



## The cephalic morphology of the Gondwanan key taxon *Hackeriella* (Coleorrhyncha, Hemiptera)



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### ABSTRACT

External and internal head structures of Coleorrhyncha, a key-taxon within the Hemiptera, are described in detail and documented using modern techniques. The main focus is on *Hackeriella veitchi*, but two additional representatives of the Gondwanan relict group were also examined, and also head structures of Enicocephalidae, a member of a potentially basal heteropteran lineage. Features were compared to those documented in literature for the Sternorrhyncha, Auchenorrhyncha, and Heteroptera. Coleorrhyncha are characterized by highly modified head structures and correspondingly an entire series of autapomorphies, such as for instance a strongly flattened head capsule with fenestrations. However, they also display features that are likely plesiomorphic compared to members of other hemipteran groups. These include the almost complete tentorium and the lack of the gula. The sistergroup relationship between Coleorrhyncha and Heteroptera is well supported by cephalic features. Potential synapomorphies are the presence of a distinct mandibular sulcus, the reduced number of antennomeres, the absence of clasping organs in the labial groove, coiled accessory salivary ducts, the presence of a small cervical muscle M1a (*M. pronotopostoccipitalis medialis*), the presence of a second mandibular promotor M14 (*M. zygomaticus mandibulae*), the presence of M28 (*M. verticopharyngalis*), and M30 (*M. frontobuccalis posterior*).

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### 1. Introduction

Coleorrhyncha is a highly aberrant group of insects and a key-taxon for the higher-level systematics of Hemiptera. It is represented by only a single recent family, the Gondwanan relict Peloriidiidae (e.g. Schlee, 1969; Austin et al., 2004; Grimaldi and Engel, 2005; Schaefer, 2009), but the fossil record suggests that this taxon was once much more diverse. The oldest fossils unambiguously classified as Coleorrhyncha are the Late Jurassic and Early Cretaceous Laurasian Karabasiidae and the Early Cretaceous Hoploridiinae (Peloriidiidae) from Transbaikalia (Popov and Shcherbakov, 1996). They show that the group was originally Pangean, with only few Southern Hemisphere species persisting until today. Much older fossils, the Late Permian to Early Cretaceous Progonocimicidae that once were widely distributed in Laurasia (e.g. Popov and Shcherbakov, 1991; Heads, 2008;

Wang et al., 2009; Szewo, 2011; Dong et al., 2012) have been classified as Coleorrhyncha (Popov and Shcherbakov, 1996), but are now tentatively considered as possible stem-group representatives of that clade (Grimaldi and Engel, 2005). Coleorrhyncha are undoubtedly one of the oldest groups of Hemiptera and represent an ancient lineage that has changed very little since Jurassic times (Pendergrast, 1962; Gullan and Cranston, 2005; Burckhardt, 2010).

Extant Peloriidiidae include 17 genera and 36 species (Larivière et al., 2011). They occur in Southeastern Australia, New Caledonia, Southern South America (Evans, 1981; Burckhardt, 2009, 2010), and with the biodiversity hotspot in New Zealand (Larivière et al., 2011). Peloriidiidae are found in temperate and subantarctic rainforests, especially those dominated by *Nothofagus* (Nothofagaceae) (Burckhardt, 2010; Burckhardt et al., 2011), although some species also occur in regions where the southern beeches are lacking (Carter, 1950). Both, habitus and life style, of peloriidiids are cryptic and they are best collected from wet moss, hepatics and leaf litter using Winkler extractors (Burckhardt, 2010; Larivière et al., 2011). Their size ranges between two and five millimeters (Burckhardt

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and Agosti, 1991; Burckhardt, 2010). Most species are brownish, and almost all are covered with self-made incrustations of excretions blended with soil particles (Burckhardt, 2010). There are several records concerning bryophyte species harbouring peloridiids (summarized in Burckhardt, 2010). For *Hackeriella veitchi*, Helmsing and China (1937) recorded an association with the moss species *Papillaria kermadecensis* (now *P. crocea* (Hampe) A. Jaeger), but this was not confirmed in a recent field study (V. Hartung, unpublished data). Recent investigations into the biology of peloridiids have revealed that they can produce sounds (Hoch et al., 2006) and that they are able to jump (Burrows et al., 2007). Well known is the occurrence of endosymbiotic bacteria which are located in mycetomes one each side of the abdomen (e.g. Pendergrast, 1962; Schlee, 1969). They are typical for phytophagous Hemiptera (Larivière et al., 2011).

The phylogenetic position of Coleorrhyncha has been discussed controversially. Initially the group was placed close to the aquatic heteropteran family Ochteridae (Breddin, 1897). Coleorrhyncha were later treated as part of the “Homoptera” and ranked equivalent to the Sternorrhyncha and Auchenorrhyncha (e.g. Myers and China, 1929; Evans, 1937, 1957, 1963; Singh, 1971). Based on phylogenetic evaluation of morphological evidence across Hemiptera, Schlee (1969) found several synapomorphies for Coleorrhyncha and Heteroptera and concluded that they likely represent sister taxa. Subsequently, molecular evidence for this sistergroup relationship started to emerge (Wheeler et al., 1993; Ouvrard et al., 2000; Bourgoïn and Campbell, 2002). The clade comprising Coleorrhyncha + Heteroptera (=Heteropterodea [or Prosorrhyncha; Sorensen et al., 1995; Schaefer, 2009]) is also strongly supported by the first multi-gene analysis with comprehensive taxon sampling of Hemiptera (Cryan and Urban, 2012) that also showed Auchenorrhyncha to be monophyletic. Building on this framework, studies focussing on the morphology of the enigmatic, species-poor and relictual Coleorrhyncha now have the potential to test hypotheses on character evolution that gave rise to one of the speciose and diverse clades among Hemiptera, the Heteroptera.

Head morphology has played an important role in investigating relationships among Hemiptera (e.g. Evans, 1937; Rieger, 1976; Hamilton, 1981). However, Rieger (1976) stressed that the poor documentation of the coleorrhynchan head leaves central homology hypotheses untested and negatively impacts systematic interpretations. Available descriptions of external and internal head structures of Peloridiidae are clearly incomplete. Line drawings of external head views have been published for several species including *Peloridium hammoniorum* (Popov and Shcherbakov, 1991), *Hemiodoecus leai* (frontal and occipital view: Myers and China, 1929; anterior portion of the adult head: Evans, 1981), and *Hemiodoecus fidelis* (Evans, 1937; Snodgrass, 1938). Ventral head structures and the tentorium of *Hemiodoecus* sp. were depicted by Hamilton (1981) and parts of the ventral head capsule, labial sensilla and internal structures of the feeding tube of *Xenophyes cascus* were treated by Brozek (2007), Burrows et al. (2007) and Burckhardt (2009). The most detailed study on internal structures of Peloridiidae was carried out by Pendergrast (1962). Nevertheless, this documentation of the inner structures of the head is very fragmentary consisting only of images of two cross sections of the head of *X. cascus* (muscles were marked, but not labelled and described in detail). A more comprehensive traditional treatment of the cephalic musculature was presented by Singh (1971) for *H. leai*.

The present study will fill the gap by providing the first detailed and well documented account of all external and internal head structures (including tentorium, muscles, nervous system and alimentary organs) of a species of Coleorrhyncha. Adults of *Hackeriella veitchi* were used for the anatomical investigation, as sufficient and appropriately preserved specimens were only

available of this species. The results are compared with external features of two other species of Peloridiidae: *Peloridium hammoniorum* and *Pantinia darwinii*. *Pantinia* and *Peloridium* are closely related to each other and both occur in South America (Popov and Shcherbakov, 1996; Burckhardt, 2009), whereas *H. veitchi* is restricted to Australia (Burckhardt, 2009). The macropterous forms of *P. hammoniorum* (both sexes) are of special interest since they are the largest of all known peloridiids (Evans, 1981). An important plesiomorphic feature maintained in this species is the capacity to fly (Burckhardt, 2009), which is lacking in all other known members of the group. For comparison, the head anatomy of a species of the heteropteran Enicocephalidae (*Systelloderes* sp.) was studied in detail. Enicocephalomorpha are possibly the sistergroup of the remaining Heteroptera (e.g., Wheeler et al., 1993; Weirauch and Schuh, 2011), even though a basal position of Nepomorpha was suggested in a recent study (Li et al., 2012). A formal numerical character analysis is not presented here. It will be carried out in a subsequent study when more detailed data on hemipteran cephalic structures are available.

## 2. Material and techniques

### 2.1. Material

The present study is based on the following specimens:

*Hackeriella veitchi* (Hacker, 1932), two females, Queensland/Australia, Springbrook National Park, Repeater Station, 2006, leg. Geoff Monteith

*Peloridium hammoniorum* Breddin, 1897, one specimen (from N.P. Kristensen, Zoologisk Museum, Copenhagen)

*Pantinia darwinii*, China 1962, one specimen, Chile: IX Reg. Pr. Malleco, PNNahuelbuta, Administración, 37°50'S 73°00'W 1100 m, 23.12.1992, D. Burckhardt # 30b, det. D. Burckhardt 2009.

*Systelloderes* sp. (Enicocephalidae, Enicocephalomorpha), Peru: Cuzco: Wayqecha Research Center, 2821 m, 13°10'22"S 71°35'32"W, 05.12.2011, leg. C. Weirauch, P11L57 sweep/beat

Specimens of *H. veitchi*, *P. hammoniorum* and *Systelloderes* sp. were preserved in 70% ethanol. *P. darwinii* was air-dried. In the following text all species will be referred to by generic name only.

### 2.2. Scanning electron microscopy

Scanning electron (SEM) micrographs of *Hackeriella* and *Pantinia* were taken with a Philips XL 30 ESEM (FEI Company, Oregon, USA) and Scandium 5.0 Software (Soft Imaging System GmbH, Münster, Germany). *Hackeriella* was completely hydrated (distilled water) over several stages and macerated in 10% KOH for 24 h at 25 °C to remove soil particles. Additionally, the specimen was cleaned twice in a Bandelin Sonorex ultrasonic bath (BANDELIN electronic, Berlin, Germany) for two seconds each time. The KOH was washed out one hour in distilled water. Subsequently, it was completely dehydrated with ethanol (100%) over several stages and dried at the critical point (EmiTech K850, Quorum Technologies, West Sussex, UK). *Pantinia* was air-dried. *Hackeriella* and *Pantinia* were sputter-coated with gold (EmiTech K500, Quorum Technologies, West Sussex, UK). A rotatable specimen holder was used to mount the samples (see Pohl, 2010). After scanning the entire specimen, *Hackeriella* was partly re-hydrated (70% ethanol) and its head was removed. After complete dehydration with ethanol (100%) over several stages, it was dried at the critical point, sputter-coated with gold and fixed on the specimen holder for scanning of cephalic details.

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