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Transition from marine to terrestrial ecologies: Changes in olfactory and tritocerebral neuropils in land-living isopods

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ABSTRACT

In addition to the ancestors of insects, representatives of five lineages of crustaceans have colonized land. Whereas insects have evolved sensilla that are specialized to allow the detection of airborne odors and have evolved olfactory sensory neurons that recognize specific airborne ligands, there is so far little evidence for aerial olfaction in terrestrial crustaceans. Here we ask the question whether terrestrial Isopoda have evolved the neuronal substrate for the problem of detecting far-field airborne chemicals. We show that conquest of land of Isopoda has been accompanied by a radical diminution of their first antennae and a concomitant loss of their deutocerebral olfactory lobes and olfactory computational networks. In terrestrial isopods, but not their marine cousins, tritocerebral neuropils serving the second antenna have evolved radical modifications. These include a complete loss of the malacostracan pattern of somatotopic representation, the evolution in some species of amorphous lobes and in others lobes equipped with microglomeruli, and yet in others the evolution of partitioned neuropils that suggest modality-specific segregation of second antenna inputs. Evidence suggests that Isopoda have evolved, and are in the process of evolving, several novel solutions to chemical perception on land and in air.

1. Introduction

Within Crustacea, representatives of five major lineages have succeeded in the transition from an aquatic to a terrestrial life style (reviews Bliss and Mantel, 1968; Powers and Bliss, 1983; Hartnoll, 1988; Greenaway, 1988, 1999). These include representatives of Isopoda (Edney, 1968; Wägele, 1989; Schmalfuss, 2003), Amphipoda (Hurley, 1968; Friend and Richardson, 1986; Morritt and Spicer, 1998), Anomura (Hartnoll, 1988; Greenaway, 2003), Brachyura (Hartnoll, 1988) and Astacoidea (Welch and Eversole, 2006). Although three of these lineages require aquatic larval stages, many species of Isopoda and Amphipoda do not, and hence are fully terrestrial. The degree to which Crustacea have partially or fully adapted to terrestrial life has been categorized into fives classes, T1 to T5 (Powers and Bliss, 1983; Hartnoll, 1988; Greenaway, 1999), T5 characterized as "a fully terrestrial species able to conduct all biological activities on land".

Amongst Crustacea, the most successful organisms in colonizing land are without any doubt members of the Oniscidea, a subgroup of the Isopoda (Powers and Bliss, 1983; Wägele, 1989; Kaestner, 1993; Schmalfuss, 2003; Schmidt, 2008). Oniscidea comprise around 3600 species (Schmalfuss, 2003), of which many have fully established the T5 grade of terrestrial life style according to Powers' and Bliss' grading of terrestrialness. The phylogeny of the Isopoda is a topic of ongoing research (e.g. Wägele, 1989; Wägele et al., 2003; Wetzer, 2002; Wirkner and Richter, 2003, 2007, 2008, 2010; Schmidt, 2008; Raupach et al., 2009; Richter et al., 2009; Wirkner, 2009), and it is still unclear if the Oniscidea invaded land several times or just once (Schmidt, 2008). Representatives that epitomize an ongoing transition from sea to land can be found amongst Ligiidae (e.g. *Ligia oceanica, Ligia exotica, Ligia occidentalis*). Members of this taxon lead an amphibious life style on rocky shores, guided by a well-developed visual system (Sinakevitch et al., 2003), and are frequently associated with washed-up sea wrack on which they feed. Depending on the species, these animals can move much faster on land than submerged (*L. exotica* and *L. occidentalis*, but not *L. oceanica*), although they walk in both habitats (Wägele, 1989). Fully terrestrial (T5) isopods are represented by, for example, Oniscidae (e.g. *Oniscus asellus*), Porcellionidae (e.g. *Porcellio scaber*), Armadillidiidae (e.g. *Armadillidium*

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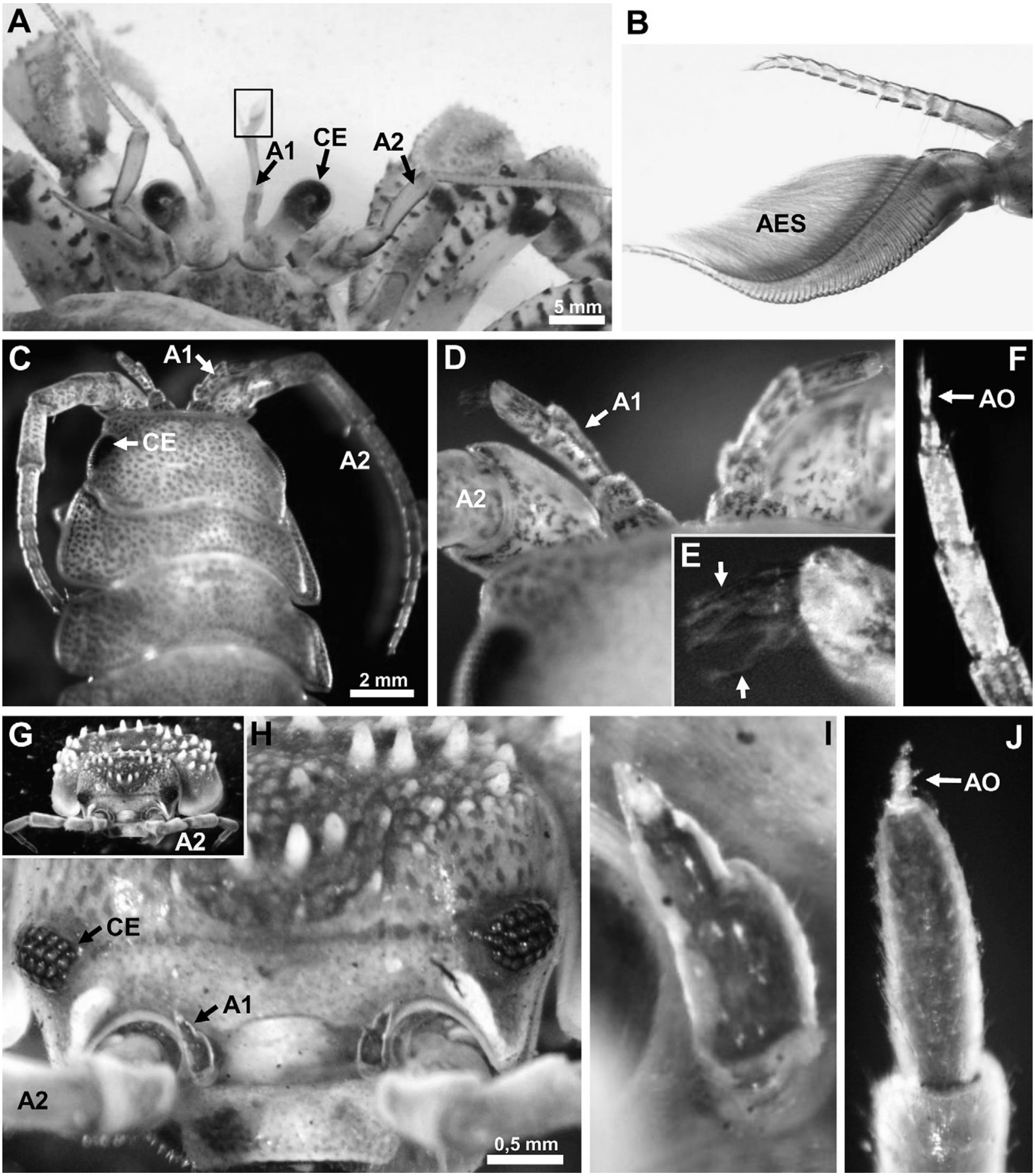

Fig. 1. A: dorsal view of the marine hermit crab *Pagurus bernhardus* to show its cephalic sensory appendages, the first and second pair of antennae. B: higher magnification of the boxed area in A showing the aesthetascs on the tips of the first antennae. C, D: dorsal views of the head of the marine isopod *Idotea baltica*. E: Aesthetascs (arrows) on the distal segment of the first antennae of *I. baltica*. F: apical organ at the distal end of the second antennae in *I. baltica*. G, H: frontal views of the head of the desert isopod *Hemilepistus reaumuri*. I: higher magnification of the left first antenna shown in H. J: apical organ at the distal segment of the second antenna of *H. reaumuri*. Abbreviations: A1 antenna one, A2 antenna 2, AES aesthetascs, AO apical organ, CE compound eyes.

vulgare) and Trachelipodidae (e.g. the xerophilic desert isopod *Hemilepistus reaumuri*).

The successful transition from marine to terrestrial life requires a number of physiological adaptations, all of which are important for survival out of water. These relate, for example, to gas exchange, salt and water balance, nitrogenous excretion, thermoregulation, molting, and reproduction (Bliss and Mantel, 1968; Powers and Bliss, 1983; Burggren and McMahon, 1988; Greenaway, 1988, 1999, 2003). Aspects of the physiological ecology of Isopoda and those morphological adaptations related to land invasion are reviewed by Edney