Chapter 4
Anti-Wetting Surfaces in Heteroptera (Insecta): Hairy Solutions to Any Problem

Pablo Perez-Goodwyn

4.1 Heteroptera, True Bugs

Insects from the order Heteroptera are called "true bugs" (Schuh and Slater, 1995). These insects go from small (few millimetres long) to very large (about 120 mm) size, with mouthparts transformed into a characteristic beak, the maxilla form an inner tube and the mandibles form the outer shaft, all protected and kept in place by the labium. The fore wings are tegminaceous or half sclerotized (hemelytra) and protect the membranous hind wings at rest. However, wing reduction is very common with all possible intermediates up to completely wingless morphs (Zera and Denno, 1997).

Heteroptera live virtually in every continental environment, including water (Saulich and Musolin, 2007). These insects conquered continental water, in almost all possible biotopes. They live in habitats ranging from big lakes and rivers to small ponds as tiny as a tree hole. They can live close to, over, or under the water surface. They live in the moist shore of water bodies, or in rocks splashed by waterfalls. They are also present in the sea, both on the coast as well as in the open ocean, being the only insect able to develop its whole life cycle in such a biotope.

The relationship with water is extensive in many representatives of Heteroptera, and happened independently several times and in several ways during their evolution. In this chapter, the basic principles of the surface adaptations to water-resistance found in Heteroptera, and their diversity throughout this insect Order will be reviewed.

Micrographs presented in this chapter, are from samples kept in 70% alcohol. These were air-dried, mounted on holders, sputter-coated with 25-nm Au–Pd, and examined and photographed using a Keyence VE 3000 (Keyence, Osaka, Japan) SEM at 15 kV. Morphometric data was obtained from micrographs using the software SigmaScan 5.0 (SysStat Inc.).

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4.2 Cuticle and its Protuberances

The insect exoskeleton is called cuticle. The cuticle functions as an armour against the hazards of the environment (e.g. dehydration, predation, parasites, infections, etc). It also serves as anchorage site for the muscles, metabolite deposits and, through coloration it can play a role in communication and defence (Gorb, 2001).

The cuticle, which is produced by an underlying epidermis, is subdivided into epi- and procuticle. The epicuticle is thin (1-2 micrometers) whereas the procuticle can more than several hundred micrometers thick. The latter can be divided into endo- and exocuticle. The epicuticle is composed of waxes, lipids, tanned proteins and covered externally by a cement sub-layer, for protection against abrasion. The function is mostly sealing off the insect from the outside environment, in order to keep water homeostasis. The procuticle in turn possesses chitin fibres embedded in a protein matrix. The chitin fibres, a structural polymer, are aligned parallel and organized in numerous layers, which in turn are rotated in relation to each other layer (Neville, 1975).
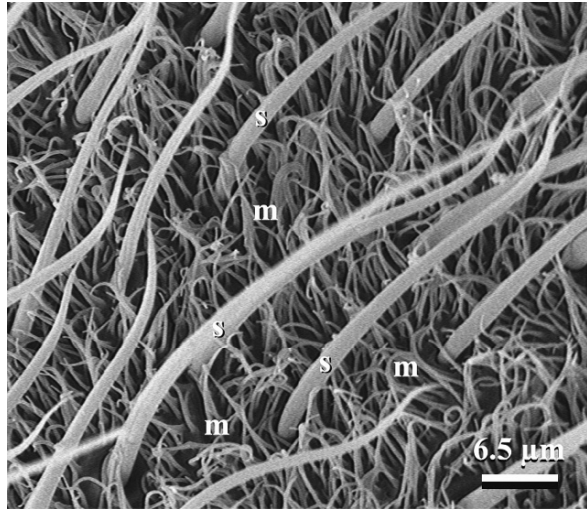
Long and thin cuticular expansions or protrusions may be called "hairs", but the actual diversity requires specific terminology. Richards and Richards (1979) proposed a scheme for classification that is widely accepted (Gorb, 2001), based on the ontogenetic origin and morphology: (1) multicellular processes (2) outgrowths originated form two differentiated epidermal cells, (3) unicellular processes, and (4) subcellular processes with more than one projection per epidermal cell.

(1) Among the multicellular type, those known as spines or thorns lack specialized cells in the underlying epidermis, and are recognized by the absence of a socket and relatively big size. (2) On the other hand, specialized cells in the epidermis originate setae, scales, specialized hairs (e.g., urticating) and sensory trichobothria, among others. These are originated by a trichogen cell (secreting the cuticle of the protrusion), a tormogen cell (secreting the socket of the protrusion) and a often sensory cell (later differentiated in a sensitive neuron or degenerated in those non-sensory function setae) (Gorb, 2001). (3) Unicellular processes include acanthae, which size can vary from relatively small (few micrometers) to large (500 μm) and posses neither socket nor innervation. (4) The subcellular processes are called microtrichia vary in shape, always small (few micrometers long). Each cell epidermal corresponds to several microtrichia. These microtrichia may reach a high density because of their small size and short distance between them.

A dense layer of hairs, conferring either a silvery-sheen or matte aspect to the insect surface, covers the body and legs of water striders. This cover varies according to the insect and its relationship with water. Below I describe a general pattern of such a cover.

Based upon Andersen's (1977) description, the *body* cover consists of two different hair layers, differing in scale and origin, the macro and micro-hair layers (Fig. 4.1). The macro-hair layer consists of long, flexible setae (macrotrichia according to Andersen, 1977) inserted in sockets in the cuticle surface (Fig. 4.1 "s"). In this layer, different lengths of setae can be recognized (Fig. 4.2 "s1", "s2"), sometimes forming more sub-layers. The most common setae are 40 to 60 μm long, about 2 μm

in diameter proximally and gradually tapering towards the apex, inclined about 30° to 50° relative to the insect surface with a density of about 3000 to 5000 setae mm^2 (according to Andersen, [1977], but according to my own measurements it may be up to 1.2×10^4 setae per mm^2, see Fig. 4.1). Scattered among these setae there is yet another kind of hair, basically the same as those described above but much longer, 100 μm or more. All the setae are striated longitudinally, with a certain pitch. The grooves are about 0.2–0.4 μm wide (Fig. 4.2).

The micro-scale layer consists of 1–10 μm long microtrichia with about a 0.5 mm diameter at the base, arising perpendicularly from the cuticle, but irregularly bent at the apex (Fig. 4.1 "m"). They occur at a density of $8–9 \times 10^5$ microtrichia per mm^2. Because of the high aspect ratio, they often tend to agglutinate and collapse in SEM preparations (Fig. 4.1).

Fig. 4.2 Leg cover of setae of *Aquarius elongatus* (Gerridae). Note two dimensions of setae (s1, s2), plus a much thicker thorn (t) in the middle of the picture. Note also the striated pattern of the setae
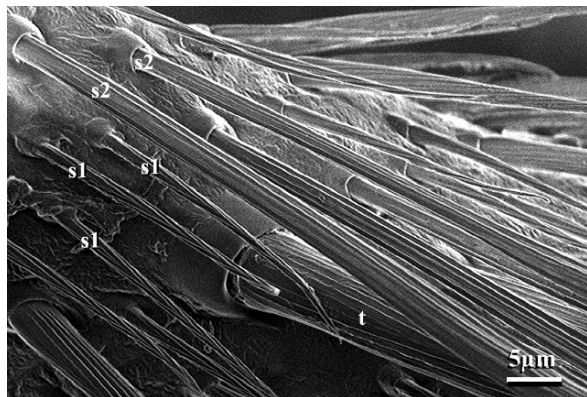
Fig. 4.3 Mid tarsus of
Halobates germanus
(Gerridae). Note full
coverage by setae, claws (cl)
and long trichobothria (tb)
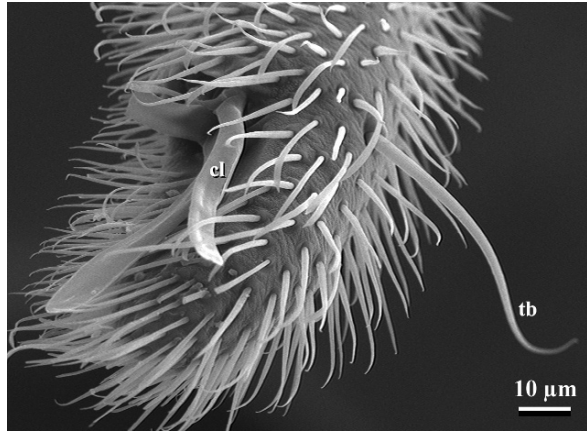
Trichobothria are also present, very long (300 μm or more) (Fig. 4.3), but with a sensory function (Lawry, 1973; Andersen, 1977; Schuh, 1975). These specialized hairs obviously do not play a significant role in water resistance.

Legs in turn are covered exclusively by setae (Figs. 4.2 and 4.3). No microtrichia are visible over the relatively smooth cuticle. The setae are also about 20–80 μm long and distally inclined. However, the density is higher than that of the body, reaching 1.2×10^4 or more setae per mm^2 in the mid and hind tarsi and hind tibia (according to Andersen, [1977], but according to my own measurements it may be 2.7×10^4 setae per mm^2). There are other specialised setae on the ventral side of the legs, which are in contact with water. These are longer, some with their tips bent, or distally spatulated as in sea skaters (Andersen, 1976). Additionally, conical thorns are present, 50–70 mm long and 6–8 mm wide (Fig. 4.2 "t").

The above-described scheme for body and legs is the basic pattern of waterproof surfaces in Heteroptera living on the aquatic environment (i.e., water striders). The pattern differs according to the ecological needs of the species and will be outlined in Section 4.3 of this chapter.

The role of a hydrophobic secretion from the metasternal gland in the waterproof function was suggested by Brinkhurst (1960) and other authors and proven incorrect by Staddon (1972). However, specialized secretions have specific protection functions during *Gerris najas* diapause, such as avoidance of freezing, antibiotic, and possibly repellent (Hauser, 1985). These secretions are deemed to be epidermal secretions carried to the surface through pore channels. Thus, the possibility of other types of secretions enhancing hydrophobicity (or increasing wettability, as in certain beetles [Dettner, 1985]) remains open.

4.2.1 Anti-Wetting Function of the Hair Cover

The surface of insect cuticle is basically hydrophobic, with a contact angle of a water drop of 90°–100° when measured over a flat, even surface (Wagner et al. 1996). This is expected due to the presence of wax on the epicuticle, but much higher contact

angles are reported for many insects, reaching over $160°$ (Wagner et al. 1996). The "super-hydrophobicity" effect of the insect cuticle first attracted attention over 50 years ago (Holdgate, 1955; many insects) and has continued up to the present (Gao and Jiang, 2004; misidentified Gerridae species). How can a common hydrophobic surface reach a super-hydrophobic effect, without changing the chemical composition?

The answer lies in the surface texture (Perez Goodwyn et al. 2008). Insect cuticle may be relatively smooth, rough, ornamented, or have numerous outgrowths. These protuberances, when arranged in the appropriate way and with the correct architecture, can achieve an increased contact angle. The formal deduction and interpretation of this effect was carried out by Cassie and Baxter (1944), based on the Wenzel's equation (Wenzel, 1936) for contact angle on rough surfaces. The contact angle θ' on a surface composed of solid and air is,

$$cos\ \theta' = f_1\ cos\ \theta - f_2 \tag{4.1}$$

where f_1 is the fraction of liquid area in contact with the solid material, f_2 is the fraction of the liquid area in contact with air, and θ is the contact angle of the solid material with water. The equation was used to describe fibres in a grid or wire grating, which produces an air and solid interface with the liquid. The bigger the f_2 proportion and the smaller the f_1, the higher the contact angle. Discussed in the context of textiles in the original paper, a broader space between fibres in this case, would allow a higher contact angle. However, a much too large interspace could allow a falling drop (i.e., rain) to pass through easily and wet the surface.

Thorpe and Crisp (1947), Crisp and Thorpe (1948), and Crisp (1950) further elaborated the mechanical theory of a hair pile in contact with water using the plastron of *Aphelocheirus* sp. as a model (see next section, Figs. 4.4, 4.6D),
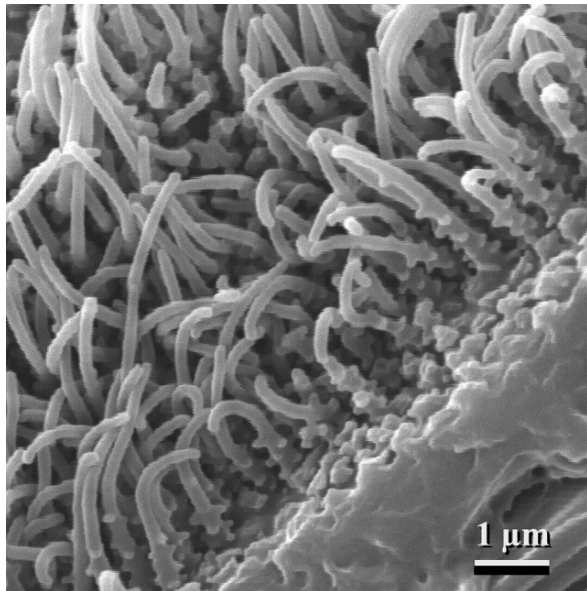
Fig. 4.4 Microtrichia of plastron of *Cryphocricos vianai*

which must resist constant water pressure. In this context I use the word "hair" to describe long and thin outgrowths, in the insects either setal or microtrichial origin. It has no relationship with mammal hairs, which are not homologous. This description is general, valid to any similar structure regardless of its biological origin.

These authors showed that in a hair pile at the interface water-air, under equilibrium pressure difference, any single hair would resist vertical deviation from the interface line. However, on the horizontal plane, the efficient resistance of the system would depend on the rigidity of the hairs. They also showed the importance of the inclination angle of these hairs in contact with the fluid. A simple, perpendicular to the interface hair pile would resist water pressure only as long as the contact angle of the bulk material was greater than $90°$. With an inclination angle the efficiency was improved; however, for achieving the most effective protection against water pressure, the optimum solution was a hair pile parallel to the interface. Also the regularity and high density of the hairs play an important role in achieving an effective water resistance. An optimum solution is observed in the plastron of *Aphelocheirus* (see next section).

In the same papers, the question of different requirements for waterproofing ("rain proofing"), and water resistance under even pressure was raised. In irregular wetting without pressure resulting from rain or a drop contacting the hair pile, there is a tendency for the hairs to be wetted only on one side. The surface tension will draw the hairs together in the wetted region, with a breakdown of the rain proofing. Thus, the hairs tend to be longer and thicker than necessary for underwater protection (i.e., plastron, Fig. 4.6) to withstand these lateral forces. A high apparent contact angle is required between the liquid and the external surface to promote runoff of the liquid. As explained before, to achieve this waterproof effect, a porous surface that is as open as possible is necessary so that the liquid will have the minimum possible contact with the solid. The best examples for this principle are the legs of water striders (Figs. 4.2, 4.3, 4.6A). The influence of density was previously highlighted (Suter et al., 2004, see also Stratton and Suter, 2009) working on various spiders including aquatic. Some spiders' hair piles were clearly adapted to irregular wetting. In that work, they applied a pressure index, as the sustainable pressure difference for a given hair pile to rate the water protection of the spiders used. Applying this index is not possible now, because the data I posses is insufficient (no contact angle of water and a single hair) and incompatible (as the density in this work is expressed as number of structures per unit area, and not per unit length as in Suter et al. 2004). However, the density of hairs in aquatic Heteroptera seems to be possibly one order of magnitude higher. It would be interesting to apply this index in a future work.

To resume, resistance to water penetration under pressure requires a fine scale structure of some rigidity with maximum solid/liquid contact, which is actually found in insect plastrons. If the hair pile is underwater, any displacement force on the hair will be a difference term due to the imposed pressure and the displacement of the structures themselves. But, if the hair pile is in the air, and a water drop contacts on one side of a hair, the displacement force will be absolute. Thus the

requirements for irregular wetting will be in the other direction: thicker hairs and bigger interspace between hairs.

Waterproofing and water resistance under pressure requirements seem to run against one another (Fig. 4.6).

4.2.2 On the Plastron and Air Bubbles

The term plastron was introduced by Brocher (1909) for a simple air cover over the body. However it was not until the work of Thorpe and Crisp (1947) that the theory of plastron respiration was thoroughly worked out.

Here I follow Thorpe's (1950) definition of plastron, with *Aphelocheirus aestivalis* as an example. Plastron is an **incompressible**, thin layer (bubble) of air, supported by specialized minute hairs (microtrichia in this case) or alveolar structures (as for instance in eggs, Hinton, 1981) on the body and in contact with the spiracles (or air exchange structure) of the insect. The gaseous exchange should be possible from the water to the plastron without requiring the insect to collect atmospheric air from the surface (Fig. 4.6D).

Many sub-aquatic arthropods have instead a **compressible** bubble (See Section 4.3, group **d.ii**). Minute hairs (microtrichia or setae, Fig. 4.6B, C) also retain this bubble, and gas exchange with the water occurs. This allows the insect to stay underwater much longer as the original air store volume would permit without gas exchange with the surrounding water. The bubble loses oxygen because the insect uses it. Hence, the nitrogen proportion will increase. If in the surrounding water there is plenty of saturated atmospheric air, oxygen will diffuse in, and at the same time nitrogen out of the bubble. And thus the insect can use this newly diffused oxygen. But as the nitrogen is diffusing out, sooner or later the bubble will reduce in size. If this bubble were not renewed, the water would invade the tracheal system at some point (Thorpe, 1950). Thus, bubble must eventually be renewed.

On the other hand, the plastron size is not changed, regardless of the gas exchange (See Section 4.3, group **d.i**). Thus, as long as there is enough saturated air in the water, a plastron will neither need renewed atmospheric air, nor bubbles in the water (as for example in Stride's (1953) classical example of the water beetle *Potamodytes tuberosus*).

Thin microtrichia may be involved in both systems (Fig. 4.6B, D). However the morphology, aspect ratio and density will be different according to the function. Following Crisp and Thorpe, (1948) and Crisp, (1950) for a properly working hairy plastron, the hairs' aspect ratio (note: r/h = radius / height as defined initially in those contributions) should be 0.2 or higher, considering the Young modulus of the insect cuticle. The microtrichia were described as 0.2 μm diameter, and 5 to 7 μm high, with the tip bent at 90°. The density of microtrichia was estimated at about 2,500,000 per mm^2. These authors assumed that the failure of the plastron under pressure (over 2 atm pressure) was due to the buckling of the microtrichia.

These authors have not provide appropriate photographs, but made hand drawings based upon light microscope observations. Later on, Parsons and Hewson (1974)

provided the first SEM micrographs. Despite the low resolution of that time's technology, they were able to accurately measure *Aphelocheirus aestivalis* and *Cryphocricos hungerfordi* (misidentified, see Sites and Nichols, 1993; Lopez Ruf and Bachmann, 2000) plastron's microtrichia. The measurements provided would make aspect ratio of 0.2 limit questionable (from 0.01 to 0.03 or 0.1 for the shortest hairs). However they described "basal nodules" present in the basal half of the microtrichia. It is difficult to determine these nodules in their micrographs, but in the present work (Fig. 6.4) and Hinton (1976), these nodules are clearly reinforcing the whole structure, preventing buckling in the basal half of the microtrichia. As is evident from the micrographs, clogging occurs only in the apical half, while the bases remain parallel. This effect would render the effective aspect ratio much higher, because only the distal half is subject to bending. This is actually the bent tip described by authors before, which is 1 to 1.5 μm long, and 0.1–0.2 μm in diameter, thus approximately 0.1 r/h. Still, the optimum aspect ratio for an effective plastron is lower than suggested. The main reason of this discrepancy is possibly that in the original paper of Crisp (1950), the measurements of the microtrichia were approximate at best. The data of Parsons and Hewson (1974), Hinton (1976) and the present contribution (Fig. 6.4) represent accurate plastron microtrichia measurements. The density of these microtrichia is very high, separated from each other by less than their own diameter (200–500 nm), and the nodules would make the structure even more compact and stable. Hinton (1976) showed that this plastron's microtrichia density is much higher than described earlier, up to 4,000,000 per mm^2 (Fig. 6.4).

The other reason for this confusion regarding the aspect ratio is found in Hinton (1976). He showed analytically that the cause of failure under pressure of the plastron is due to simple water penetration through the hairs, much before the whole structure collapses. His estimations, based on accurate measurements of both density and morphology, show that over 40 to 96 atm would be necessary to buckle one single microtrichium. Hence, the plastron collapse was deemed to be a cause of wetting.

On the other hand, microtrichia cover of **compressible** air stores or bubbles (Fig. 4.6B, C), would have a r/h one order of magnitude lower (0.01 to 0.005, for *A. paludum*, see Fig. 4.1) or even lower in setae cover (Fig. 4.5, *Belostoma oxyurum*. See also Wichard et al., (2002) *Ilyocoris cimicoides*, *Nepa cinerea*, and *Notonecta glauca* as well as Heckman, (1983) *Hesperocorixa* sp). In these setae cover compressible bubbles, there is as well a lower density of prolongations per mm^2.

Nevertheless, the cause of collapse in breathing compressible bubbles is due to the bending under pressure, when the air is disappearing. The microtrichia of compressible bubbles start to bend from the base, or close to it. Thus, even under low pressure, a very long and thin filament will easily bend and collapse the air space under it. In a plastron, the microtrichia do not bend, but withstand pressure perpendicularly, with the tips of the hairs creating the optimum configuration for water resistance (Crisp and Thorpe, 1948): fibres parallel to the interface liquid-air.

In this context, and keeping this different behaviour in mind, and at a certain density, the aspect ratio is a valuable tool for recognizing a true hairy plastron.

Fig. 4.5 Setae coverage of the compressible air bubble of *Belostoma oxyurum* 3rd instar larva (Belostomatidae) in the ventral abdominal store
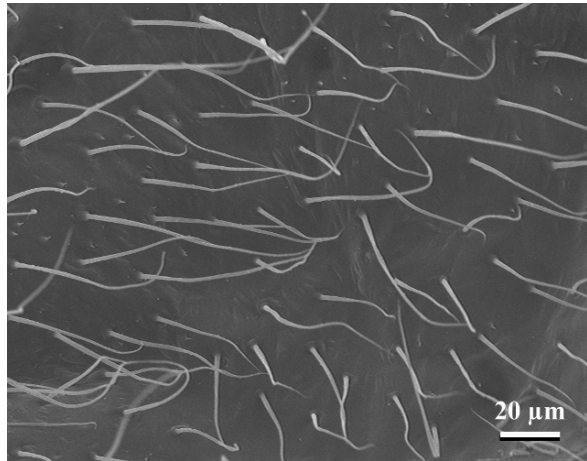
Hairs with an effective aspect ratio (i.e. considering the free bending part of the prolongation) of approximately 0.1 may work as plastron, and those with 0.01 or lower, will not resist water pressure when the air bubble is collapsing.

4.3 Heteroptera in/on/Near Water

Many Heteroptera live in, on, or near aquatic habitats and thus, have evolved diverse adaptations to water. The focus of the following classification is on the adults and immature stages except eggs. Many eggs do have water protection structures, namely a plastron, not only in aquatic but also in many terrestrial bugs. This kind of plastron is from the alveolar type and it is extremely diverse (Hinton, 1969a, 1981; Cobben, 1968). It is adapted to keep eggs from drowning during accidental submersion; unlike adults and larvae, eggs cannot crawl away.

The first and easiest division to describe the diversity of water-resistance adaptations, may be terrestrial and aquatic bugs. However, this distinction is misleading and does not reflect the real diversity of adaptations. Many taxa that live in intermediate points, such as those on the water surface (Gerromorpha) or those shore dwellers (Saldidae, Gelastocoridae), as well as mixed environment requirements during the life cycle blur the picture.

Based upon the water-resistance adaptations in adults and larvae (except eggs) the heteropteran bugs can be divided into four large groups:

a. Living in marginal biotopes, close to water or very high humidity
b. Living in air, but on the water surface
c. Living in a middle point between water and air. Resisting immersion for short but regular periods.
d. Living under water

Group (a) Many representatives of Heteroptera live in close relation to water, without venturing onto its surface. They live in the gravel or stones close to water bodies, in moss, algae masses and tufts and with a very high humidity.

The setae cover of these insects is prepared to resist wetting only occasionally (waterproof); it consists of long setae with bare parts of cuticle exposed. No development of dense thin microtrichia is present, or this is relatively scarce (e.g., Macroveliidae, Hebridae and some Mesoveliidae). These species' pilose cover is adapted to avoid being trapped in the water surface layer if it accidentally falls on it. The setae are not dense, but are resistant to accidental water contact, promoting fast runoff (similar to the pattern of Figs. 4.2, 4.3).

According to Andersen (1982) this is the ancestral environment for Gerromorpha. The Gerromorpha living farthest from the water are Macroveliidae (McPherson et al. 2005), some Mesoveliidae (Madeoveliinae and some species of Mesoveliinae), primitive Hydrometridae (e.g., Heterocleptinae), as well as some *Hydrometra* (Polhemus and Polhemus, 1987) and also Eotrechinae (Gerridae) (Andersen, 1982) dwelling in moss, litter, under stones up to several meters away from water. Most Hebridae belong to this group (Andersen, 1981).

Among the Leptopodomorpha, most Saldidae (except *Enosalda mexicana, Paralosalda mexicana, Saldula palustris* (Stock and Lattin, 1976), *Halosalda lateralis* (Brown, 1948) see "group **c**") and Leptopodini (Leptopodidae) can be placed in this group (Polhemus, 1985; Yamazaki and Sugiura, 2004).

Dipsocoridae (Dipsocoromorpha) are mostly shore inhabitants of rivers (Štys, 1970; Schuh and Slater, 1995). They are covered by a dense pile of long setae and presumably can survive flooding of their environment. A possible plastron has been suggested (Schuh and Slater, 1995), but it seems unlikely, despite the lack of detailed morphological information on the hair cover.

Among the Pentatomorpha, Lygaeidae species are chiefly terrestrial, with very diverse feeding habits; some of them are considered pests (Schuh and Slater, 1995). In the subfamily Rhyparochrominae however, *Lipostemmata* spp. are peculiar (Ashlock, 1970; Lopez Ruf and Mazzucconi, 1999). They live and feed on floating water ferns (*Salvinia* sp. see Cerman et al., 2009), but, in case of danger, they will crawl to the underwater side of the floating plant. Presumably they retain a bubble of air, which allows them to stay there for "several minutes" (Baranowski and Bennett, 1979). Undoubtedly this is a compressible bubble around the body, due to the relative dense pilosity (probably setae) similar to that described by Slater and Woodward (1982) of an allied genus.

Another exception is found in Cimicomorpha. This infraorder is probably the largest in number of species. However, only one species, *Nabis gagneorum*, seems to be associated with water. It lives in riparian habitats close to and on wet midstream rocks. The genus (with several hundred species worldwide) underwent an insular radiation in the Hawaii archipelago, occupying niches otherwise uncommon in the continental distribution (Polhemus, 1999).

The Gelastocoridae and Ochteridae, both Nepomorpha, share the same habitat (Menke, 1979a, b) with a different adaptation. Water-resistant hairs do not cover the bodies of these groups' species (even though Ochteridae are called "velvety shore

bugs"). Their bodies are mostly bare cuticle, either rugose or more or less smooth, and strongly sclerotized. In case of accidentally falling into water, they can breathe as the 1st abdominal respiratory spiracles open to this cavity (Parsons, 1970). The air trapped under the wings should last until they can crawl out of the liquid.

Group (b) Within this group, the highest number of species of Gerromorpha (Gerridae, Hydrometridae, Mesoveliidae, Veliidae) are represented. According to Andersen's (1982) habitat classification, this would include those species ranging from living on plant-covered water surface, to completely free water surface, either lotic or lentic (excluding open sea water). The basic hair pattern described (Section 4.2) is present in these species (Andersen, 1982; Andersen and Weir, 2001). The development of the microtrichia cover is characteristic and extensive, with a density of 80,000 per mm^2 or higher. Thus, there is a double protection layer, one waterproof promoting fast runoff in case of droplets contacting (the big setae layer), and the other, useful in case of submersion (the microtrichia layer) (Fig. 4.1 "m")

There are some bugs that are completely covered by water resistant microtrichia like the Gerridae, or covered only in part as in Mesoveliidae (Andersen and Weir, 2001; 2004), or Veliidae (Mazzucconi, 2000). In the case of coastal marine water striders, such as Mesoveliidae (*Mesovelia polhemusi* Spangler, (1990) which live in crevices between mangroves' roots (and thus, it are not strictly surface water dwellers), and certain Veliidae (*Haloveloides, Halovelia, Xenobates*, Lansbury, 1996; Andersen, 1999; Andersen and Weir, 1999) having special adaptations. In these marine insects the density of microtrichia is exceptionally high (over 10^6 per mm^2) compared to freshwater species, probably due to a risk of exposure to lower surface tension in the sea water (see also section c.ii. *Halobates* sp.). This risk was described by Baudoin (1976) as "the deadly foam trap", which, according to this author, should be the biggest obstacle for insects' invasion of seawater. A similar case in fresh water is presumably the foam dweller species (e.g. genus *Oiovelia* (Veliidae), see Mazzucconi and Bachmann, 1997) with an increased density of the microtrichia cover.

Even though the microtrichia cover is present, the aspect ratio of these prolongations is quite low, 0.01 or less. The main function is to survive accidental or circumstantial immersion (i.e. many Gerridae lay their eggs under water, thus at least the female must submerge for some time, to oviposit). On the other hand, the setae, long and stable, are much more important, to promote fast runoff of uneven wetting. These setae appear typically with a density of 12,000 per mm^2 (Gerridae) or lower (Hydrometridae, Hebridae etc. (Andersen, 1977)).

Group (c) In this group only marine insects are represented, either intertidal or open sea inhabitants. These insects can be divided into two subgroups based upon their adaptations for water-resistance: (c.i) those adapted to survive underwater for a certain period of time on a regular basis, (c.ii) water surface dwellers, which are very often submerged. Basically, in this group also there is a double protection layer, one promoting fast runoff in case of droplets contact (the big setae layer), and the other useful in case of submersion (the microtrichia layer). Some specializations are present nevertheless.

(c.i) In the first subgroup, Aepophilidae (monobasic for the species *Aepophilus bonnairei*), Omaniidae (both Leptopodomorpha, Kellen, 1960; Cobben, 1970), Hermatobatidae (Cheng, 1977; Foster, 1989), certain *Halovelia* (Veliidae) are included (Kellen, 1959; Andersen and Polhemus 1976; Andersen, 1999; Andersen and Weir, 1999) (all Gerromorpha). These are intertidal inhabitants, sheltering in crevices of rocks or corals during high tide, when they presumably remain motionless (except *Hermatobates* see below).

Among the Leptopodomorpha, a "plastron" was described in *Aepophilus bonnairei*, restricted to certain parts of the body (King and Ratcliffe, 1970), and fitting the definition of Thorpe and Crisp (1947) under a more or less loose interpretation. Even though no experimental data support this assumption, the circumstantial evidence suggests the ability to remain submerged for "up to several days" (King and Fordy, 1984), with probably no available air bubbles in rock crevices. A compressible bubble may not last that long, however, no experiments are available to confirm this hypothesis.

Among Saldidae species, *Enosalda mexicana, Paralosalda mexicana,* (Polhemus, 1985), *Saldula palustris* (Stock and Lattin, 1976), and *Halosalda lateralis* (Brown, 1948), are usually covered regularly by high tides. However, in none of them is a plastron developed. Presumably these insects would either find crevices with some air store or depend on an unspecialised compressible air bubble around their bodies.

Hermatobatidae species are called intertidal coral dwellers or treaders, which survive tides submerged (Foster, 1989; Andersen, 1999). These insects present an interesting microtrichia pile. Each hair is from 1 to 3 micrometers long, and ends in a ball tip. The tips are approximately twice as wide as the shaft. These microtrichia form a uniform and dense cover on most of the body. This configuration was actually predicted by Crisp (1964), unaware of its existence in nature. It was described as a hypothetical sub-optimal to achieve efficient water protection (even with low contact-angle materials) before the optimal configuration, which hairs parallel to the water surface. Even though a plastron function seems reasonable according to the morphology, this is probably not the only respiration method on which these animals depend. Foster (1989) found these insects strictly associated with stones containing air-bubbles. He suggested the importance of the presence of free available air for the survival of this species in the wild. When forced to submerge in laboratory conditions, they remained active for 4 hours and survive for over 13 hours. This performance suggests an inefficient plastron, or normal compressible bubble behaviour.

Other Gerromorpha that survive submersion periods include *Halovelia* species which, except for higher density of microtrichia cover, do not have any adaptation, thus probably it is totally dependent on trapped air in crevices.

(c.ii) In the second sub-group *Halobates,* (Gerridae) and *Haloveloides* (Veliidae) are the only open sea water dwellers (Andersen, 1999). Only *Halobates* has an outstanding water protection structure (Cheng, 1973, 1974, 1981; Andersen, 1977, 1982). The microtrichia pile is composed of specialized prolongations. Each microtrichium has a thickened head, several times wider than the shaft, and usually tilted to one side like a golf club (Fig. 4.6). On the shaft itself, there are up to 4

Fig. 4.6 Diagrammatic representation of anti wetting setae and/or microtrichia coverage with different functions **A**: Stiff setae, over 50–70 μm long, simple waterproofing, against irregular wetting, high aspect ratio. **B**: Common microtrichia about 7–9 μm long, compressible bubble, high aspect ratio. **C**: Setae over 50–70 μm long, compressible bubble, high aspect ratio **D**: Special microtrichia 5 μm long, with basal nodules and bent tip, true plastron, low aspect ratio. **E**: Setae with underlying microtrichia: double function cover, waterproofing and air bubble. m: microtrichia, s: setae
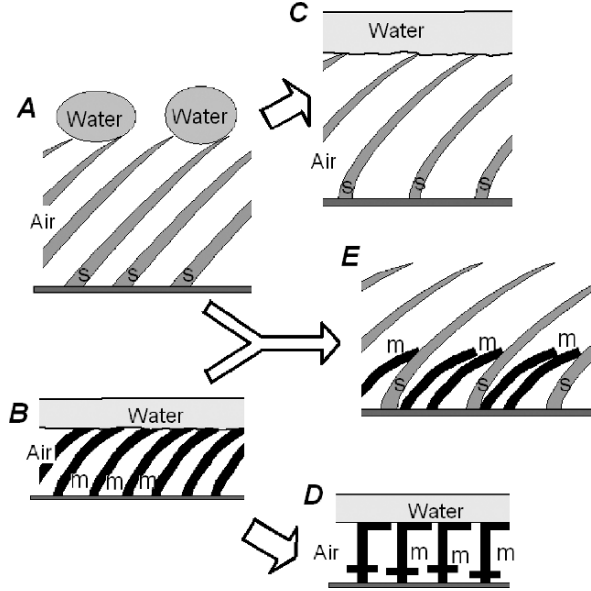
perpendicular branches interlocking the microtrichia. The microtrichia shafts are 0.8 to 1.05 micrometers apart (compare with *Cryphocricos*'s plastron Fig. 4.3); however the heads are much closer. This structure would provide effective water protection, in case of being submerged, which should occur frequently in the open ocean. However, these insects are not able to survive long periods of submersion (Cheng, 1981, 1985). This microtrichia cover seems to be an ultimate water protection, not effective as a plastron, as extra protection against accidental submersion in the sea, where much lower surface tension may be expected (Baudoin, 1976; Guthrie, 1989). In this genus, the cover of long setae also is very dense (12,000 to 17,000 per mm^2 according to Andersen, (1977), but about 30,000 according to my measurements [Fig. 4.7]), much more than fresh-water related genera. This would enhance the waterproofing effect.

Fig. 4.7 Thoracic microtrichia cover of *Halobates germanus* (Gerridae). Note "golf-club" shape heads and interlocking prolongations (*). S: setae
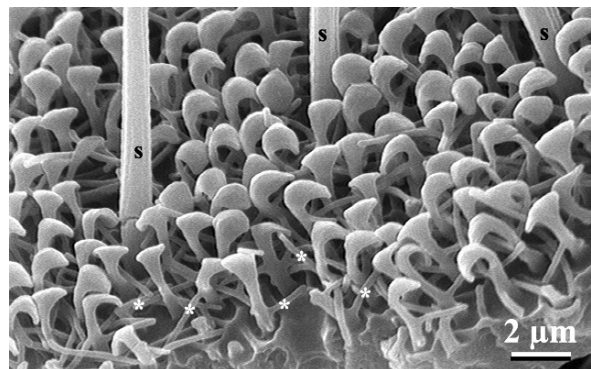
The (**c**) group is characterized by an enhanced microtrichia layer, aided by a waterproof setae layer. The microtrichia may have simply an increased density and lower aspect ratio (*Aepophilus* sp., *Halovelia* sp.) or improved morphology to resist wetting (*Hermatobates* sp. and *Halobates* sp.).

Group (d) here we also have two groups: (d.i) true plastron breathers (with an incompressible bubble and no need to renew the air [Fig. 4.4]) and (d.ii) compressible bubble breathers, with a bubble that must be renewed from time to time (Fig. 4.5).

(d.i) Apehlocheriridae (Messner et al., 1981), and some Naucoridae like *Chryphocricos hungerfordi*, (Parsons and Hewson, 1974; Sites and Nichols, 1993), *C. barozzii* (Lopez Ruf and Bachmann, 1996; Lopez Ruf et al., 2000) and *C. vianai* (Fig. 4.3). Also probably *Heleocoris mexicanus* (Hinton, 1969b, 1976 also suggested *Idiocarus* sp. but the microtrichia are much too long), and Helotrephidae, *Neotrephes usingeri* (Hinton, 1976). Polhemus (2000; after Mahner, 1993) stated in a broad context regarding subaquatic Nepomorpha that "available evidence suggests that at least all of the genera exhibiting brachyptery possess a plastron" describing the probable breathing habits of the fossil family Leptaphelocheiridae. I think this is a reasonable assumption. This family is probably the oldest known group of plastron breathers, although nothing is known about their habits. There still are the possibilities that this insect had an exposed bubble or even used cutaneous respiration, and of course it might travel often to the surface. In the context of the hypothetical elaboration of a fossil's habits, it seems reasonable. However, extending this to all extant species seems questionable. Especially because the definition of plastron is so accurate, and so many intermediate conditions are present (see group c.i, above). The plastron function was assessed only in *Aphelocheirus aestivalis*. The microtrichia structure of *Chryphocricos* spp. is the only one practically identical to that of *A. aestivalis*. All the other presumably Nepomorpha "plastron" function hair piles are either longer microtricha, and/or its base is not described, thus in this review, they are quoted as probable plastron.

Under the plastron category *Plea minutissima* is a special case. Pleidae bugs have an exposed bubble on the abdominal sternites, plus a subhemelytral reserve (Gittelman, 1975). This behaves as a normal compressible bubble gill. However Kovac (1982) suggested and empirically proved that during winter diapause, this insect can switch to plastron respiration. The effectiveness of this system is questionable, although it allows the insect to survive for up to months without replenishing the air due to its notably reduced metabolism. However it is unlikely that it can survive under non-diapause metabolic needs exclusively on the plastron.

(d.ii) truly aquatic Heteroptera, which develop their whole life cycle under water, are the representatives of this group. Most Nepomorpha (except Aphelocheiridae, Gelastocoridae, and Ochteridae) are included here, namely Nepidae, Belostomatidae, Corixidae, Naucoridae, Potamocoridae, Notonectidae, Helotrephidae, and Pleidae.

These Heteroptera have mostly the same basic respiratory system. It consists of a subhemelytral air store, which may be connected and supplemented with an exposed bubble on the ventral side of the abdominal sternites (Parsons, 1970, 1972).

There are several modifications related to this mode of renewing the air in the store. Both in adult Nepidae and Belostomatidae, there are siphons that can connect the air chamber with the water-air interface, without forcing the insect to surface (Menke, 1979c). These siphons, which are retractile in Belostomatidae, are basically two straps (Belostomatidae) or half pipes (Nepidae), covered internally by long setae, creating a virtual air tube. There is no ventral exposed bubble in Nepidae adults, and only an almost non-functional hydrophobic hair stripe that has some air attached in Belostomatidae (Parsons, 1972). In Corixidae, the sub-hemelytral air store extends to the anterior border of the prothorax. Through a slit between head and pronotum, this store is exposed directly to the air interface for a few milliseconds during a fast-upward trip of the bug, which lives attached to submerged substrata when resting. The Notonectidae, mostly neustonic, directly expose their ventral abdominal store to the air, with their body ventral side up.

All larval stages of these families possess only the exposed ventral bubble due to the lack of wings (Fig. 4.5).
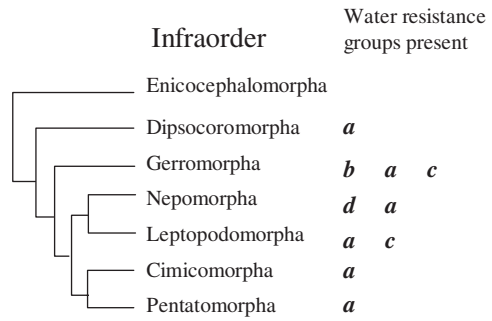
The exposed bubble in all cases is supported by long setae, which hold the bubble against the body as an even cover (Fig. 4.5) or as a two-sloped roof. The latter is found both in larval Nepidae, forming two grooves along the abdomen, as well as in Notonectidae adults also forming two grooves, but occupying all of the abdominal width (Wichard et al., 2002). These setae have a very high aspect ratio, 200 – 400 µm long, striated, and located in single rows close to one another. When extended with an air bubble under them, they contact the setae on the other side of the groove. Larval Belostomatidae, Pleidae (compressible bubble gill part), Helotrephidae, Naucoridae (Sites, 1991; Lopez Ruf, 1996) (except those of group **d.i**), Corixidae (exposed part of the air store, on abdomen, part of the thorax and legs (Heckman, 1983) and possibly Potamocoridae have an evenly distributed bubble over the ventral side of the abdomen. In this case, the setae are more widely spaced (10 to 30 µm), however also with a high aspect ratio, and up to several hundred micrometers long.

Regarding the Helotrephidae, Hinton (1976) suggested that *Neotrephes* has a plastron. This author provided SEM pictures, and based on the morphology his suggestion seems to be correct (see above section **d.i**). However, Papaček et al. (1988) stated that *Trephotomas compactus* also has a "plastron". They describe a "macroplastron", but based on the pictures and description they provide, *T. compactus* may have a compressible bubble, working presumably functioning similarly to that described above for most of the Nepomorpha.
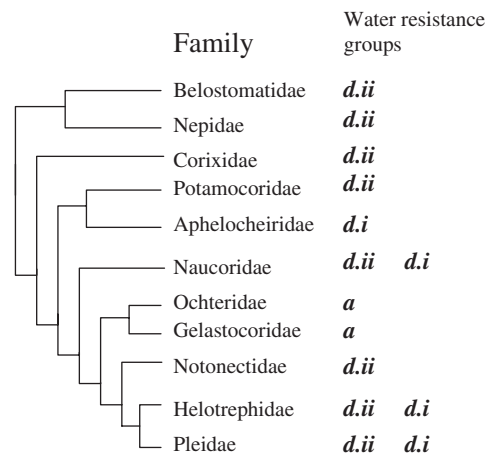
4.3.1 Phylogeny

The phylogeny of Heteroptera shows that both the microtrichia cover and the setae with a water resistance function appeared independently several times (Fig. 4.8). Trends are evident however. The Gerromorpha and Leptopodomorpha are related to water, but never completely sub-aquatic (Andersen, 1982). Nepomorpha on the other hand seems to be mostly sub-aquatic (Mahner, 1993).

Fig. 4.8 Phylogeny of
Heteroptera, adapted from
Wheeler et al. (1993) and
Tree of Life web project.
Letters to the right of
infraorder names, correspond
to water-resistant types
according to this chapter. The
order of the letters represents
the frequency of each type in
the lineage

Infraorder	Water resistance groups present		
Enicocephalomorpha			
Dipsocoromorpha	*a*		
Gerromorpha	*b*	*a*	*c*
Nepomorpha	*d*	*a*	
Leptopodomorpha	*a*	*c*	
Cimicomorpha	*a*		
Pentatomorpha	*a*		

In Nepomorpha (Fig. 4.9) we see a clear reversal from the main subaquatic trend
in the group Ochteridae+Gelastocoridade (Mahner, 1993, Hebsgaard et al., 2004).
The evolution of plastron respiration may have different interpretations. In Fig. 4.9,
the phylogenetic hypothesis Hebsgaard et al. (2004) is represented. Here Naucori-
dae and Aphelocheiridae are in separated monophyletic groups, and hence, the
plastron presumably evolved independently in both. However if we consider the
phylogenetic hypothesis Mahner's (1993), we have Naucoridae + Aphelocheiridae
as a monophyletic group, making the evolution of plastron a common character
(either simplesio- or sinapomorphy). In Helotrephidae and Pleidae, the shared plas-
tron character seems to be newly evolved because of the few cases observed in
each family (see Hebsgaard et al. [2004] for a comprehensive up-to-date revision of
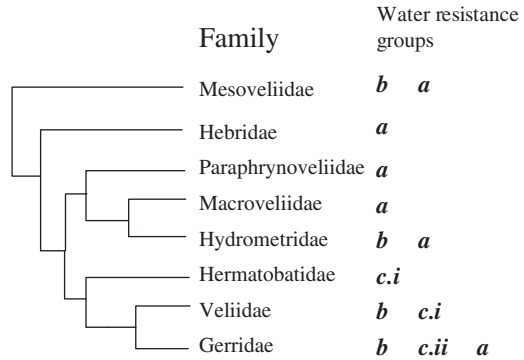Nepomorpha phylogeny).

In Nepomorpha, the only sub-aquatic group, we see that either compressible
bubble or plastron respiration has evolved. Both of them may have neither the
same origin nor the same structure. However both illustrate the principle of water
resistance under even pressure. The hairs (microtrichia or setae) are either densely
or loosely packed, thin, and may be relatively ineffective against rain or uneven

Family	Water resistance groups	
Belostomatidae	*d.ii*	
Nepidae	*d.ii*	
Corixidae	*d.ii*	
Potamocoridae	*d.ii*	
Aphelocheiridae	*d.i*	
Naucoridae	*d.ii*	*d.i*
Ochteridae	*a*	
Gelastocoridae	*a*	
Notonectidae	*d.ii*	
Helotrephidae	*d.ii*	*d.i*
Pleidae	*d.ii*	*d.i*

Fig. 4.9 Nepomorpha
phylogeny according to
Hebsgaard et al. 2004. Letters
on the right are the same as in
Fig. 4.8

Fig. 4.10 Phylogeny of Gerromorpha according to Andersen (1982). Letters on the right are the same as in Fig. 4.8

Family	Water resistance groups		
Mesoveliidae	*b*	*a*	
Hebridae	*a*		
Paraphrynoveliidae	*a*		
Macroveliidae	*a*		
Hydrometridae	*b*	*a*	
Hermatobatidae	*c.i*		
Veliidae	*b*	*c.i*	
Gerridae	*b*	*c.ii*	*a*

wetting. These animals live mostly underwater, thus they need not to be concerned about getting trapped in the surface tension layer. The main concern of these bugs is respiration under water, and hence, the adaptations we find.

On the other hand, both Gerromorpha (Fig. 4.10) and Leptopodomorpha are close or even on the water, but they must avoid by any means being wetted. The development of strong and stable setae (which never get clogged together even under very high densities) guarantees the resistance to water drops. This also promotes easy runoff of water by increasing the proportion of air in the contact interface. In this functional context, the microtrichia cover has only an "emergency submersion" water resistant function, and not a stable breathing one. The modifications present in marine, intertidal or foam dwellers' microtrichia cover seems to be adapted to factors other than continuous respiration, such as an increased risk of lower surface tension. Increasing the density and/or changing the morphology will improve the resistance against water, at least for a certain period of time. This trend is visible also in an unusual invasion of water surface by representatives of Lygaeidae, with no other close phylogenetically related group, not even in the whole Pentatomorpha infraorder.

4.4 Final Remarks

In the context of water protection with a setal or microtrichial pile, different requirements resulted in the evolution of structures adapted to either submersion resistance or waterproofing. The literature cited represent only those works in which a specific reference and/or appropriate SEM photographs or drawings are available regarding protection against water, plus some personal data and micrographs. Heteroptera present the entire range of protection adaptations according to their ecological needs. In the case of waterproofing or uneven wetting protection requirements, large and stable setae are present at a relatively low density, promoting fast runoff of water (group a). On the other extreme, the submersion resistance requirements are met with long and thin setae or microtrichia in a compressible bubble, or with short, thin and high-density microtrichia as in the case of a plastron (group d). An optimum

compromise between these two extremes is met with a cover of long and stable setae promoting fast runoff of droplets, and an underlying cover of thin microtrichia serving in case of temporal submersion (groups b and c).

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