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Harpactoxanthopsis quadrilobata (Desmarest, 1822) from the Eocene of Slovakia and Italy: the phenomenon of inverted images of fossil heterochelous crabs

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Abstract

This short note provides details on a specimen of *Harpactoxanthopsis quadrilobata* (Desmarest, 1822) deposited in the Natural History Museum of Slovak National Museum in Bratislava which was figured in the monograph by Lőrenthey and Beurlen (1929). The phenomenon of inverted images of fossil heterochelous crabs in the literature published in the 19th century is documented on the example of *H. quadrilobata* from the Eocene of Italy.

Key words: Brachyura, *Harpactoxanthopsis*, Eocene, Slovakia, Italy, heterochely

Introduction

Harpactoxanthopsis quadrilobata (Desmarest, 1822) is a well known brachyurous crab species reported from numerous Eocene localities across Europe (De Angeli and Garassino, 2006). In Slovakia, its occurrence is restricted to the Borové Formation (middle–upper Eocene) (Hyžný, 2010). The first report is that by Dornyay (1913). There is one specimen of *H. quadrilobata* (SNM Z-277) deposited in the Natural History Museum of Slovak National Museum in Bratislava. It actually represents a near-complete female individual figured by Dornyay (1913: pl. 2, fig. 7) and later re-figured by Lőrenthey and Beurlen (1929: pl. 9, fig. 4). Hyžný (2010) mentioned that the specimen was given to SNM in 1955 as a gift from the Liptov Museum, but he failed to provide a figure. This short note aims to give more information on this particular specimen and to provide new photographs. In this respect, it is interesting to note that the heterochely in *H. quadrilobata* documents inverted images in works published in the 19th century and earlier. As an example, the case of the figures published in Bittner (1875) is discussed.

Repositories: GBA—Geologische Bundesanstalt, Wien, Austria; SNM—Natural History Museum, Bratislava, Slovakia.

Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Carpilioidea Ortmann, 1893
Family Zanthopsidae Vía Boada, 1959
Genus *Harpactoxanthopsis* Vía Boada, 1959
Type species: *Cancer quadrilobatus* Desmarest, 1822.
Included fossil species: see Schweitzer *et al.* (2010).

Harpactoxanthopsis quadrilobata (Desmarest, 1822)

(Fig. 1A–F)

1822 *Cancer quadrilobatus* Desmarest, p. 93, pl. 8, figs. 1–2.
1862 *Harpactocarcinus quadrilobatus* (Desmarest); A. Milne Edwards, p. 74, pl. 3, fig. 2, pl. 4, fig. 1, pl. 5, fig. 1.
1875 *Harpactocarcinus quadrilobatus* (Desmarest); Bittner, p. 89, pl. 2, figs. 4–5, pl. 3, figs. 1–2.
1895 *Cancer* (*Palaeocarpilius*) *gecchelinensis* De Gregorio, p. 14, pl. 4, fig. 3.
1913 *Harpactocarcinus quadrilobatus* (Desmarest); Dornyay, p. 25, pl. 2, figs. 6–7.
1929 *Xanthopsis quadrilobata* (Desmarest); Lőrenthey and Beurlen, p. 208, pl. 9, figs. 3–4, pl. 10, fig. 7.
1969 *Harpactoxanthopsis quadrilobata* (Desmarest); Vía Boada, p. 276, pl. 30, figs. 1–2, pl. 31, figs. 1–2, pl. 32, figs. 1–2.

1994 *Harpactoxanthopsis quadrilobata* (Desmarest); Beschin *et al.*, p. 186, pl. 8, figs. 1a–b.

1998 *Harpactoxanthopsis quadrilobata* (Desmarest); Beschin *et al.*, p. 24, figs. 9(5), 12, 13, 15(1).

2006 *Harpactoxanthopsis quadrilobata* (Desmarest); De Angeli and Garassino, p. 77–78.

2010 *Harpactoxanthopsis quadrilobata* (Desmarest); Hyžný, p. 119, figs. 2A–F.

Material examined: A near-complete left-handed female specimen (SNM Z-277) from the Eocene of the Borové Formation, Slovakia (Fig. 1A–C); two right-handed female specimens (GBA 354868, 1875/05/0033 and GBA 354869, 1875/05/0033) from the Eocene of the Castelgomberto Formation, Italy (Fig. 1E–F).

Remarks: Taxonomically, the specimens fit the original description (Desmarest, 1822) in all aspects. The only peculiarity is that major chela of SNM Z-277 apparently represents a cutter claw, whereas the minor chela may be either another cutter claw or a regenerated crusher claw (see below). In heterochelous decapods the robust chela is usually termed the crusher (typically a major chela) and the slender morphotype is termed the cutter.

The actual specimen differs somewhat from the published figure (Dornyay, 1913: pl. 2, fig. 7): the most distal elements of the appendages on the right side are missing, most probably due to careless handling or as a consequence of transport from the Liptov Museum to Slovak National Museum in the fifties of the 20th century.

The other two studied specimens represent the material of Bittner, originally depicted as inverted images (see below) in Bittner (1875: pl. 2, fig. 4; pl. 3, fig. 1). The larger chela of both specimens represents a typical crusher claw (Fig. 1E–F).

Handedness in *Harpactoxanthopsis quadrilobata*

Harpactoxanthopsis quadrilobata is a heterochelous species; *i.e.* it is characterized by the bilateral asymmetry due to morphologically dissimilar chelae. This phenomenon is not rare among decapods crustaceans; it can be observed for instance in the infraorders Caridea (*e.g.* in alpheid shrimp, Anker *et al.*, 2006), Astacidea (*e.g.* in lobster and crayfish, Wahle *et al.*, 2012; Tobo *et al.*, 2012), Axiidea (*e.g.* in ghost shrimp, Biffar, 1971), Anomura (*e.g.* in hermit crabs, McLaughlin, 2003; Tudge *et al.*, 2012) and also Brachyura (*e.g.* Warner, 1977; Schweitzer and Feldmann, 2010). The heterochely can result from several factors, *i.e.* feeding technique in durophagous decapods (Schweitzer and Feldmann, 2010) or mating behaviour in fiddler crabs and allies (Salmon *et al.*, 1978; Mariappan *et al.*, 2009). Interestingly, the ratio between crushers and cutters in studied populations of selected decapods taxa varies (Mariappan *et al.*, 2009). Whereas in the lobster *Homarus gammarus* Linnaeus, 1758 (Przibram, 1931) or ghost shrimps (MH pers. obs.) the distribution of right and left handedness is equal, it is highly unequal in crabs like the box crab *Calappa philargius* (Linnaeus, 1758) (Ng and Tan, 1985), the shore crab *Carcinus maenas* (Linnaeus, 1758) (Pynn, 1998), or members of the fiddler crab *Uca* Leach, 1814 (Barnwell, 1982; Jones and George, 1982). Nevertheless, it is important to note that under specific circumstance the handedness can change (for details see *e.g.* Hamilton *et al.*, 1976; Pynn, 1998; Mariappan *et al.*, 2009). The studied specimen SNM Z-277 possesses a major chela that apparently represents a cutter claw; it is slender, without molariform teeth or a pronounced gap between fingers, and differs markedly from large crusher claws of *H. quadrilobata* depicted for instance by Bittner (1875: pl. 2, fig. 4, pl. 3, fig. 1; see also Fig. 1E–F), Vía Boada (1969: pl. 31, fig. 1, pl. 32, fig. 2) and Beschin *et al.* (1998: figs. 12, 13). Nevertheless, suggesting reversed handedness in the studied specimen is premature. Exhaustive quantitative study is needed to further evaluate this phenomenon in *H. quadrilobata*; such study is, however, beyond the scope of the present paper. Another interpretation is that the right chela (Fig. 1C) represents a regenerated crusher claw. It is relatively stout and the fixed finger appears to possess molariform denticles. However, because the fixed finger has been broken (Fig. 1A) it cannot be decided which the case is.

To my knowledge, no quantitative studies on handedness in fossil decapods have been published. If that type of study is attempted in the future, one must be careful about using figures from works published before 20th century as references. Stephen Jay Gould (1941–2002), in one of his famous essays (Gould, 1995a, b), discussed the phenomenon of figuring gastropod shells as inverted images as a consequence of the engraving technique. At the end of the essay he encouraged others to do some investigation in old literature with the focus on heterochelous crabs. Based on the previously stated hypothesis (Gould, 1995a, b), he concluded that most pre-eighteenth-century engravers, artists and authors were indifferent to whether illustrations of assymetrical organisms (such as snails and some crabs) were presented as inverted images. Allmon (2007) investigated major illustrated works printed before 1758 and as a result, he confirmed the hypothesis. Standards of accuracy in natural history illustration improved later, but still, it is recommended to check the figures with the actual specimens. The studied *Harpactoxanthopsis quadrilobata* specimen (SNM Z-277) is presented by Dornyay (1913) as observed, which is in fact not surprising as it was done in the time when engraving was no longer used to produce images. However, it is not the case of older figures of the same species. Allmon (2007) presented numerous cases when in pre-Linnaean works heterochelous crabs were depicted as inverted images. Herein, a brief report is given about inverted images of fossil crabs in 19th century works. During the re-examination of the material published by Alexander Bittner and deposited at

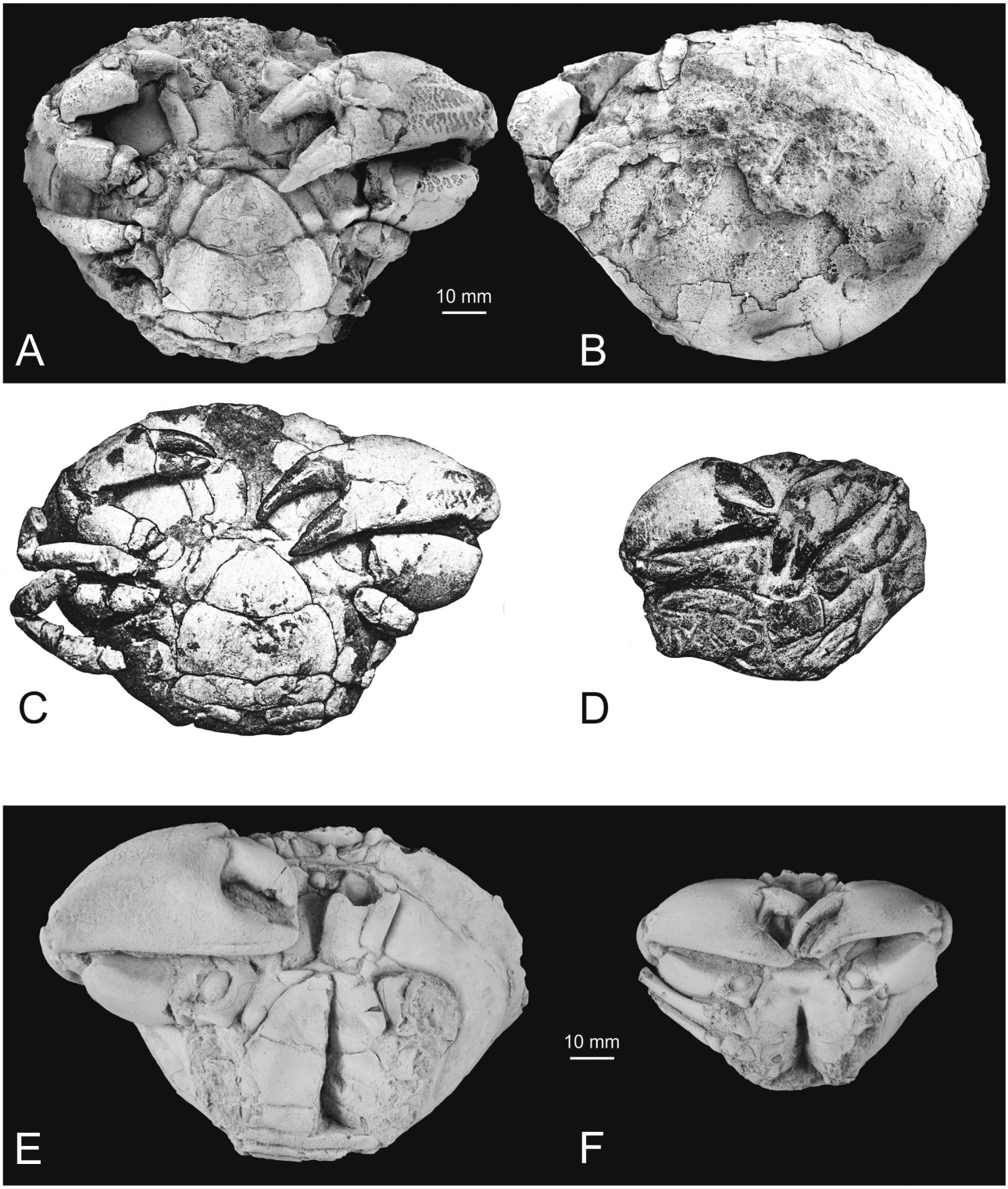


Fig. 1. *Harpactoxanthopsis quadrilobata* (Desmarest, 1822): A–B—a near complete female specimen from the Eocene of Slovakia (SNM Z-277), ventral (A) and dorsal (B) aspect; C–D—digital images of Dornyay (1913: pl. 2, figs. 6–7), later re-figured by Lőrenthey and Beurlen (1929: pl. 9, figs. 3–4), Cactually represents SNM Z-277; E–F—complete female specimens (GBA 354868, 1875/05/0033 and GBA 354869, 1875/05/0033) from the Eocene of Italy, compare with their inverted images published in Bittner (1875: pl. 2, fig. 4, pl. 3, fig. 1). Specimens in A, B, E, F were covered with ammonium chloride prior the photography.

Geologisches Bundesanstalt in Vienna, it was noted that figures in Bittner's works are not presented uniformly. Whereas crabs figured in Bittner (1883) are presented as observed, the figures in his earlier work (Bittner, 1875) are not. In fact, specimens of *H. quadrilobata* depicted in Bittner (1875: pl. 2 fig. 4, pl. 3 fig. 1) are inverted images (compare with Fig. 1 E–F).

For future studies on handedness of *H. quadrilobata* (or any other fossil heterochelous crab figured before the 20th century) it is essential to pay attention to the engraving image techniques and their published products.

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