

Sternites and spiracles – The unclear homology of ventral sclerites in the basal millipede order Glomeridesmida (Myriapoda, Diplopoda)



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ABSTRACT

We report the discovery of a ventral plate in the basal and little-known chilognath millipede order Glomeridesmida. This ventral plate, interpreted here as a 'true sternite', is clearly separate from both the coxa and the more lateral stigma-carrying plates commonly referred to as 'diplopod sternites'. Therefore, the lateral, stigma-carrying plates of the Diplopoda, previously referred to as sternites, are not sternal elements, but subcoxal elements associated with the limb base. This discovery changes the nomenclature used for the ventral plates in Diplopoda, with the formerly named 'sternite' better referred to as 'stigma-carrying plate'. In helminthomorph Diplopoda, the stigma-carrying plates are apparently secondarily fused with the sternite.

The main argument for the independent evolution of tracheae in insects and myriapods, the different location of their respective spiracles, no longer holds true. In all Myriapoda and Hexapoda the spiracles associated with subcoxal elements are located lateral to the limb base. This discovery shows that the arguments for an independent origin of tracheae in insects and myriapods are not uncontested.

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1. Introduction

Latreille, when defining the taxon Arthropoda in 1829, included the major groups of recent arthropods – the crustaceans, arachnids, and insects, and considered the Myriapoda as a group within the latter (Latreille, 1829). Over the following decades and centuries, almost all possible relationships among the main arthropod groups have been proposed, and the monophyly of the taxon Arthropoda and its main subgroups was repeatedly questioned and debated (see Fig. 1 in Bäcker et al., 2008). Originally, morphological characters and their homology hypotheses furnished the deciding characters (= apomorphies) for taxon delineation and relationship hypotheses (Klass and Kristensen, 2001; Bitsch and Bitsch, 2004; Bäcker et al., 2008; Fanenbruck, 2009; Liu, 2009; Grimaldi, 2010). Current hypotheses on the phylogeny of major arthropod taxa are dominated by results of molecular analyses (Min et al., 1998; Dove and Stollewerk, 2003; Anderson et al., 2004; Mallatt et al., 2004; Negrisolo et al., 2004; Pisani et al., 2004; Regier et al., 2010; Giribet and Edgecombe, 2011; Rota-Stabelli et al., 2011; Reumont et al., 2012). The majority of the resulting phylogenies from these

studies accepted multiple, independent origin of complex morphological structures (see also Kück et al. 2012). An example is the tracheal system:

The homology of the tracheae within the Arthropoda and within the putative taxon Atelocerata (Hexapoda + Myriapoda) has been discussed in the literature for nearly 80 years (e.g., Ripper, 1931; Hilken, 1998). Tracheae of Atelocerata were assumed to be convergent and analogous, and evolved independently four (Kraus, 1998) or even six times (Dohle, 1988, 1997). Differences in structure (Hilken, 1998) and function (Dohle, 1985, 1997), in segmental arrangements (as in symphylans and collembolans) and location of stigma openings (= tracheal openings) are invoked as support for the independent origin. Furthermore, the tracheae of Collembola, Diplura and Protura are considered autapomorphic (Hilken, 1998; Bitsch and Bitsch, 2004). Many recent studies in arthropod phylogeny employing molecular data (Boore et al., 1995; Friedrich and Tautz, 1995; Hwang et al., 2001) support a Pancrustacea-Hypothesis (Crustacea + Hexapoda) and thus argue in favor of the independent origin of the tracheal system in the 'Atelocerata'. However, judging from their unique structure and arrangement, tracheae of Atelocerata were considered homologous by other authors (e.g., see Tiegs, 1940; Minelli, 1993; Wägele and Stanjek, 1995; Klass and Kristensen, 2001; Bäcker et al., 2008), structural differences were interpreted as the result of evolutionary changes after the tracheae evolved.

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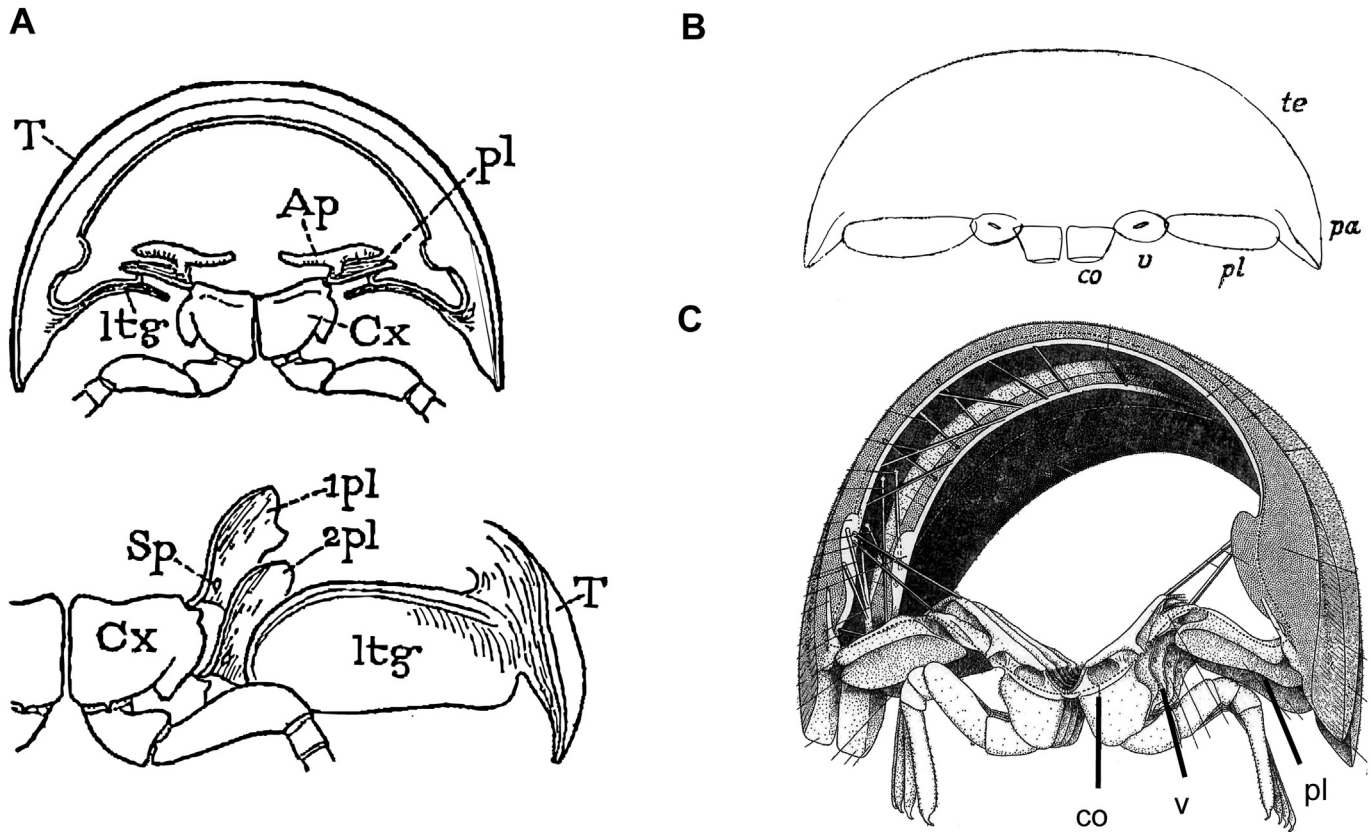


Fig. 1. Viewpoints on the ventral sclerites in Diplopoda, especially of the subclass Pentazonia. **A:** Snodgrass view (slightly modified from Snodgrass, 1958), Sphaerotheriida; **B:** Verhoeff's view of a Sphaerotheriida (from Verhoeff, 1928), which is quite similar to (C); **C:** Sphaerotheriida, from Manton (1954). **Abbreviations:** 1pl, 2pl = first and second pleurite; Ap = apodeme; co = coxa; Cx = coxa; ltg = latero-tergite; pa = paratergite; pl = pleurite; Sp = stigma opening; T = tergite; te = tergite; v = stigmatic plate.

Klass and Kristensen (2001) discussed the morphological details for these competing hypotheses. They conclude that "...the hypothesis of a tracheal system with pleural stigma openings on many trunk segments ... being the groundplan autapomorphy of a taxon Atelocerata cannot at present be discarded for many compelling reasons...".

Because of the enormous diversity of the Arthropoda in terms of species and clades, research advances have not been employed in all groups equally. There are numerous understudied clades for which detailed morphological studies (and genetic data) as well as catalogs and keys are not yet available.

The Diplopoda are a case in point; many morphological features frequently employed in phylogenetic reconstructions have not been examined. Investigations into organ systems, which provide frequently invoked apomorphies, were only studied in the early 1900s or before and morphological data were derived from only small sets of taxa; e.g., the Tömösváry organ of land-living arthropods (also called 'head organ') was most recently examined histologically in millipedes by Hennings more than 100 years ago (Hennings, 1904, 1906), the homology with a similar organ occurring in crustaceans (Klass and Kristensen, 2001) has never been examined in detail.

1.1. The ventral sclerites in the Diplopoda

The German myriapodologist Verhoeff interpreted the stigma-carrying plates in the majority of Diplopoda as sternites. Verhoeff (1928: 388) emphasized the importance of this primary homology hypothesis by attributing law-like qualities to this hypothesis: "Ein chaotischer Wirrwarr hätte hier entstehen können, wenn Verfasser

nicht durch das Gesetz, daß bei den Chilognathen die beintragenden freien Sternite stets die Träger der Stigmen- und Tracheentaschen sind, soweit solche überhaupt vorkommen, für die Beurteilung eine feste Grundlage gewonnen hätte." (Translation: A chaos [in the naming of the ventral plates in Diplopoda] could have erupted if the author [Verhoeff] had not designated the following law as a firm foundation: *the leg-carrying free sternites are, when present, the carriers of the stigmata and tracheal pouches in the chilognathes [Diplopoda ex Polyxenida].*)

Current millipede textbooks (e.g., Blower, 1985; Hopkin and Read, 1992) and systematic treatments (Enghoff, 1984; Sierwald et al., 2003) follow Verhoeff's view: all list one pair of sternites, each carrying two spiracles as the groundplan of chilognath diplosegments (see Fig. 1B, C). Verhoeff (1928: 385) argued that movable pleurites, connected to tergites and sternites via membranes, dominate in millipede fossils (see Fritsch, 1901a, 1901b), while in the recent millipede taxon Helminthomorpha, the pleurites are fused to the tergites, a character usually cited as an apomorphy for the clade. In the orders Glomeridesmida, Glomerida and Sphaerotheriida (= clade Pentazonia), paired plates located laterally to the legs are identified as 'pleurites'. In addition to the paired pleurites, the Pentazonia are also assumed to possess divided 'sternites', located between pleurites and leg coxae, carrying a single spiracle each (see Fig. 1B, C). These divided 'sternites' form an often cited apomorphy of the Pentazonia (Enghoff, 1984; Sierwald et al., 2003). Applying Verhoeff's 'law', any plate carrying a stigma, regardless of its position, is automatically a sternite. Inside the Diplopoda, all taxonomic, phylogenetic (Enghoff, 1984; Sierwald et al., 2003), and even Evo-Devo (e.g. Janssen et al., 2006) publications still apply Verhoeff's 'law'.

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