

A general definition of the term “plastron” in terrestrial and aquatic arthropods

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Abstract The term “plastron”, as it applies to terrestrial and aquatic arthropods, has been used in a variety of ways. A generalised and simple definition of this term is provided based on a classification of its structural and functional aspects.

Keywords Respiration · Physical gill · Compressible gill · Incompressible gill · Structural plastron · Functional plastron

When submerged in water some arthropod species and their eggs are able to envelope in a thin layer of air merely a few microns thick. This film of air can occur around the entire body or only over specific areas, depending on the mode of respiration of the particular arthropod (Crowe and Magnus 1974; Hebets and Chapman 2000; Messner and Adis 2000; Krisper et al. 2008; Fielden et al. 2011). This phenomenon is commonly known as the arthropod plastron. The term was established by Brocher (1912a, b, c) and refers to the French term for a cuirass. The structure and function of an arthropod plastron can be quite diverse and complex. Many different and sometimes inconsistent descriptions and definitions of the term “plastron” are found in the literature. An early description was given by Thorpe (1950): “The term plastron is restricted to a ‘gas store’ communicating with the tracheal system and usually in the form of a thin film of constant and negligible volume and large surface area retained in position

by a system of hydrofuge hairs or scales”. Several authors used the term “plastron” as if it is synonymous with “physical gill” (Crisp and Thorpe 1948; Hebets and Chapman 2000). Schmidt-Nielsen (1997) defined a plastron as “a non-compressible gill consisting of hydrophobic hairs into which oxygen diffuses from the water up to a pressure of 3.5 to 5 atm.”. Others preferred to define only the function of these structures as compressible or incompressible gas gills (Rahn and Paganelli 1968; Chaui-Berlinck et al. 2001). The definition of Schaefer and Tischler (1983) includes only small hairs as plastron structure and excludes the function as compressible or incompressible gill. Therefore, in a revised version of this definition, in addition to hairs, Messner (1988) specified more cuticular structures (scales, bulbs and projections) and secretions (wax, cocoons or webs) as possible plastron structures of different arthropod taxa. However, this definition lacks the term for the functional subdivision between compressible and incompressible gas gills. In a new definition, Fielden et al. (2011) describe plastron as “an alternative respiration system that can absorb oxygen from water via a thin layer of air trapped by hydrophobic hairs or other cuticular projections”. These examples show the variety of uses and definitions of the term plastron in the literature and underline the need for a classification that includes structural and functional viewpoints (see Table 1).

Types of structures

Many water-repellent structures exist in terrestrial and aquatic arthropods, which are able to create a thin layer of air surrounding the entire body or around the stigmata or spiracles of the tracheal system. Messner and Adis (1994, 2000) divided such structural plastra into direct cuticular formations such as bent hairs or comb-like projections, and

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Table 1 Different plastron structures in several arthropod groups with functional subdivision into compressible and incompressible plastrons

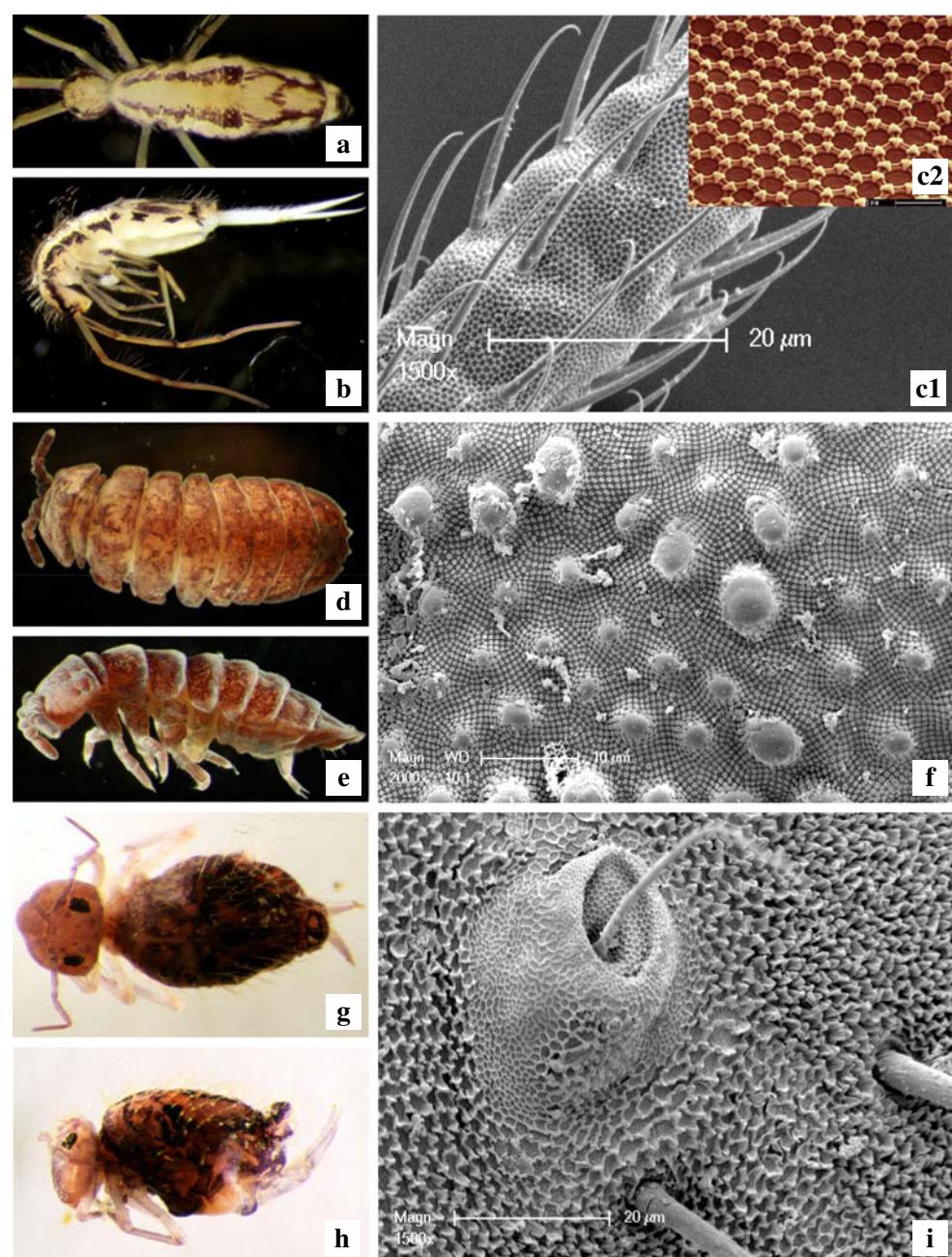
Taxon	(Structural) Plastron	Function		Reference
		Compressible Plastron	Incompressible Plastron	
Arachnida				
<i>Nanorchestes antarcticus</i> (Prostigmata; Acari)	Grooves on the entire body surface	x		Rounsevell and Greenslade (1988)
<i>Platyseius italicus</i> (Mesostigmata, Acari)	Peritremata with microtrichia	x		Hinton (1971); Crowe and Magnus (1974)
<i>Hydrozetes lacustris</i> (Oribatida; Acari)	Cerotegument		x	Messner et al. (1992)
<i>Dermacentor variabilis</i> (Ixodida; Acari)	Spiracular plate with aeropyles and arial chambers	x		Fielden et al. (2011)
<i>Phrynx marginemaculatus</i> (Amblypygi)	Cuticular projections on ventral opisthosomal surface	x		Hebets and Chapman (2000)
<i>Cryptocellus adisi</i> (Ricinulei)	Navicular and calyx like setae and microtrichia	x		Adis et al. (1999)
<i>Argyroneta aquatica</i> (Araneae)	Dense coat of bristles (microtrichia) around the opisthosoma	x		Braun (1931); Heckman (1983)
Myriapoda				
<i>Gonographis adisi</i> (Pyrgodesmidae; Diplopoda)	Cuticular wax secretion around stigmata and tergal plates in juvenile and subadult stages		x	Adis (1986); Messner and Adis (1988)
<i>Polydesmus denticulatus</i> (Polydesmidae; Diplopoda)	Microtrichia and structure of the stigmata	x		Messner et al. (1996)
Insecta				
<i>Acentria nivea</i> (Pyralidae; Lepidoptera)	Web or cocoon based by gland secretion		x	Messner et al. (1987)
<i>Lipsothrix remota</i> (Tipulidae; Diptera)	Superficial cuticular air channels on the surface of spiracular gills		x	Hinton (1967)
Some genera of Cercopidae and Cicadidae (Auchenorrhyncha)	Cuticular wax secretion in juvenile stages	x		Messner and Adis (1992)
Elmidae (Coleoptera)	Subelytral and abdominal dense-arranged setae and scales		x	Thorpe (1950); Hinton (1976); Brown (1987)
<i>Macroplea</i> sp. (Chrysomelidae; Coleoptera)	Larvae with two tracheal connected abdominal hooks	x		Wesenberg-Lund (1943); Thorpe and Crisp (1949); Kölisch and Kubik (2011)
<i>Aphelocheirus</i> sp. (Naucoridae; Heteroptera)	Microtrichia on the entire body surface		x	Thorpe and Crisp (1947a)
<i>Dinotoperla</i> sp. (Gripoterygidae; Plecoptera)	Exochorion of eggs with aeropyles		x	Yule and Jardel (1985)
<i>Agriotypus armatus</i> (Ichneumonidae; Hymenoptera)	Silk cocoon with ribbon-like appendage based by gland secretion		x	Thorpe (1950); Messner (1965)
<i>Paulianina</i> sp.; <i>Edwardsina</i> sp. (Blephariceridae; Diptera)	Spiracular gills		x	Arens (1995)
Enthognatha				
Japygidae (Diplura) from blackwater sites in Brazil	Cocoon based by gland secretion		x	Adis et al. (1989)
Many springtail species (Collembola)	Cuticle structure with microtuberles and hydrophobic lipid layer	x		Noble-Nesbitt (1963); Lawrence and Massoud (1973); Ghiradella and Radigan (1974)

cuticular secretions such as wax and gland secretions making cocoons or webs. The diversity of morphological characters that serve as structural plastrons suggests a polyphyletic origin (Hinton 1967; Messner and Adis 2000). Springtails (Collembola) are a good example of a hexapod order that employs gaseous exchange across the entire body

cuticle (Hopkin 1997). Springtails are primarily small animals with a high surface area to volume ratio, and their cuticle is almost entirely hydrophobic due to the complex structure of hexagonal subunits comprising microtuberles (Fig. 1). The unwettable properties of the springtail cuticle produce the thin air layer that

prevents euedaphic species from submersing and enables surface-living (hemi-and epedaphic) species to drift passively on the water surface (Coulson et al. 2002; Moore 2002; Hawes et al. 2008; Lessel et al. 2011). The exact microstructure of the cuticle varies between different species (Lawrence and Massoud 1973; Eisenbeis and Wichard 1985). Many collembolan species inhabit epigaeic terrestrial habitats wherein the cuticle assumes primarily an anti-wetting and self-cleaning function. The existence of an epicuticular hydrophobic lipid layer was demonstrated by Ghiradella and Radigan (1974) for springtails. After removing this layer with solvents, the cuticle becomes wettable (Noble-Nesbitt 1963).

Fig. 1 Different aspects of the epicuticular structure of selected collembolan species. (a–c1) *Entomobrya muscorum* (Nicolet, 1842) (Arthropleona: Entomobryidae): Habitus dorsal (a), lateral (b) and the typical hexagonal microtubercle structure of the furca (c1). (c2) Arthropleona (©Borensztajn 2001): Higher resolution (bar 1 μm) of the hexagonal microtubercle structure (note the occasional pentagonal and septagonal aberrations). d–f *Tetrodontophora bielanensis* (Waga, 1842) (Arthropleona: Onychiuridae): Habitus dorsal (d), lateral (e) and formation of thoracal macrotubercles that are generated from fused tetragonal microtubercle structures (f). g–i *Allacma fusca* (Linnaeus, 1758) (Symphypleona: Sminthuridae): Habitus dorsal (g), lateral (h) and fusion of the abdominal hexagonal microtubercles to protuberances (i)



Respiratory function

The first scientific evidence of a respiratory function for this structure was demonstrated by Ege (1918) in aquatic insects. The structure and respiratory function of the plastron of the stream-dwelling bug *Aphelocheirus* (Heteroptera: Aphelocheiridae) was described and documented in detail by Thorpe and Crisp (1947a, b, c, 1949). However, as early as 1828, Strauss-Durckheim suggested “...that in cases, where the air reservoir is exposed to the water, the reduction of the respired oxygen-content should be followed by absorption of dissolved oxygen from the ambient water into the air

bubble." (cited from Wolfekamp 1955). In addition, both Dutrochet (1833, 1837) and Comstock (1887) argued for a respiratory function of the air layer, whereas Brocher (1912a, b, c) was later to ascribe only a hydrostatic function. This was demonstrated by the riffle beetle *Elmis* (Coleoptera; Elmidae), where the air reservoir of the subelytral chamber can be condensed to compensate for the change of the specific weight under submerged conditions. With this adaptation, the beetle is able to move vertically between the water surface and the bottom substrate (Thorpe and Crisp 1949, Thorpe 1950; Wolfekamp 1955).

The mechanics and chemistry of plastron respiration are well understood (Stride 1953, 1955, 1958; Hinton 1976; Hinton and Jarman 1976; Chau-Berlinck et al. 2001; Shirtcliffe et al. 2006; Bush et al. 2008; Flynn and Bush 2008). Two basic types of structural plastron are recognized: one compressible and the other incompressible (Rahn and Paganelli 1968). Some authors prefer the term physical gill (the term was first mentioned by Jordan (1929, page 147)) instead of the term compressible gill. The compressible gill has only a limited lifespan, especially depending on the diving behaviour of the arthropod. Being positioned just below the surface extends the underwater time of an air breather more than eight-fold; however, the lifespan of the compressible gill at a greater depth is greatly reduced due to the diffusion of N₂ into the water and the subsequent reduction and gradual collapse of the gas phase (Rahn and Paganelli 1968). Therefore, arthropod species with a compressible gill are permanently forced to move to the water surface to replenish their air supply. The exchange of CO₂ and O₂ between the gas phase and the water is relatively constant in running water. Standing water bodies cause localised oxygen depletion and only a few small-sized and akinesic air-breathing arthropod species such as the aphid *Aspidaphium cuspidati* (Stroyan, 1955) (Homoptera: Aphididae) or the leaf beetle *Macroleptus mutica* (Fabricius, 1792) (Coleoptera: Chrysomelidae) can survive permanently under these conditions (Messner and Adis 2000).

In contrast to the compressible gill, the incompressible gill shows a stable N₂-ratio between the gas phase and the surrounding water. This equilibrium provides arthropod species with incompressible gills with independence regarding the water surface and allows deeper diving behaviour from 10 to 50 metres depth. Below this depth the incompressible gill experiences a functional limitation due to the surrounding water pressure and the subsequent collapse of the gas phase (Messner et al. 1992, Messner and Adis 2000). Deeper diving arthropods, such as the sucking louse of seal *Echinophthirius horridus* (Olfers, 1816) (Anoplura: Echinophthiriidae), display a strong closing system of the spiracle

structure, which serves as a small backup of air in the tracheal system of the louse under high pressure conditions (Webb 1946; Messner et al. 1998; Messner and Adis 2000).

The need for a standard definition and terminology

To sum up, it is necessary to distinguish between the structural and functional aspects surrounding the term "plastron". Indeed, the structural plastron can be divided functionally into a compressible plastron and an incompressible plastron (up to a maximum water pressure of 5 atm). Some examples for the subdivision are given in Table 1. In this context the term "gill" was no longer used because it is not comparable to the "true" gills of aquatic crustaceans. The following definitions are suggested:

(Structural) plastron Any water-repellent structure of terrestrial and aquatic arthropods that allows air-breathing arthropods to use their respiration system under water. This consists of a thin air layer with a thickness of a few microns around the entire body (cuticular-breather) or over certain body parts connected with the stigmata (tracheal breathers). It can be subdivided functionally into two subcategories depending on the physical and chemical properties of the gas gills:

Incompressible plastron Requires the trapping of only small amounts of air. A stable N₂-ratio between the gas phase and the surrounding water is maintained; this allows the arthropod to be mostly independent of the water surface and provides a deep diving capability in some species due to low buoyancy. The O₂-partial pressure of the gas phase is constantly lower than in the surrounding water, which causes a permanent diffusion of O₂ into the air layer. Examples include air trapped in spiracle systems and the subelytral air chamber in beetles.

Compressible plastron Needs higher air-volumes, which results in increased buoyancy and often reduced diving capability. Diffusion of N₂ into the surrounding water causes a continuous reduction and gradual collapse of the air layer. The reduced O₂-partial pressure of the gas phase will be renewed from the surrounding water up to eight times the primary O₂-content of the air layer. Arthropods with a compressible gill are adapted to submerged conditions but are permanently forced to return to the water surface (or other sources of air) to replenish their air supply (e.g. cuticular breathers).

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