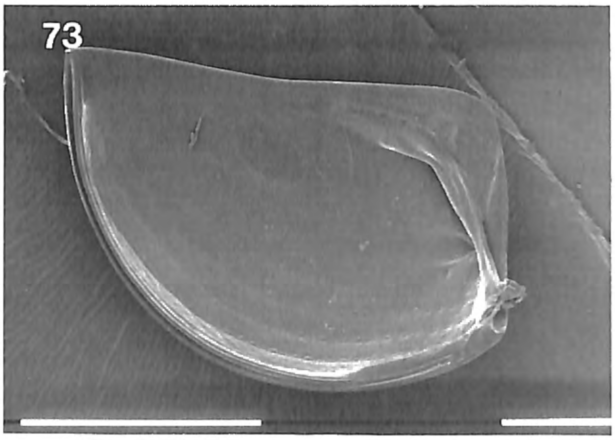
In *Derallus* the first urosternite has a medial longitudinal carina; the apical notch has the bottom produced in a triangular tooth; the lateral edges of the sternites (which means the posterior edge of the fifth) are smooth.

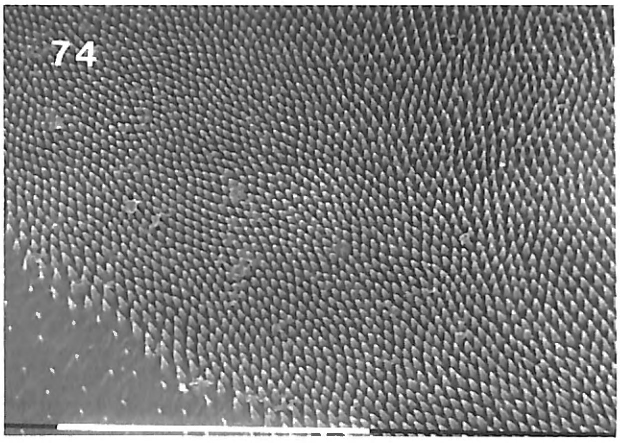
In *Hemiosus* the first apparent urosternite has three longitudinal carinae, the two lateral ones incomplete; the second to fourth urosternites often have short basal carinae; all these carinae are usually flat (fig. 30). The apical notch has the bottom produced into a triangular tooth, rarely into a pair of fine teeth or a weak rounded projection. The lateral edges of the urosternites are crenulate in many species, smooth in a few ones.

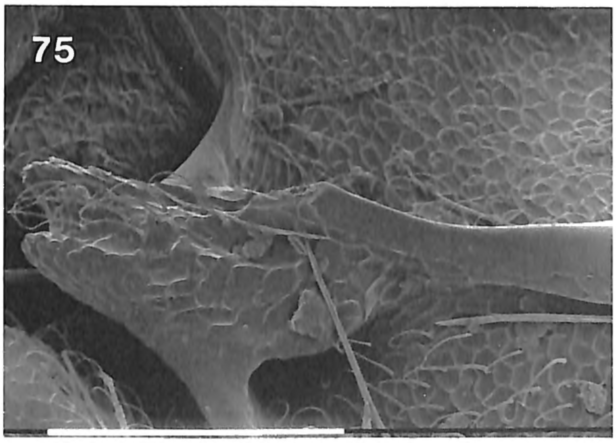
In *Berosus* there is only a medial carina on the first urosternite, but in many Neotropical species a pair of depressions, bordered by long trichobothria, appears near the lateral edges (fig. 62). These structures may be related to perception of the curve of the ventral bubble; they usually appear in species that have what appear to be hydrodynamic specializations. Only a few species have carinae on the second to fourth urosternites. A little more frequent – but still far from being the general case – is the presence of a carina or raised tooth on the fifth urosternite, in front of the apical notch; this feature is sometimes restricted to males. The lateral edges of urosternites may be crenulate (fig. 39), serrate or smooth; in some cases only the fifth is serrate, the others smooth. There appears to be a tendency to lose the crenulation in several separate lineages (OLIVA, 1989).

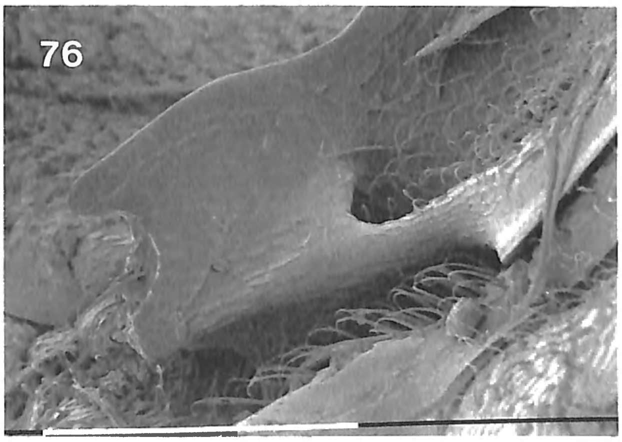


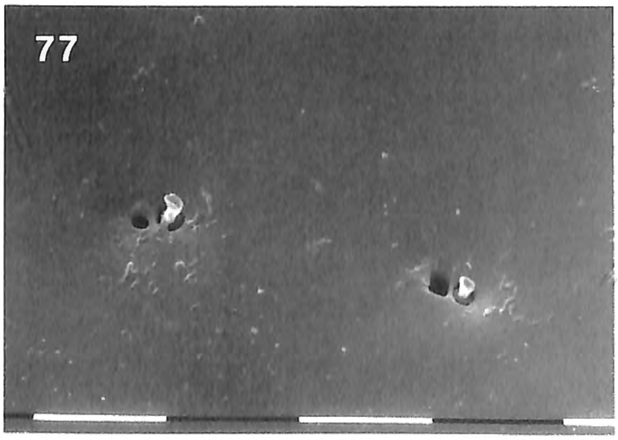












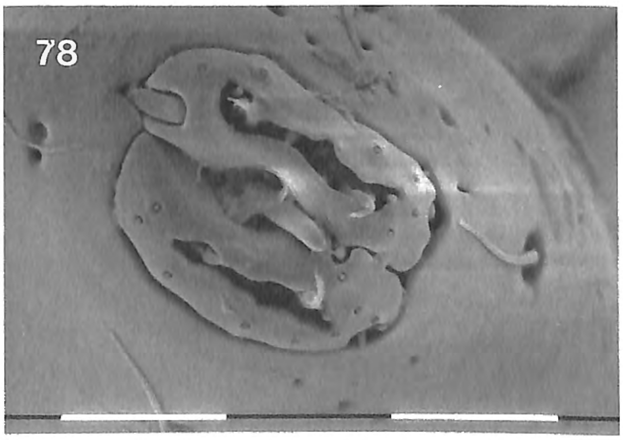
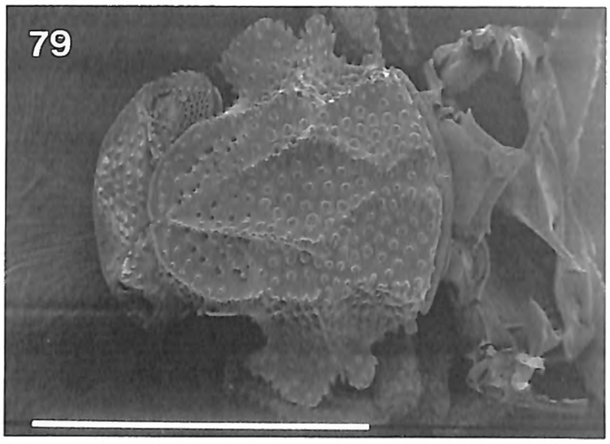
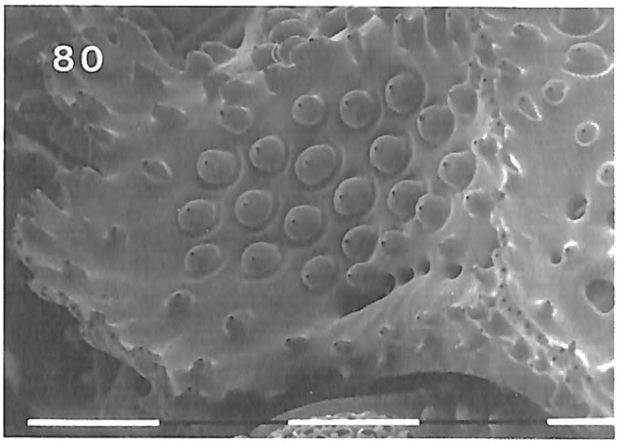
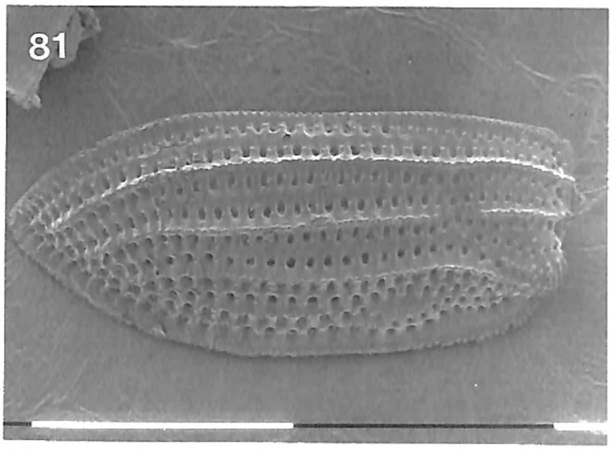
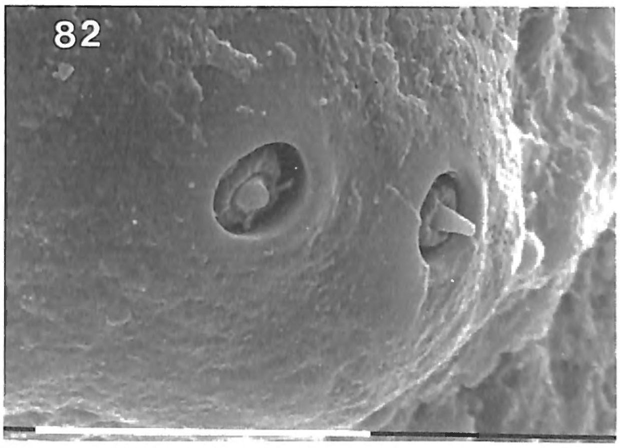


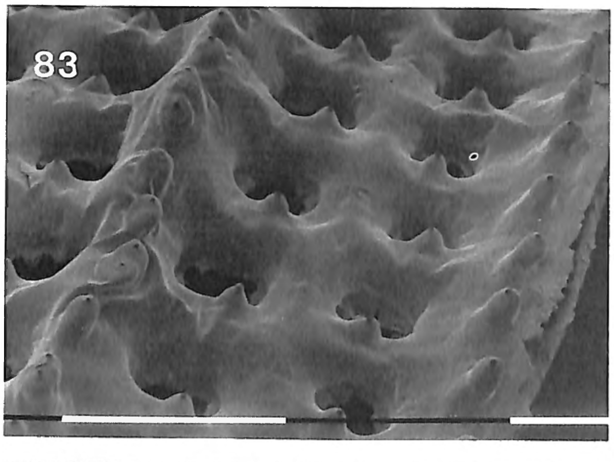
Plate X:
Fig. 71-75: *D. altus*. – Fig. 71: head and pronotum, 60 X. – Fig. 72: puncture on elytral stria, 10,000 X. – Fig. 73: elytron, inner face, with plectron, 42.6 X. – Fig. 74: detail of plectron, 1,050 X. – Fig. 75: mesosternal process (anterior tooth broken), 845 X. – Fig. 76-78: *D. ambitus* Fig. 76: mesosternal process, 573 X. – Fig. 77: puncture on elytral stria, 2,400 X. – Fig. 78: apex of maxillary palpus, with apical complex of sensilla, 2,900 X.

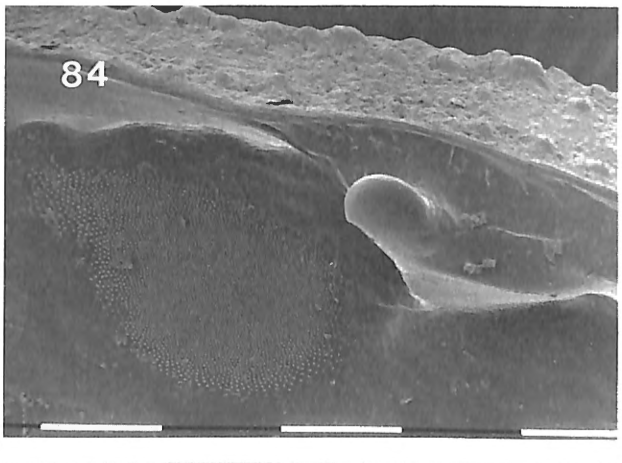


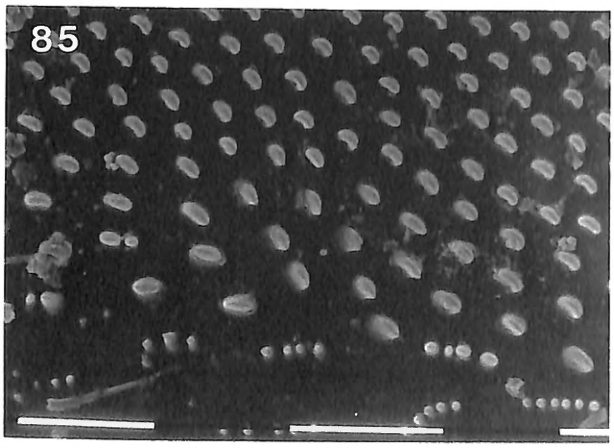












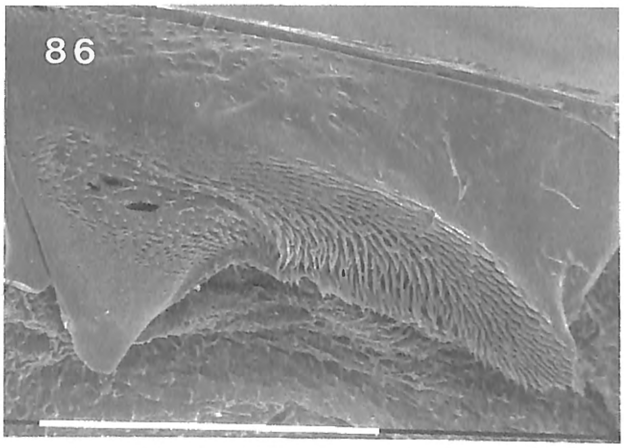
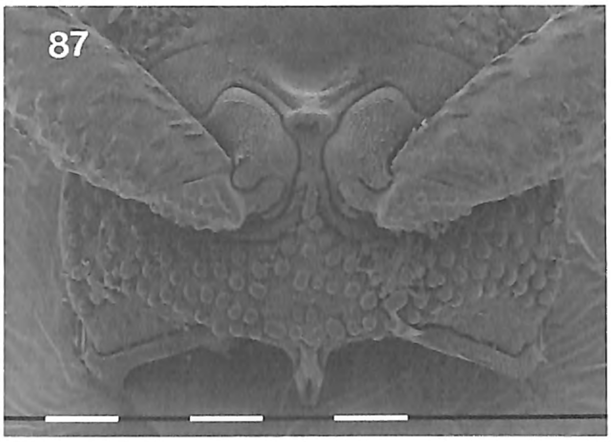
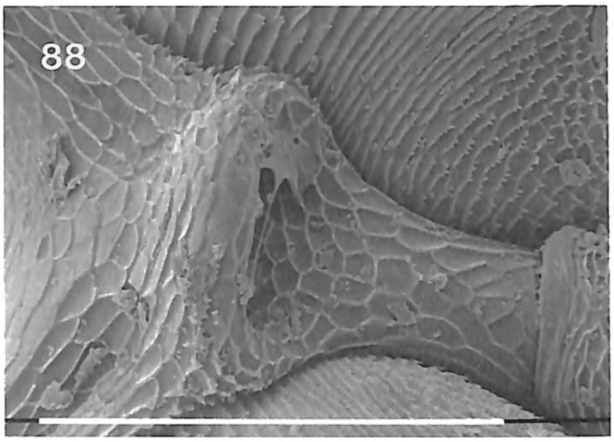
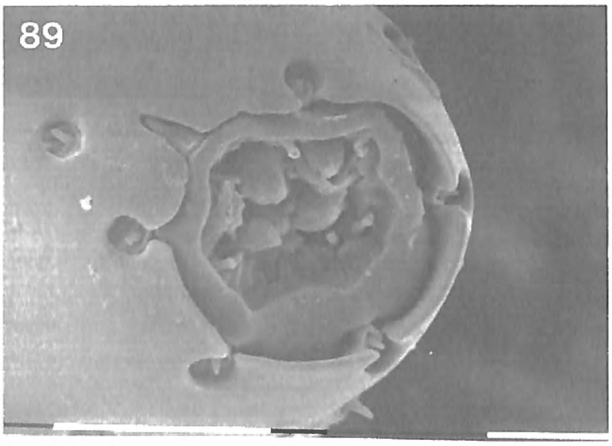


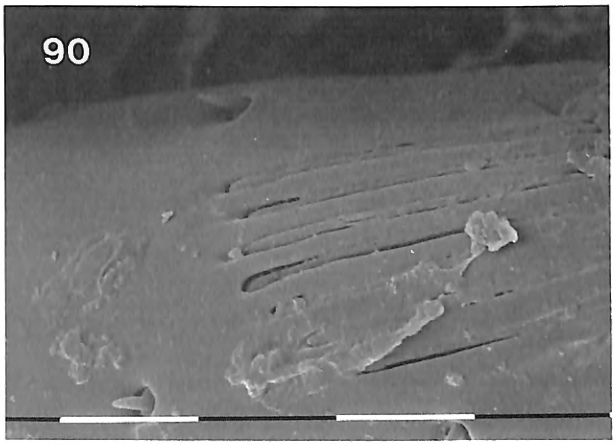
Plate XI:

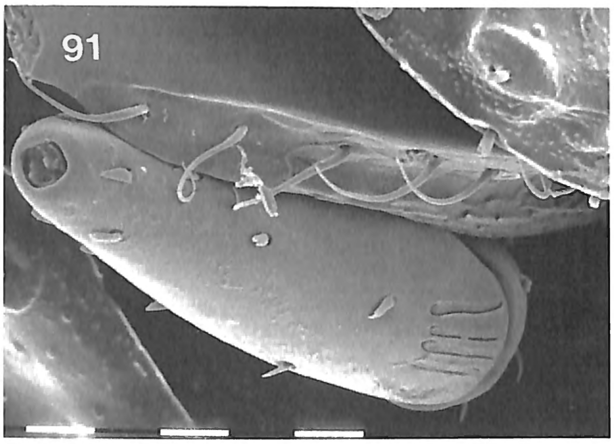
Fig. 79-86: *Epimetopus trogoides*. – Fig. 79: head and pronotum, 60 X. – Fig. 80: anterolateral angle of pronotum, 231 X. – Fig. 81: Elytron, outer face, 46 X. – Fig. 82: detail of granules, 5,950 X. – Fig. 83: elytron, outer face, showing disposition of granules, 406 X. – Fig. 84: elytron, inner face, with plectron and inner ridge, 212 X. – Fig. 85: detail of plectron, 2,400 X. – Fig. 86: laterosternite of first urite, 573 X.

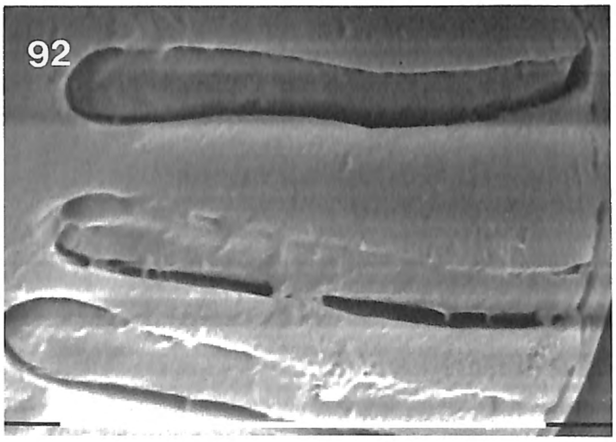


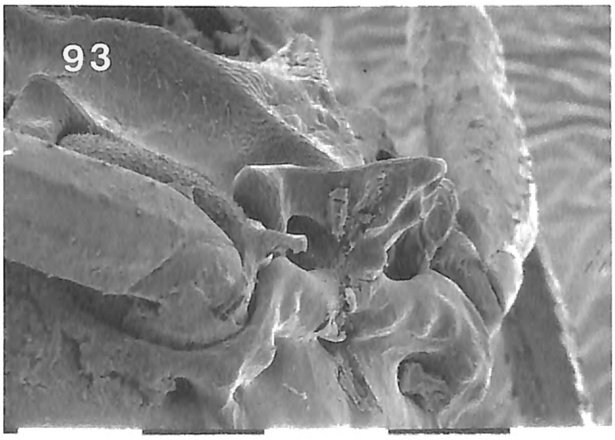












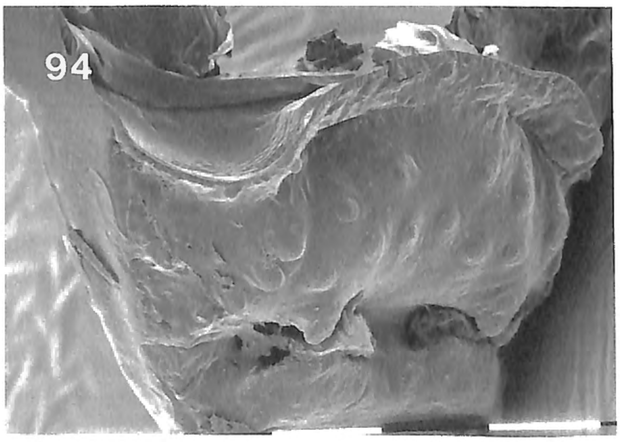


Plate XII:
Fig. 87-90: *E. trogoides*. – Fig. 87: meso- and metasternum, ventral view, 131 X (notice smooth granules on reticulate cuticle, and spines on ventral face of femora). – Fig. 88: mesosternal process, 845 X. – Fig. 89: apex of labial palpus with apical complex of sensilla, 3,860 X. – Fig. 90: maxillary palpus: sunken sensilla at base of distal segment, 2,500 X. – Fig. 91-94: *Georissus laesicollis*. – Fig. 91: maxillary palpus: sunken sensilla at base of distal segment, 1,150 X. – Fig. 92: detail of sunken sensilla, 8,500 X. – Fig. 93: mesosternal process, 845 X. – Fig. 94: first urosternite, 186 X.

7.4. *The genus* Hydrochus

The examined species of *Hydrochus* have three carinae on each urosternite (fig. 115), save on the modified fifth. The carinae are broad and flat, with thick hairs among which appear minute granules that may be lumps of secretion (cf HAUSER, 1985); on each medial carina there are two trichobothria, one behind the other (fig. 116). On the fifth urosternite a depression filled with granulate matter takes up a great part of the surface. The posterior third of the urosternite forms a broad smooth plate (translucent under light microscope), set with conical, almost spine-like hairs and with some long, supple hairs (fig. 117). Some species of *Hydrochus* have a serrate margin on at least the fifth apparent urosternite.

7.5. *The genus* Georissus

The apparent urosternites are more or less modified, specially the first (fig. 94). Data obtained in this study are not sufficient for an interpretation.

8. Maxillary palpi

In most Hydrophilidae, the antennae are adapted for air captation, and therefore are not used for exploration of the substratum under water. This function is taken up by the maxillary palpi, often remarkably elongate. It has been observed that in all the genera examined under SEM there is a complex of sensilla at the very tip of the palpus, (which appear truncate under light microscope). Nonaquatic, and specially nonswimming genera of Hydrophilidae have short maxillary palpi, the distal segment of which is usually ensiform. The labial palpi also bear apical sensilla (fig. 89).

8.1. *The* Helophorus (Empleurus)

The species that make up this genus show some striking characters, some of them primitive (they are not aquatic, have no swimming hairs on tarsi, etc). The most striking of these has been disclosed by examination under SEM: the apical palpite bears on its outer face a field of twelve slit-like sunken sensilla (fig. 14). Similar structures are known from other families of Coleoptera, v.g. Staphylinidae (DRUGMAND & WAUTHY, in press), but none have been found in *Helophorus* of other subgenera.

8.2. *Nonswimming genera*

Sunken sensilla have been found in three other genera, although with a different disposition than in *Helophorus (Empleurus) porculus*. In the riparian *Georissus crenulatus* and *Epimetopus trogoides* the sensilla (four in the first case, seven in the second) form a row at the base of the distal palpite, set parallel one to another and narrowly spaced (fig. 89, 90, 91). In *Hydrochus* three subapical sunken sensilla have been found (fig. 118).

8.3. *Swimming Hydrophilidae*

No sunken sensilla have been found in the following species: *Helophorus brevitarsis, H. arvernicus, H. aquaticus, Hemiosus mulvianus, Berosus zimmermanni, B. patruelis, B. coptogonus, B. obscurifrons, Derallus angustus, D. ambitus.* In all these, there is an apical complex of sensilla; the rest of the apical palpite bears only hairs without special modifications (fig. 33, 70, 78).

8.4. *A tentative interpretation*

The basal field of sunken sensilla is probably the primitive condition. DRUGMAND (personal communication) has found half-sunken, thick sensory hairs with a similar disposition in very primitive Staphylinidae (Aleocharinae Falagriini, n. gen. n. sp.). The condition in *Helophorus (Empleurus) porculus* would appear to be a secondary acquisition. The three subapical sensilla in *Hydrochus* could come from the reduction of such a field. For beetles that creep through a maze of vegetation, some advantage may be found in concentrating the sensilla near the tips of the palpi. The riparian *Georissus* and *Epimetopus* retain the primitive condition.

The complex of varied sensilla at the apex (for contact exploration?) is set on a distinct plate (fig.33), which may represent the vestigial fifth palpite (cf. COULON 1989 on Staphylinoidea). Although, as it has been said, no sunken sensilla have been found in swimming Hydrophilidae, there are what may be termed "semisunken" sensilla at the edge of the apical plate (fig. 33, 78). More exhaustive studies would be necessary to clear up this interesting subject.

Some species of *Hemiosus* and *Berosus* show sexual dimorphism in the maxillary palpi; in other species the melanization of the apical palpite is distinctively extense when compared with that of allied species. Some cases of these two characters have been examined under SEM, but no special cuticular structures were found.

9. Femoral vestiture

9.1. *Riparian forms*

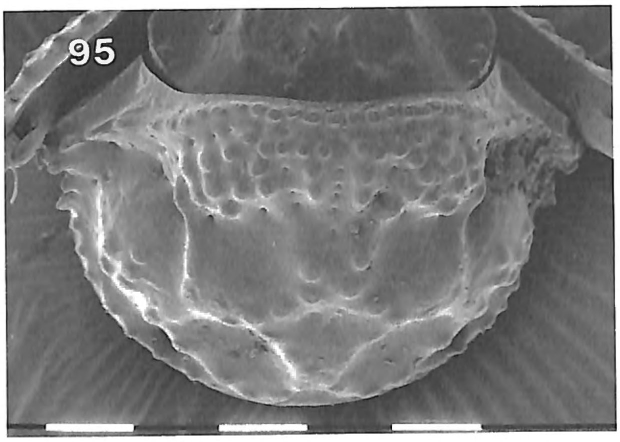
Articulate, decumbent spinelike hairs (probably tactile) appear on the ventral face of the femora in *Georissus*,in *Helophorus (Empleurus)* (fig 13) and in *Epimetopus* (fig. 87); in the last they are specially large and dense.

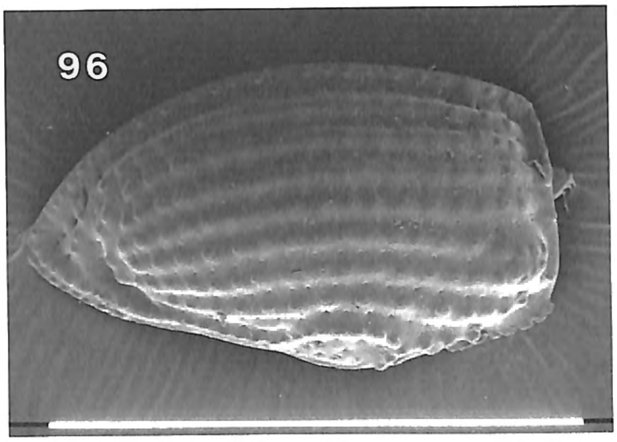
9.2. *The aquatic* Helophorus

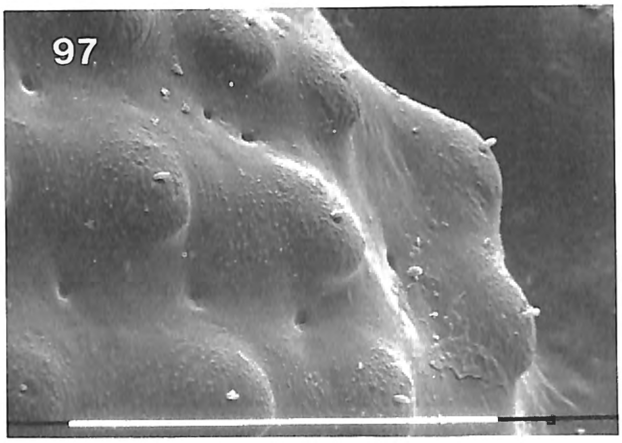
Both spines and sparse, supple hairs (quite different from the sternal pubescence) have been found in *H. brevipalpis* (fig. 22).

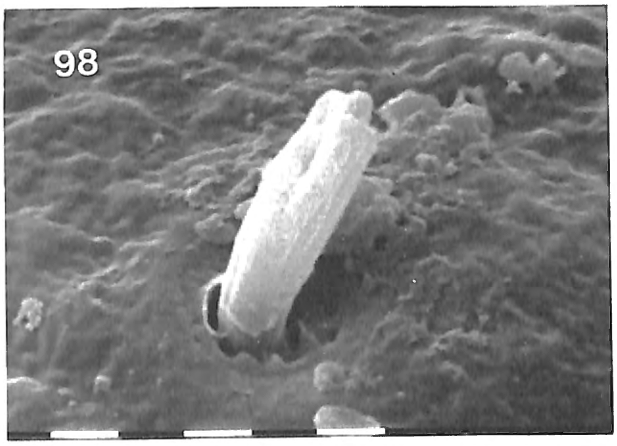
9.3. *The Berosinae*

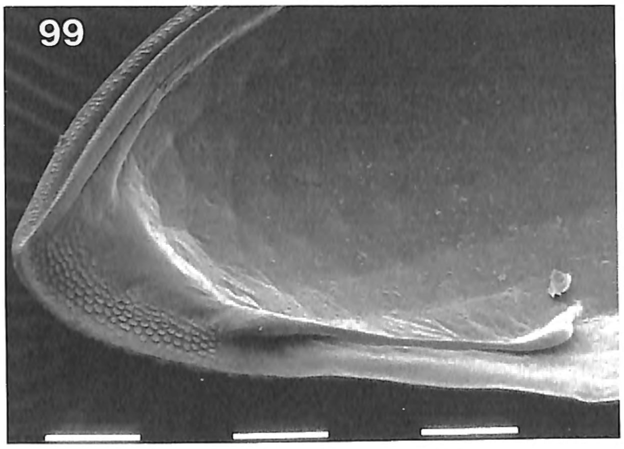
In this subfamily the sternal pubescence (which covers

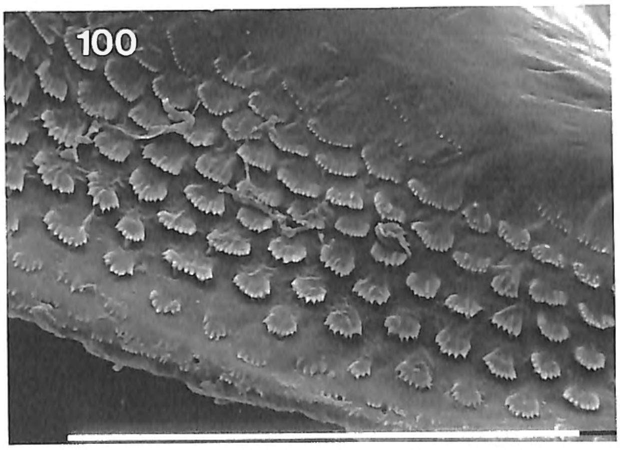












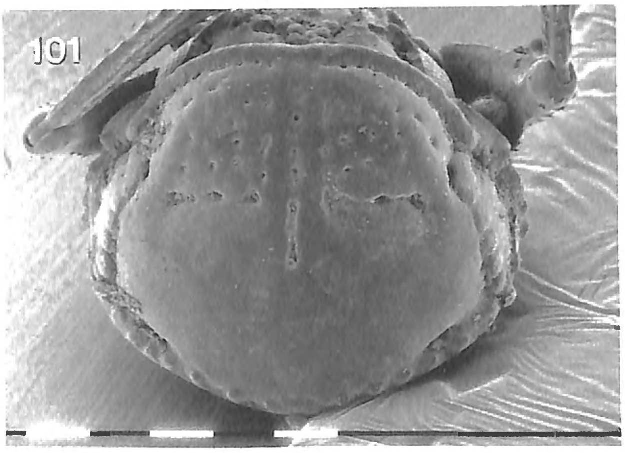
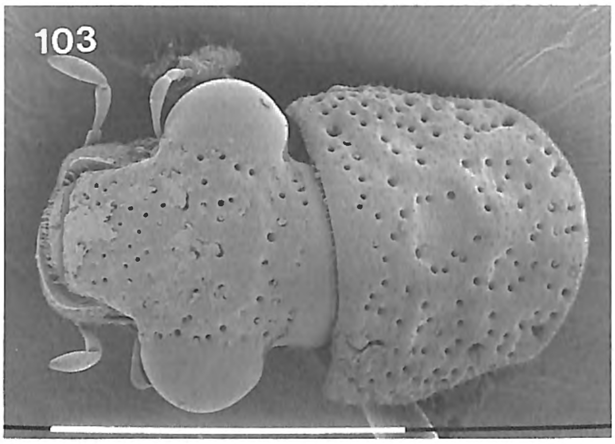
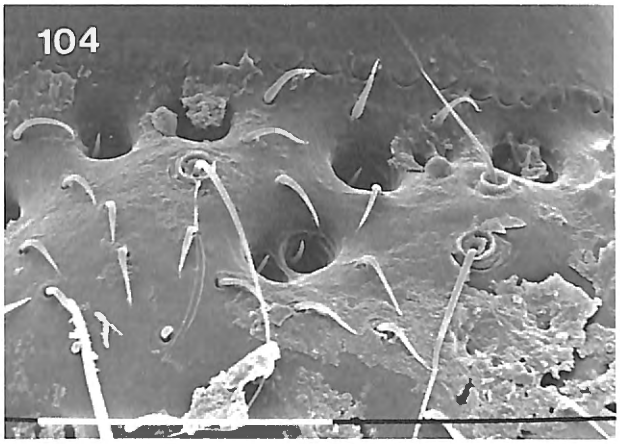
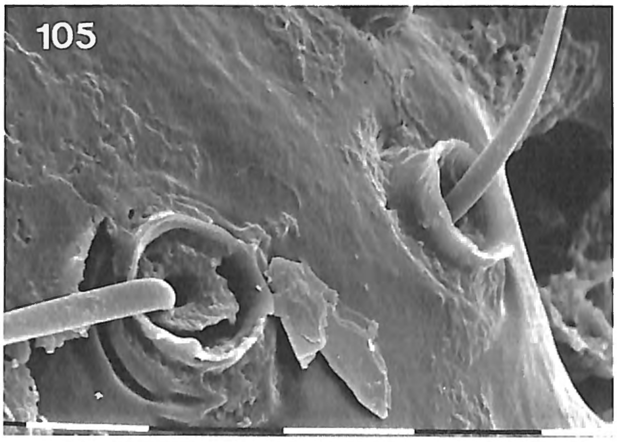
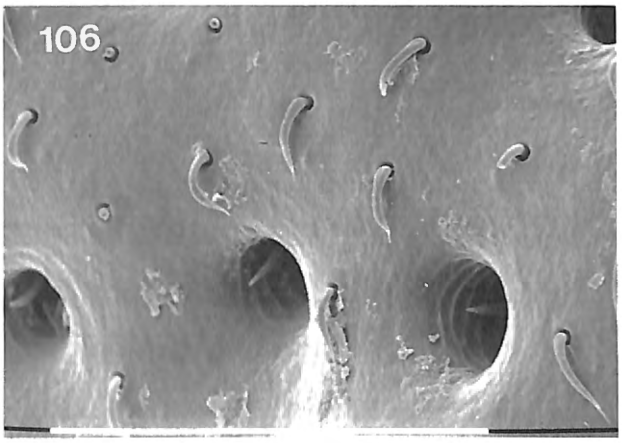


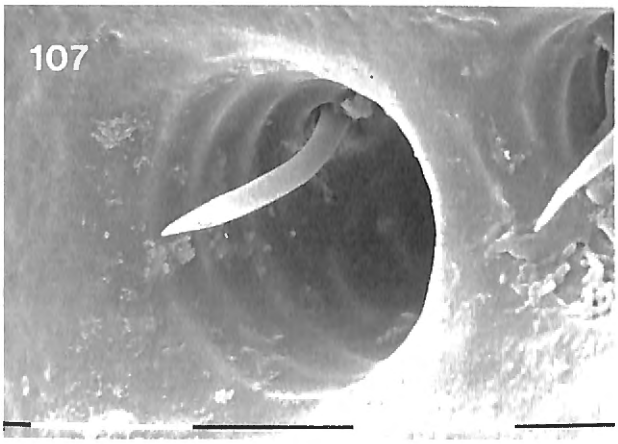
Plate XIII:
Fig. 95-100: *G. laesicollis*. – Fig. 95: pronotum, 150 X. – Fig. 96: elytra, outer face, 93 X. – Fig. 97: detail of strial punctures and protruding sensilla on granules, 745 X. – Fig. 98: detail of sensilla, 11,400 X. – Fig. 99: elytron, inner face with ridge and apical microtrichia, 163 X. – Fig. 100: detail of apical microtrichia, 885 X. – Fig. 101-102: *Georissus crenulatus*. – Fig. 101: pronotum, 106 X. – Fig. 102: elytron, inner face, 85 X.

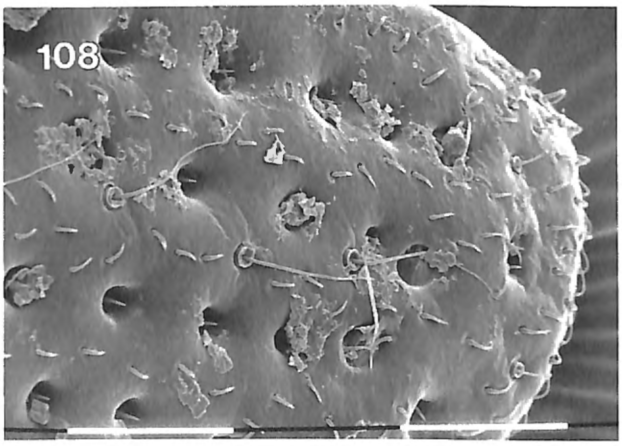


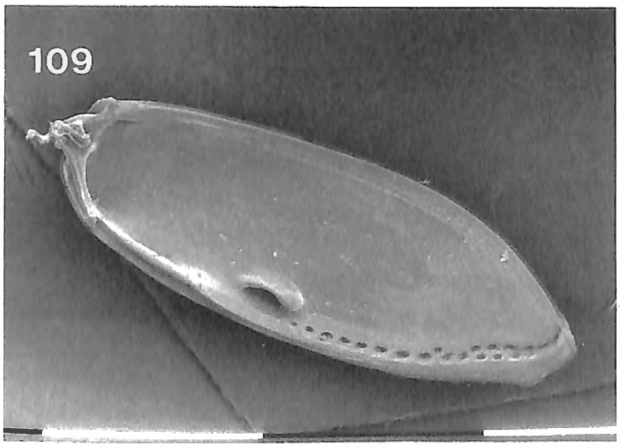












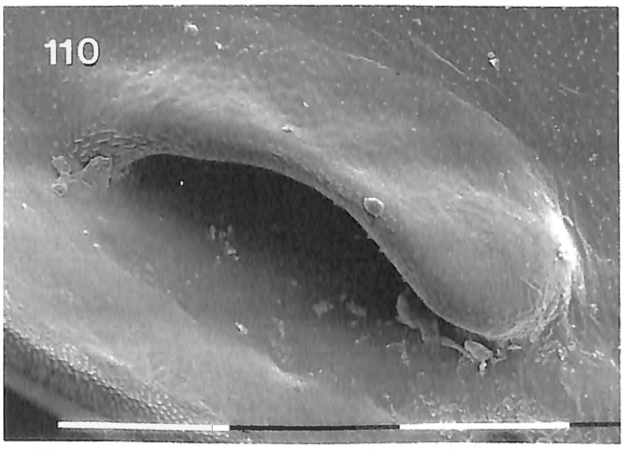


Plate XIV
Fig. 103-110: *Hydrochus* spp. – Fig. 103: head and pronotum, 63 X. – Fig. 104: detail of punctures and trichobothria, 526 X. – Fig. 105: trichobothrion, 2,300 X. – Fig. 106: pronotal sculpture, 775 X; broken hairs show hollow. – Fig. 107: enlarged puncture on pronotum, 2,840 X. – Fig. 108: elytron, outer face, apex, 500 X. – Fig. 109: elytron, inner face, 39 X. – Fig. 110: detail of ridge, 300 X.

as well the coxae and trochanters) extends to the base of the femora. It has been remarked that the Berosinae are active swimmers; the extension of the pubescence to the femoral bases may affect the shape of the ventral bubble, which in its turn might have influence on the hydrodynamics of the beetle. The glabrous part of the femora carries spinelike hairs, often minute in size. These are larger in *Derallus perpunctatus* (see 2) that in any other species of the genus, or indeed in any Berosinae that I have examined.

The femoral pubescence is narrow in *Derallus*, *Regimbartia* and *Allocotocerus*. In *Hemiosus* it is rather extense, always disposed obliquely along the femur, so that most of the anterior margin is glabrous. In *Berosus* there is a wide variation from one species to another, but when the pubescence is oblique it is never disposed as in *Hemiosus*.

9.4. The genus Hydrochus

The species of this genus have a dense sternal hydrofuge pubescence that covers the coxae and trochanters, and also a small basal area of the femora, which bear sparse hairs and a few spines (fig. 114).

10. Conclusions

10.1. The Helophorinae

It has been mentioned that the species of the subgenus *Empleurus* have no swimming hairs on their tarsi and are not aquatic. When taken together with the remarkable sunken sensilla on the palpi, with the absence of metallic sheen, that is present in all other subgenera and with the accentuated pronotal relief, it is evident that the *Empleurus* have evolved along different lines from the aquatic *Helophorus*. At first,I had been tempted to consider *Empleurus* as a separate genus, but the arguments of Dr M.HANSEN (personal communication) have persuaded me that this is not justified, since these characters are all plesiomorphic. The basal intercalary stria on the elytra is also retained in this subgenus (fig. 9).

The subgenera *Meghelophorus* and *Atracthelophorus* are aquatic, as it has been mentioned. In the first, the intercalary elytral stria is retained, but the distal maxillary palpite is long and asymmetrical. In the second, the intercalary stria has disappeared and the palpite is symmetrical, of much the same shape as that of nonaquatic genera. The asymmetrical palpite of *Megalhelophorus* is similar to that of *Hemiosus*, which also retain an intercalary stria, and in some species a colour pattern like the helophorine one. The main difference between a *Helophorus (Meghelophorus)* and a *Hemiosus* is that the latter has prominent meso- and metasternal processes. These, and specially the first, affect the shape of the ventral bubble. Other characters of *Hemiosus* are: presence of femoral pubescence, convex shape and swimming hairs on the tibiae as well as on the tarsi of the middle and rear legs. All these go to produce a more efficient swimming, the first by affecting in its own way the shape of the ventral bubble. I have observed *Helophorus aquaticus* in the water; their swimming is hampered by a remarkable degree of yawing. It is tempting to picture the ancestral Berosine as stemming from somewhere near the *Helophorus (Meghelophorus)*, yet it must be admitted that most of the similarities are either primitive traits or due to aquatic life. In the light of present data, the cladogram given by HANSEN (1992) appears as the best proposed so far.

10.2. The position of the Epimetopinae

As mentioned in 2), the colour pattern and pronotal relief of *Epimetopus trogoides* differ only in degree from those of *Helophorus (Empleurus) rufipes*. The field of sunken sensilla at the base of the apical palpite is certainly a primitive character. The sturdy legs with rows of large spines and the ridges on odd-numbered elytral striae are found in several other families of Coleoptera. I agree with HANSEN (1992) when he places Epimetopidae near Helophoridae, on the one hand, and to the Georissidae-Hydrochidae stock on the other.

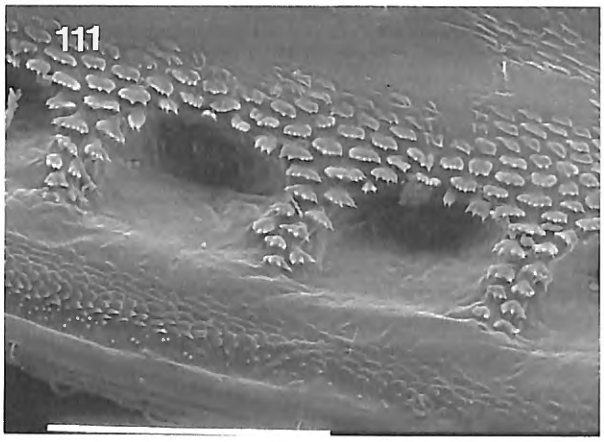
10.3. The position of the Berosinae

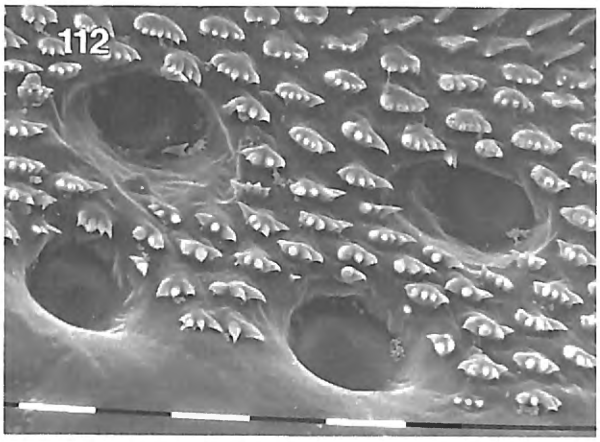
This subfamily includes beetles of decidedly aquatic habits, although swimming is mainly used in fleeing and in going up for air, and the beetles spend most of the time on the substratum.

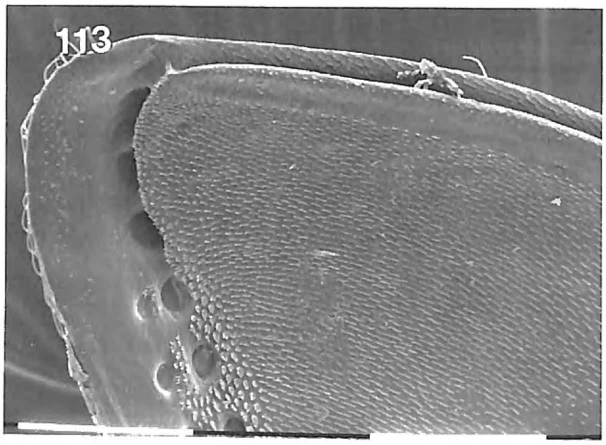
In point 1) I have exposed the main similarities and differences between the *Helophorus (Meghelophorus)* and the *Hemiosus* which retain certain primitive characters among the Berosinae. I had been tempted to suggest that the Berosinae had branched off from Helophorinae already adapted to aquatic life. However, most of the characters common to Helophorinae and Berosinae are plesiomorphic, and those that are not (as the asymmetrical apical palpite) may be explained by independ adaptation to aquatic life, which has been far more successful for the Berosinae.

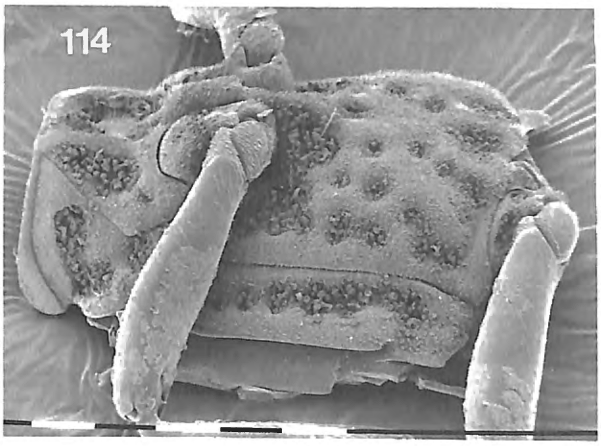
There can be no doubt as to the close relationship of *Hemiosus* and *Berosus*. The shape of the mesosternal process, the disposition of the femoral pubescence and the different type of male genitalia (cf. OLIVA, 1989) are the main differences between these two genera. One common character that they do not share with any other genera is the size and prominence of the eyes. This may be connected in some way with the dispersion flights. The stridulatory apparatus is much the same in *Hemiosus* and in *Berosus* although in the second some special modifications of the plectrum occur (see V).

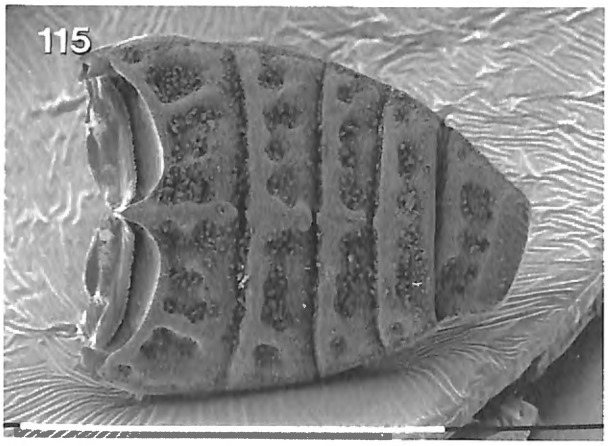
As suggested in part 2, it appears probable that the genus *Derallus* has evolved from an ancestor ressembling a minute *Hemiosus*. These genera are both restricted to the Neotropical area, and a great number of species of *Berosus* including, I think, the greater variety of forms, is also found there. For this reason, I had assumed in

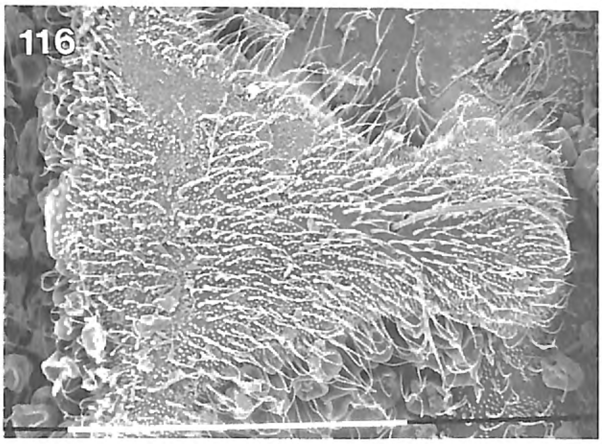


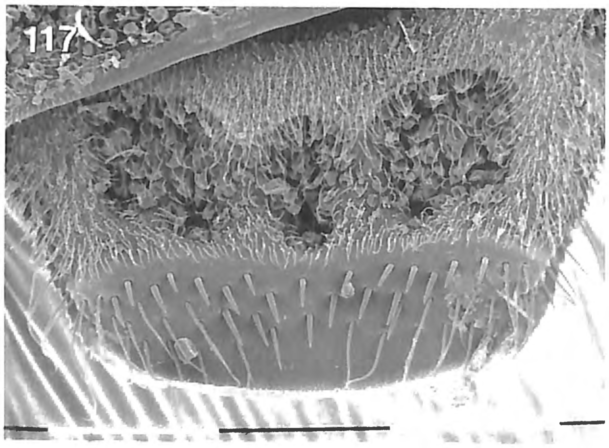












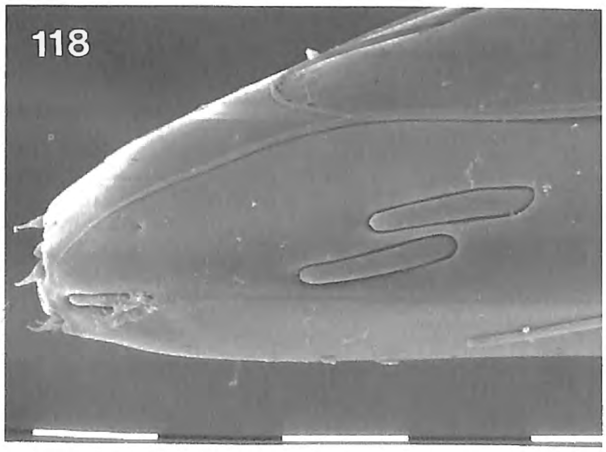


Plate XV:

Fig. 111-118: *Hydrochus* spp.Fig. 111, 112: microtrichia in two species, 503 X and 1,360 X. – Fig. 113: elytral apex, inner face, 312 X. – Fig. 114: ventrolateral view, showing meso- and metasternum, depressions filled with granulate matter and femora with sparse hairs and some spines, 110 X. – Fig. 115: apparent urites, 75 X. – Fig. 116: detail of middle carina of second urosternite, 600 X. – Fig. 117: fifth urosternite, 300 X. – Fig. 118: sunken sensilla on maxillary palpus, 4,200 X. Ẑ 300 X.

an earlier work (OLIVA, 1989) that the last genus had a Neotropical origin from a stock near *Hemiosus*. This would not be incompatible with an Afrotropical origin for the subfamily, which would explain present-day distribution. Some characters of *Regimbartia* and of *Allocotocerus* suggest a long evolution, specially the abdomen with only four visible sternites. In any case, the Berosinae show a clear instance of hydrodynamic efficience attained through two different types of adaptation. In *Hemiosus* and *Berosus* the shape is rather angular because of the prominent humeral humps (a primitive character) and rather gibbous pronotum. Both have an extense femoral pubescence and long legs; in the case of *Berosus* there is a remarkable tendency, appearing in several lines, to a smoother dorsal surface, first on the elytra, then on the whole dorsum; this goes often with modifications of the elytral apices and/or with spine-shaped hairs on the posterior half of the elytra (fig.57, 58).

On the other hand, the genera *Derallus*, *Regimbartia* and *Allocotocerus* show a tendency to the streamlining of the dorsum, with effacement of the humeral humps, loss of the intercalary stria and a general smoothing of the dorsal sculpture. The high shape appears to prevent rolling in such species of *Derallus* as I have been able to observe in nature, but yawing remains a problem.

10.4. The genus Hydrochus

This worldwide genus comprises beetles adapted to life under water, but on submerged plants; they have a sternal hydrofuge pubescence and antennae modified for air captation, but no adaptations for swimming. The long, sparse femoral hairs look much like those of *Helophorus*. I have taken as a working hypothesis that the *Hydrochus* have specialized early from a primitive stock which, however, had a disposition of sunken sensilla on the palpi rather like that of *Helophorus (E.) porculus*. Since the microtrichia and the locking device on the inner elytral face suggest a close relation to *Georissus*, and since, on the other hand, the condition in *Helophorus porculus* is not primitive, it must be accepted that the basal sunken sensilla have been lost, then apical sunken sensilla acquired, perhaps because concentration of sense organs at the tips of the palpi is an advantage to beetles that creep through a maze of vegetation.

10.5. The genus Georissus

This obviously primitive genus (riparian, worldwide with few species) should be placed next to *Hydrochus* on the strength of the microtrichia and ridges on the inner elytral face (see above). The basal sunken sensilla as in *Epimetopus* are a retained primitive trait. In any case, no doubt can remain that *Georissus* should be included in the Hydrophilidae, or in the Hydrophiloidea according to the criterium employed.

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