



Recent developments on the morphology of the brachyuran foregut ossicles and gastric teeth

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Abstract

The complexity of the brachyuran foregut, in particular the foregut ossicles and gastric teeth, were investigated and documented in 66 brachyuran taxa employing a new staining method. The brachyuran groundpattern is proposed to consist of 41 ossicles. Most of the ossicles show a very conservative pattern with only a few variations. A previous classification scheme proposed by Nauck (1880) with the grouping of the recent brachyuran crabs in Heterodontea and Cyclodontea is not supported by this study. The study also shows that the Heterodontea and Cyclodontea are not monophyletic.

Key words: Brachyura, phylogeny, stomach morphology, foregut ossicles, gastric teeth, Heterodontea, Cyclodontea

Introduction

Apart from numerous investigations on the morphology of the foregut of the Crustacea (Herbst 1796; Brandt 1833; Baer 1834), H. Milne Edwards' (1837) fundamental work *Histoire naturelle des Crustacés* (1837) was the first detailed study of the anatomy of the decapod stomach. He established the first nomenclature for foregut-ossicles, which was accepted for a long time and by many later authors (e.g. Parker 1876, Huxley 1877, 1880). Based on his studies Milne-Edwards (1837) came to the conclusion that the general arrangement of the ossicles in all decapods is the same, but these structures exhibit characteristics diagnostic to the generic level. Of special importance was the work of Huxley (1880), who in addition to studies of the history, physiology and ecology of decapods also undertook investigations on comparative morphology. In his descriptions he coined the term "gastric mill". Parallel to Huxley, Nauck (1880) examined the foreguts of approx. 70 different species of the Brachyura. Based on his data on the foregut-ossicles and the gastric teeth, he suggested a classification of the Brachyura into the Heterodontea and the Cyclodontea (see tab. 3). The fundamental division of this classification was not accepted, however, by any subsequent author (see also discussion). Mocquard (1883) described the foreguts of more than 100 decapods and came to the conclusion that all decapod foregut structures were basically uniform and the recognisable differences are the result of losses or fusions of the ossicles. He postulated a complete set of ossicles and a powerful gastric mill for ancestral decapods.

Patwardhan (1934, 1935a–e) concluded from investigations of reptant and natant decapod foregut structures, that the efficiency of the internal digesting apparatus (principally the gastric mill) must be correlated with the efficiency of the mouthparts. Patwardhan showed that natant decapods possess strong mandibles and weakly developed gastric mills in contrast to the reptant decapods.

Maynard & Dando (1974) as well as Meiss & Norman (1977) described and illustrated the ossicles of a further 15 reptant decapods with a revised ossicle nomenclature and created the basis for a uniform identification of the ossicles. A different view regarding the mandibles and their correlation with the development of the gastric mill comes from Felgenhauer & Abele (1989). They employed numerous examples to argue that the structure of the gastric mill and the mandibles is correlated not inescapably with the food spectrum, but rather with the phylogeny.

Brösing *et al.* (2002) described the foregut ossicle system of three dromiid species with the conclusion that they are part of a monophyletic taxon Brachyura. A revised ossicle nomenclature with six additional ossicles was proposed based on a new staining method. Descriptions of the gastric teeth of additional decapod species have more recently expanded our knowledge about foregut structures (Castro & Bond-Buckup 2003, Abrunhosa *et al.* 2006, Melo *et al.* 2006, Sakai & Sawada 2006, Sakai *et al.* 2006 and Huespe *et al.* 2008). The foregut ossicles and gastric teeth of more than 66 brachyuran species were examined and are here described and documented in detail.

Material and methods

The foregut-ossicles and the gastric teeth of 66 brachyuran and two outgroup species were examined (see also