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On the Miocene *Cyprideis* species flock (Ostracoda; Crustacea) of Western Amazonia (Solimões Formation): Refining taxonomy on species level

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Abstract

The Miocene mega-wetland of western Amazonia holds a diverse, largely endemic ostracod fauna. Among them, especially the genus *Cyprideis* experienced a remarkable radiation. Micropalaeontologic investigations of a 400 m long sediment core (~62 km SW Benjamin Constant, Amazonia, Brazil) permitted a taxonomic revision of about two-thirds of hitherto described *Cyprideis* species. We evaluate the diagnostic value of shell characters and provide an extensive illustration of the intraspecific variability of species. Based on comparative morphology, the 20 recorded *Cyprideis* species are arranged in groups and subgroups. The "smooth" group comprises *C. amazonica*, *C. kotzianae*, *C. kroemmelbeini*, *C. machadoi*, *C. multiradiata*, *C. olivencai*, *C. paralela* and *C. simplex*; the "ornate" group *C. curucae* nom. nov., *C. cyrtoma*, *C.* aff. *graciosa*, *C. inversa*, *C. ituiae* **n. sp.**, *C. matorae* **n. sp.**, *C. minipunctata*, *C. munoztorresi* nom. nov., *C. pebasae*, *C. reticulopunctata*, *C. schedogymnos* and *C. sulcosigmoidalis*. Five species have been revalidated, two renamed, two synonymised and two are new descriptions. Along with 10 further formally established species, for which a review is pending, *Cyprideis* keeps at least 30 endemic species in that region during Miocene times. Up to 12 *Cyprideis* species have been found to occur sympatrically, representing >90 % of the entire ostracod fauna. Ostracod index species enable a biostratigraphic allocation of the well succession to the *Cyprideis minipunctata* to *Cyprideis cyrtoma* biozones, corresponding to a late Middle to early Late Miocene age (late Serravallian–early Tortonian).

Key words: Brazil, fossil ostracods, Cytherideidae, taxonomy, morphology

1. Introduction

Species flocks (e.g. Greenwood 1984; Lecointre *et al.* 2013) as the result of accelerated divergence of closely related species within a certain ecosystem concern fundamental aspects of biologic evolution (i.e., modes, patterns and pace) and substantially affect past and current biodiversity (e.g. Glaubrecht & Köhler 2004; Schön & Martens 2004). Celebrated examples for such bursts of species originate from isolated islands and long-lived lakes as well, however, they are not restricted to them (e.g. Eastman & McCune 2000; Sullivan *et al.* 2002; Kocher 2004; Wilson *et al.* 2004; Wesselingh 2007; Grant & Grant 2008; Wilke *et al.* 2008; Köhler *et al.* 2010).

Among recent ostracods, the *Cyprideis* species flock of East African Lake Tanganyika forms an intensively studied example (e.g. Wouters & Martens 1992, 2001, 2008; Schön *et al.* 2000; Schön & Martens 2012). For the Neogene period, comparable radiations in fossil *Cyprideis* are well recognized from Lake Pannon (Central Europe; Kollmann 1960; Krstić 1968a, b; Van Harten 1990), the Palaeo-Mediterranean realm (Decima 1964; Bassiouni 1979; Ligios & Gliozzi 2012), and the Caribbean area (Van den Bold 1976) as well as from western Amazonia (Purper 1979; Whatley *et al.* 1998).

In Miocene times an enormous, predominately fluvio-lacustrine wetland (~1 million km^2) shaped western Amazonia (Hoorn & Wesselingh 2010; Hoorn *et al.* 2010a; for diverging views see e.g. Westaway 2006; Latrubesse *et al.* 2010), which holds an amazingly diverse, largely endemic bivalve, gastropod and ostracod fauna. While detailed taxonomic evaluations (e.g. Nuttall 1990; Wesselingh 2006a) already provide a firm base for considerations on e.g. mollusc phylogeny and causes of speciation (Wesselingh 2006b, 2007; Anderson *et al.* 2010), ostracodologic research lags behind and still remains in the stage of alpha taxonomy.

Whereas first descriptions of fossil western Amazonian molluscs date well back to the 19th century (Gabb 1869; see Wesselingh 2008 for a historical review), studies on ostracods started with the seminal monograph of Purper (1979; as conference proceedings: Purper 1977)—more than one century later. Subsequently, Sheppard & Bate (1980), Purper & Pinto (1983, 1985), Purper & Ornellas (1991) and Swain (1998) continued that work. Later, the comprehensive research of Muñoz-Torres *et al.* (1998, 2006) and Whatley *et al.* (1998, 2000) appreciably advanced ostracod taxonomy, leading to an ostracod-based biozonation as well as to initial phylogenetic hypotheses. It was up to these authors to formulate the western Amazonian *Cyprideis* species flock. Further publications come from Ramos (2006), Celestino & Ramos (2007), and Ramos *et al.* (2009). Wesselingh & Ramos (2010) reviewed the state of the art. Recent contributions are by Linhares *et al.* (2011), Gross *et al.* (2013) and Nascimento *et al.* (2013).

The current paper investigates *Cyprideis* species from a ~400 m deep, continuously cored drill-hole from western Amazonia (Fig. 1). While the investigation of natural outcrops in this area (e.g. exposures along river banks) enables more detailed sedimentologic analyses (e.g. Hoorn 1994a, b; Gross *et al.* 2011), their stratigraphic range is usually limited, compared to such long drillings (Wesselingh *et al.* 2006a).

morphometrics). This allows for conclusions on the taxonomic value of observable valve characters as well as for a demonstration of intraspecific variability (as far as possible including sexual and ontogenetic polymorphism).

Based on our observations, we refine existing *Cyprideis* species definitions (5 species are revalidated, 2 synonymised, 2 renamed and 2 defined) as well as earlier proposed species (sub-)groupings. Due to the occurrence of some ostracod index species, the core comprises sediments of the *C. minipunctata* to *C. cyrtoma* ostracod zones, corresponding to the *Grimsdalea* pollen zone and a late Middle to early Late Miocene age.

We regard the current study as a base for upcoming, more advanced analyses (e.g. geometric morphometric approaches or geochemical analyses) as well as a further step in illuminating the amazing *Cyprideis* species flock of western Amazonia's geological past.

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Note. Specimens on all plates are figured at the same scale (except additional details, which are marked by a vertically aligned scale bar). Abbreviations: C = carapace, L = left valve, R = right valve; d = dorsal view, e = external view, i = internal view; ♀ = female, ♂ = male, j = juvenile. In brackets length (l) and height (h) are indicated in millimetres (e.g. 0.88/0.49 = length 0.88 mm, height 0.49 mm; the length of spines is not included) followed by a specimen code (sample number_specimen number; e.g. AM10-7_85. For corresponding inventory numbers, see ESM 2).

Electronic supplementary material

ESM 1. Dataset of the occurrences of *Cyprideis* species in core 1AS-10-AM.

ESM 2. Dataset of measured and photographed specimens.