



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

Brösing *et al.* 2007) (tab. 1).

Preparation and ossicle-staining. The foreguts of the selected taxa were dissected and cleaned by heating in 10% KOH solution at 100°C for 60 min. All calcified structures of the foregut were stained by adding alizarin red to the heated potassium-solution for 10–15 minutes. After staining, the foreguts were washed in distilled water and stored in 70% ethanol (Brösing 2002, Brösing *et al.* 2002). The results are intact stomachs with red-stained ossicles *in situ*.

Scanning electron microscopy. For scanning electron microscopy, the gastric teeth were dissected and separated from the remaining foregut, dehydrated in absolute ethanol, and critical-point-dried. Finally, the teeth were coated with gold and examined with the following scanning electron microscopes:

Scanning electron microscope (JSM-840), ZMUC, Copenhagen;
 stereo scanning electron microscope (S 360), Humboldt-University Berlin;
 digital scanning electron microscope (LEO 1430), Humboldt-University Berlin;
 digital scanning electron microscope (LEO 1450 VP), Museum für Naturkunde Berlin;
 digital scanning electron microscope (CamScan, Elektronenoptik GmbH), Senckenberg, Forschungsinstitut und Naturmuseum Frankfurt.

TABLE. 1. List of species examined; AMS, Australian Museum, Sydney; FSBC, Florida Marine Research Institute, St. Petersburg; MNHN, Muséum national d’Histoire naturelle, Paris; MB, Muséum national d’ Histoire naturelle; a.c., author’s collection; QM, Queensland Museum, Brisbane; SMF, Senckenbergmuseum Frankfurt; ZMB, Zoologisches Museum, Berlin; ZMUC, Zoological Museum, Copenhagen.

<i>Orconectes limosus</i> (Rafinesque, 1817)	Cambaridae Hobbs, 1942	SMF 37108
<i>Lithodes maja</i> (Linnaeus, 1758)	Lithodidae Samouelle, 1819	ZMUC CRU-4417
<i>Paradynomene tuberculata</i> Sakai, 1963	Dynomenidae Ortmann, 1892	MP-B. 26608
<i>Dynomene praedator</i> A. Milne-Edwards, 1879	Dynomenidae Ortmann, 1892	MNHN-B. 6903
<i>Dynomene filholi</i> Bouvier, 1894	Dynomenidae Ortmann, 1892	Author’s collection
<i>Metadromia wilsoni</i> (Fulton and Grant, 1902)	Dromiidae de Haan, 1833	MNHN-B. 26255
<i>Sternodromia spinostris</i> (Miers, 1881)	Dromiidae de Haan, 1833	SMF 36913
<i>Dromia personata</i> (Linnaeus, 1758)	Dromiidae de Haan, 1833	SMF 9685
<i>Lauridromia intermedia</i> (Laurie, 1906)	Dromiidae de Haan, 1833	MP-B. 26370
<i>Hypoconcha spinosissima</i> Rathbun, 1933	Dromiidae de Haan, 1833	FSBC I 48297 EJ67063
<i>Homola ranunculus</i> Guinot and Richter de Forges, 1995	Homolidae de Haan, 1839	MNHN-B. 19869
<i>Homola barbata</i> (Fabricius, 1793)	Homolidae de Haan, 1839	SMF 14939
<i>Paromola cuvieri</i> (Risso, 1816)	Homolidae de Haan, 1839	SMF 36914
<i>Dagnaudus petterdi</i> (Grant, 1905)	Homolidae de Haan, 1839	AMS P 53426
<i>Latreillia valida</i> de Haan, 1839	Latreilliidae de Haan, 1840	ZMB 27446
<i>Latreillia metanasa</i> Williams, 1982	Latreilliidae de Haan, 1840	ZMB 27447
<i>Cymonomus granulatus</i> (Norman, in Wyville Thomson, 1873)	Cymonomidae Bouvier, 1898	SMF 36916
<i>Raninoides bouvieri</i> Capart, 1951	Raninidae de Haan, 1839	MNHN-B. 16176
<i>Raninoides hendersoni</i> Chopra, 1933	Raninidae de Haan, 1839	MNHN-B. 13401
<i>Raninoides personatus</i> Henderson, 1888	Raninidae de Haan, 1839	MP-B. 11558
<i>Lyreidus brevifrons</i> Sakai, 1937	Raninidae de Haan, 1839	MP-B. 18959
<i>Lyreidus tridentatus</i> de Haan, 1841	Raninidae de Haan, 1839	MNHN-B. 13368
<i>Lysirude channeri</i> (Wood-Mason, 1887)	Raninidae de Haan, 1839	MP-B. 11562
<i>Notopoides latus</i> Henderson, 1888	Raninidae de Haan, 1839	MP-B. 18964
<i>Ranina ranina</i> (Linnaeus, 1758)	Raninidae de Haan, 1839	MNHN-B. 16183

continued next page

TABLE 1. (continued)

<i>Hyas araneus</i> (Linnaeus, 1758)	Majoidea Samouelle, 1819	ZMUC CRU-4411
<i>Hyas coarctatus</i> Leach, 1815	Majoidea Samouelle, 1819	ZMUC CRU-4412
<i>Inachus dorsettensis</i> (Pennant, 1777)	Inachidae MacLeay, 1838	ZMUC CRU-4413
<i>Libinia dubia</i> H. Milne Edwards, 1834	Majoidea Samouelle, 1819	SMF 36914
<i>Calappa granulata</i> (Linnaeus, 1758)	Calappidae de Haan, 1833	SMF 6025
<i>Spinolambrus notialis</i> (Manning and Holthuis, 1981)	Parthenopidae MacLeay, 1838	ZMUC CRU-4409
<i>Dorippe sinica</i> Chen, 1980	Dorippidae MacLeay, 1838	SMF 15134
<i>Medorippe lanata</i> (Linnaeus, 1767)	Dorippidae MacLeay, 1838	ZMUC CRU-4405
<i>Ilia spinosa</i> Miers, 1881	Leucosiidae Samouelle, 1819	ZMUC CRU-4407
<i>Philyra variegata</i> (Rüpell, 1830)	Leucosiidae Samouelle, 1819	ZMUC CRU-4408
<i>Bellidilia laevis</i> (Bell, 1855)	Leucosiidae Samouelle, 1819	SMF 36917
<i>Leucosia anatum</i> (Herbst, 1783)	Leucosiidae Samouelle, 1819	SMF 36918
<i>Portunus (Portunus) pelagicus</i> (Linnaeus, 1758)	Portunidae Rafinesque, 1815	SMF 36919
<i>Liocarcinus depurator</i> (Linnaeus, 1758)	Portunidae Rafinesque, 1815	ZMB 16417
<i>Carcinus maenas</i> (Linnaeus, 1758)	Portunidae Rafinesque, 1815	SMF 37107
<i>Callinectes sapidus</i> Rathbun, 1896	Portunidae Rafinesque, 1815	SMF 36920
<i>Cancer pagurus</i> Linnaeus, 1758	Cancridae Latreille, 1802	SMF 36921
<i>Carpilius convexus</i> (Forskål, 1775)	Carpiliidae Ortmann, 1893	MP-B. 7669
<i>Austinograea alayseae</i> Guinot, 1990	Bythograeidae Williams, 1980	SMF 37109
<i>Segonzacia mesatlantica</i> (Williams, 1988)	Bythograeidae Williams, 1980	SMF 37110
<i>Hexaplex megalops</i> Doflein, 1904	Hexapodidae Miers, 1886	SMF 36922
<i>Trapezia cymodoce</i> (Herbst, 1801)	Trapeziidae Miers, 1886	ZMUC CRU-4410
<i>Trapezia lutea</i> Castro, 1997	Trapeziidae Miers, 1886	ZMB 27450
<i>Tetralia glaberrima</i> (Herbst, 1790)	Tetraliidae Castro, Ng & Ahyong, 2004	SMF 36923
<i>Leptodius sanguineus</i> (H. Milne Edwards, 1834)	Xanthidae Dana, 1851a	ZMB 15618
<i>Rhithropanopeus harrisi</i> (Gould, 1841)	Panopeidae Ortmann, 1893	SMF 36924
<i>Potamonautes lirrangensis</i> (Rathbun, 1904)	Potamonautidae Bott, 1970	ZMUC CRU-4406
<i>Nepinnotheres villosulus</i> (Guerin-Meneville, 1831)	Pinnotheridae de Haan, 1833	AMS G 4226
<i>Retropluma quadrata</i> de Saint Laurent, 1989	Retroplumidae Gill, 1894	SMF 36925
<i>Pseudopalicus declivis</i> Castro, 2000	Palicidae Bouvier, 1898	SMF 36926
<i>Parapalicus clinodentatus</i> Castro, 2000	Palicidae Bouvier, 1898	ZMB 27449
<i>Micropalicus vietnamensis</i> (Zarenkov, 1968)	Palicidae Bouvier, 1898	ZMB 27448
<i>Crossotonotus spinipes</i> (De Man, 1888)	Crossotonotidae Moosa & Sèrene, 1981	SMF 36927
<i>Ocypode cursor</i> (Linnaeus, 1758)	Ocypodidae Rafinesque, 1815	SMF 12165
<i>Ocypode gaudichaudi</i> Milne Edwards & Lucas, 1843	Ocypodidae Rafinesque, 1815	SMF 6844
<i>Uca (Gelasimus) tetragonon</i> (Herbst, 1790)	Ocypodidae Rafinesque, 1815	SMF 36928
<i>Uca (Minuca) rapax</i> (Smith, 1870)	Ocypodidae Rafinesque, 1815	SMF 36929
<i>Mictyris longicarpus</i> Latreille, 1806	Mictyridae Dana, 1851b	ZMUC CRU-4415
<i>Mictyris platycheles</i> H. Milne Edwards, 1852	Mictyridae Dana, 1851b	ZMUC CRU-4416
<i>Cardisoma armatum</i> Herklots, 1851	Gecarcinidae MacLeay, 1838	SMF 36930
<i>Discoplax hirtipes</i> Dana, 1851	Gecarcinidae MacLeay, 1838	ZMUC CRU-4414
<i>Eriocheir sinensis</i> H. Milne Edwards, 1853	Varunidae H. Milne Edwards, 1853	SMF 37106
<i>Pseudosesarma moeschi</i> de Man, 1888	Sesarmidae Dana, 1851	QM W 25869

Results

Gross morphology of the brachyuran stomach

The intestinal tract of the Brachyura can be generally divided into three different anatomical sections; the foregut, midgut and hindgut. The foregut section starts with the mouth opening surrounded by the mandibles, the first and second maxillae, and the first to third maxillipeds. Then the oesophagus follows, leading postero dorsally into the first part of the stomach, the gastric mill. The “gastric mill” contains several gastric teeth, setae and a sack-like membranous chamber. The pyloric filter follows posteriorly, separated from the gastric mill by the cardio-pyloric valve.

In consequence of its ectodermal origin, all parts of the foregut have a chitinous intima and are involved in the molting-cycle just the hindgut. The short midgut is of endodermal origin and without a chitinous intima. The stomach (gastric mill and filter) is located within the antero dorsal part of the cephalothorax. Its position is fixed by a series of muscles connected with dorsal apodemes of the cephalothorax (Maynard & Dando 1974). In most of the investigated specimens the position of the stomach is recognisable by deep furrows on the dorsal carapace. All stomach muscles are differentiated anatomically by their origin and also physiologically by their innervation (Maynard & Dando 1974; Heinzel *et al.* 1993; Böhm 1996, Böhm *et al.* 1997, 2001).

During the feeding process, food particles are manipulated and shredded by the first pair of pereopods and the mouth parts. The transport of the food into the gastric mill is the result of peristaltic movements of the oesophagus (Böhm *et al.* 1997).

The basis for an efficient grinding of the food is the interaction between the stomatogastric nervous system, the stomach-muscles and the foregut ossicles with the gastric teeth.

With the passage through the filter, liquid food components are separated from the solid particles and transported into the midgut-gland. There the liquid components are digested and absorbed.

General morphology of the foregut ossicles and the gastric teeth

The different, moveable ossicles in some cases with remarkable tooth structures, are essentially responsible for the grinding of the food particles. Within the last two centuries the ossicles received a series of different names. Some of the ossicles (III, VII, XVI, XVII, XVIII, XXI, XXIII) are unpaired and arranged at the midline of the stomach (Fig. 1). All other ossicles are usually paired.

The ossicles of the dorsal gastric mill (I, II, III, IV, V, VI and VII) are essentially responsible for the shaping and stabilisation of the gastric mill as well as for the function of the gastric teeth. Ossicles I, II and VII cover the dorsal part of the gastric mill. The lateral section of the gastric mill is limited by the zygo-cardiac ossicle (V). In some cases the membranous part of the gastric mill is laterally extended (Raninidae, Bythograeidae and Ocypodidae) or anteriorly (Dorippidae, Leucosiidae (*Ebalia*) and Majidae). The zygo-cardiac ossicle of both sides carries the lateral teeth, which have family-level diagnostic characteristics. The single dorso-median tooth is formed by the posterior part of the urocardiac ossicle (VII).

The function and motility of the gastric teeth is regulated by the interaction of various stomach-muscles and the ossicles. The unpaired pyloric ossicle (III) usually covers the transition from the gastric mill to the posterior pyloric filter. This ossicle can also be greatly reduced (such as in representatives of the Raninidae and Dorippidae).

The ossicles of the lateral gastric mill (VIII, IX, X, Xa, XI, XII, XIII, XIV and XV). Some of these ossicles are also involved in the stabilisation of the membranous parts of the stomach in particular the thin calcified stomach plates XI and XII are responsible for a more or less stable shape of the stomach sac, independent of the degree to which it is filled.

The pectinal ossicle (VIII) carries the accessory teeth. The number of teeth varies from one tooth (in Raninidae, Dorippidae and Leucosiidae) up to 15 or 16 teeth (Grapsidae and Gecarcinidae).

Ossicles of the cardio-pyloric valve (XVI, XVII and XVIII). These ossicles work together as the cardio-pyloric valve, which partly separates the anterior gastric mill and the posterior pyloric filter. The dorsal part of the valve is characterized by family-specific teeth or bristles. In representatives of the Dromiidae, Homolidae,

Calappidae and Dorippidae it has a nearly pointed shape with numerous setae. Characteristic tooth-like structures on the antero dorsal part of the valve were present in the samples of xanthoid crabs, *Leptodius sanguineus* and *Rhithropanopeus harrisi*. Furthermore in representatives of the Ocypodidae, Gecarcinidae and Mictyridae the leading edge of the cardio-pyloric valve is even more pronounced. It carries a tooth-like projection and the posterior plate is covered with strong setae.

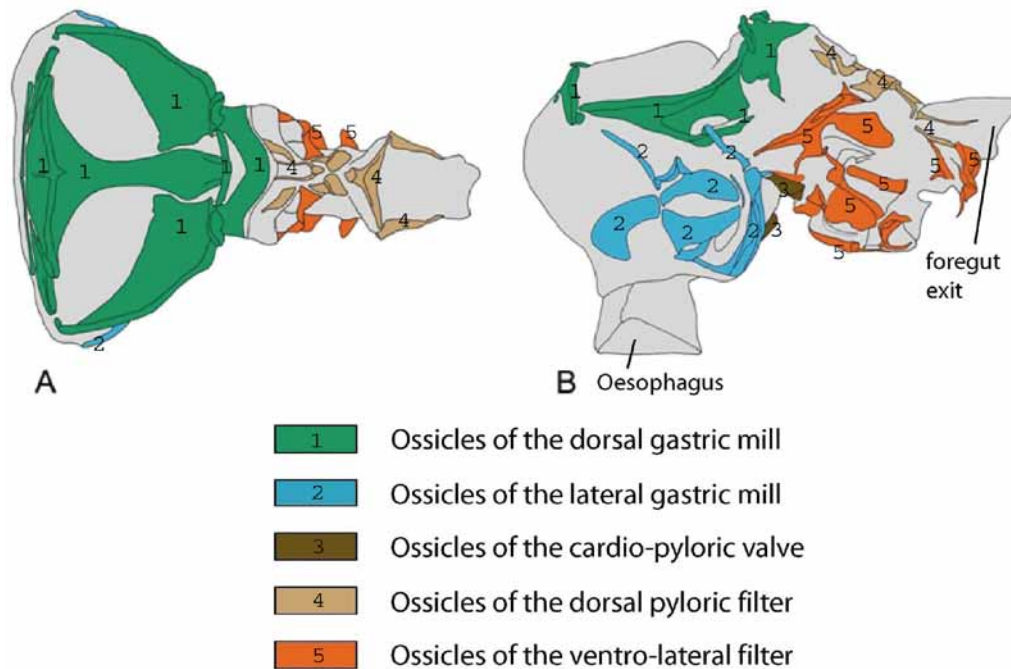


FIGURE 1. Different functional regions of the brachyuran foregut ossicles. A. dorsal view; B. lateral view, left = anterior, right = posterior (modified after Brösing *et al.* 2002).

Ossicles of the dorsal pyloric filter (XIX, XIXa, XX, XXI, XXIa and XXIb). The pyloric filter is joined to the posterior part of the gastric mill. It is supported dorsally by six different ossicles (XIX, XIXa, XX, XXI, XXIa and XXIb). Whereas the anterior mesopyloric ossicle (XIX) and the lateral mesopyloric ossicle (XIXa) are usually small and weakly calcified, the paired mesopyloric posterior ossicle (XX) is often strongly raised in relief. Muscles inserted on these ossicles and connected via an apodeme with the dorsal carapace stabilise the pyloric filter in its dorsal position. The posteriorly following unpaired uropyloric ossicle (XXI) has in most of the investigated species a crescentic shape, sometimes connected with very thin plates. The uropyloric ossicle (XXI) extends most of the width of the pyloric filter. Posteriorly joins the uropyloric ossicle (XXI) with the paired, very long extended posterior uropyloric ossicles. In most of the examined species, ventrally of the ossicles (XXIb) there are the very small infra-uropyloric fragments (XXIa).

Ossicles of the lateral and ventral pyloric filter (XXII, XXIII, XXIV, XXV, XXVI, XXVIa, XXVII, XXVIII, XXIX, XXX, XXXI, XXXII and XXXIII). These ossicles contribute the main part of the filter function of the stomach. With the exception of ossicles XXIII and XXVII, all other ossicles of this region are paired. Superficially on the lateral pyloric filter at least two layers of different stomach-muscles are recognisable. They insert mostly on the ossicles described above (Maynard & Dando 1974). These muscles are controlled by the pyloric network, part of the stomatogastric nervous system (Heinzel *et al.* 1993); and are responsible for the movement of the ossicles and the pyloric filter.

Ossicle nomenclature

Most of the described ossicles are paired; unpaired ossicles are given in the singular form. We recognised 41 different ossicles including six newly described ones (IIa, IIb, Va, XIXa, XXIb and XXVIa) (tab. 2).

TABLE. 2. Revised ossicle-nomenclature.

I	mesocardiac ossicle	Ossicles of the dorsal gastric mill
IIa	prepterocardiac ossicles	
II	pterocardiac ossicles	
IIb	postpterocardiac ossicles	
III	pyloric ossicle	
IV	exopyloric ossicles	
V	zygocardiac ossicles	
Va	prezygocardiac ossicles	
VI	propyloric ossicle	
VII	urocardiac ossicle	
VIII	pectineal ossicles	Ossicles of the lateral gastric mill
IX	prepectineal ossicles	
X	postpectineal ossicles	
Xa	quill of the postpectineal ossicles	
XI	anterior lateral cardiac plates	
XII	posterior lateral cardiac ossicles	
XIII	inferior lateral cardiac ossicles	
XIV	subdentate ossicles	
XV	lateral cardio-pyloric ossicles	
XVI	anterior ossicle of the cardio-pyloric valve	Ossicles of the cardio-pyloric valve
XVII	posterior ossicle of the cardio-pyloric valve	
XVIII	lateral ossicle of the cardio-pyloric valve	
XIX	anterior mesopyloric ossicle	Ossicles of the dorsal pyloric filter
XIXa	lateral mesopyloric ossicles	
XX	posterior mesopyloric ossicles	
XXI	uropyloric ossicle	
XXIa	infra-uropyloric fragments	
XXIb	posterior uropyloric ossicles	
XXII	preampullary ossicles	Ossicles of the lateral and ventral pyloric filter
XXIII	anterior inferior pyloric ossicle	
XXIV	inferior ampullary ossicles	
XXV	ampullary-roof-ossicles, lower portion	
XXVI	ampullary-roof-ossicles, upper portion	
XXVIa	anterior process of the ampullary-roof-ossicles, upper portion	
XXVII	posterior inferior pyloric ossicle	
XXVIII	anterior supra-ampullary ossicles	
XXIX	middle supra-ampullary ossicles	
XXX	posterior supra-ampullary ossicles	
XXXI	anterior pleuropyloric ossicles	
XXXII	middle pleuropyloric ossicles	
XXXIII	posterior pleuropyloric ossicles	

Comparison of the foregut ossicles

The description of the different foreguts follows Brösing *et al.* (2002). Only noteworthy particularities or deviations from other brachyuran species examined here are mentioned below. In some cases, ossicles are not separable from one another and no suture lines are recognisable. Therefore these ossicles will be mentioned as “mixed ossicles”.

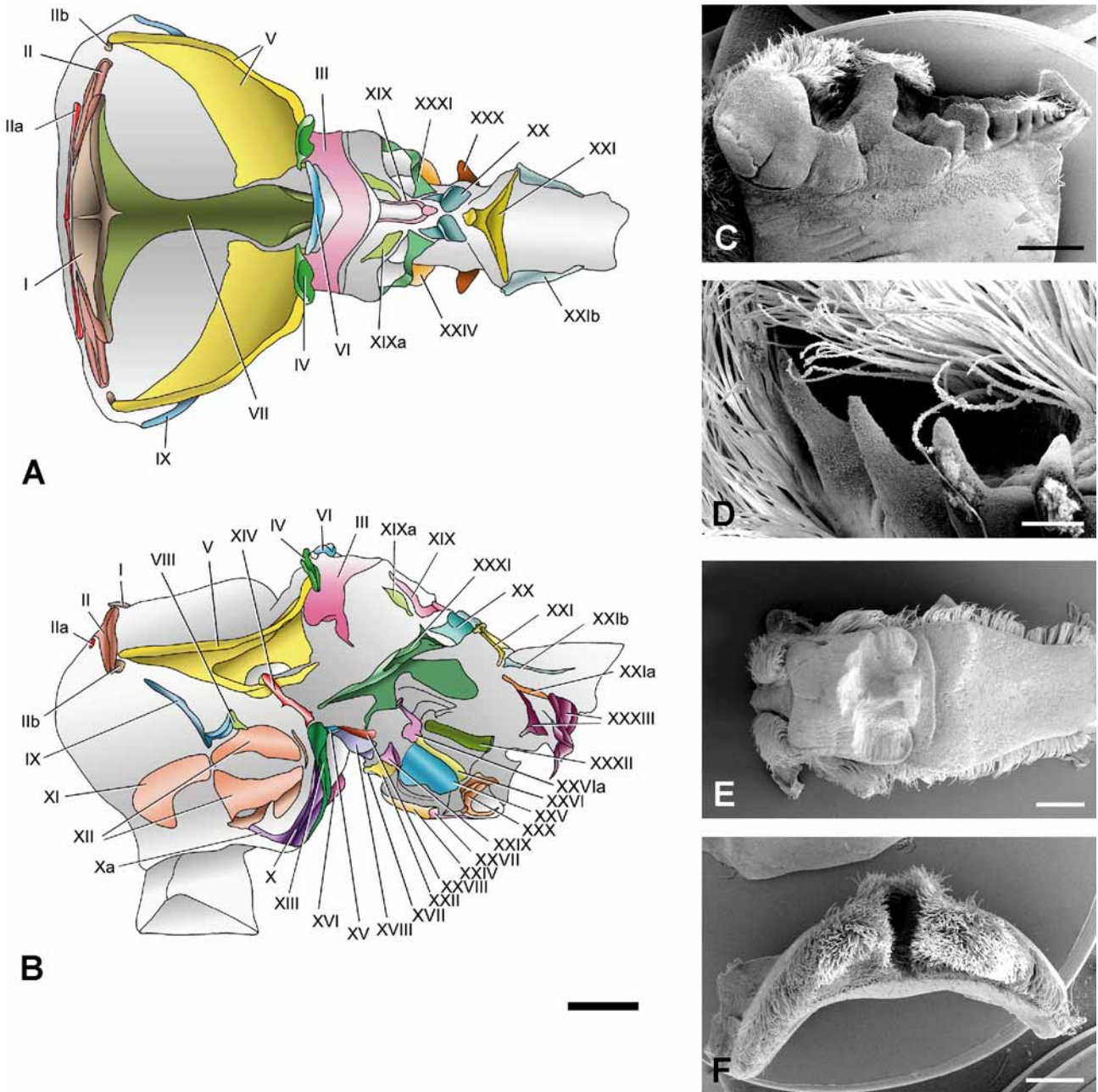


FIGURE 2. Foregut ossicles of *Stenodromia spinostris* (Miers, 1881), A. dorsal view, B. lateral view; gastric teeth of *Dromia personata* (Linnaeus, 1758), C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. - F. 1mm, D. 200µm.

Dromiidae de Haan, 1833

A detailed description of three dromiid foregut-ossicles (*Metadromia wilsoni*, *Dromia personata* and *Lauridromia intermedia*) is given in Brösing *et al.* 2002. Remarkable deviations from two further dromiid species (*Stenodromia spinostris* and *Hypoconcha spinosissima*) are as follows:

Stenodromia spinirostris (Miers, 1881) (Fig. 2A, B)

The paired prepterocardiac ossicle (IIa) lies anterior to the mesocardiac ossicle (I). Both have a form of narrow, transversally elongated strips.

Hypoconcha spinosissima Rathbun, 1933

The prepterocardiac ossicle (IIa) is unpaired.

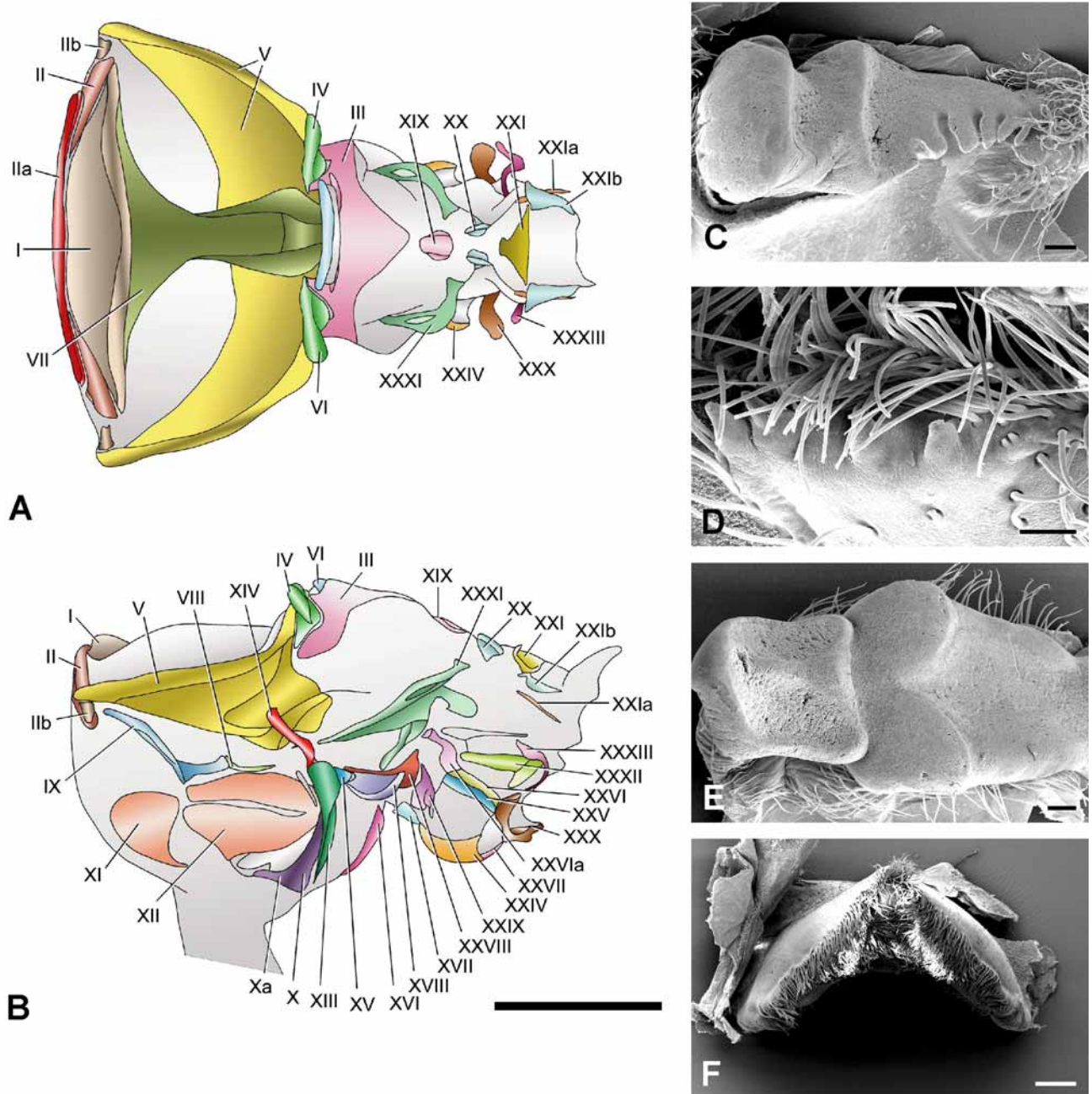


FIGURE 3. Foregut ossicles of *Dynomene filholi* Bouvier, 1894, A. dorsal view, B. lateral view; gastric teeth of *Paradynomene tuberculata* Sakai, 1963, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 200µm, D. 100µm, E. 200µm, F. 500µm.

Dynomenidae Ortmann, 1892

Dynomene filholi Bouvier, 1894 (Fig. 3A, B) and *Dynomene praedator* A. Milne-Edwards, 1879

The unpaired prepterocardiac ossicle (IIa) consists of a single narrow strip in front of the mesocardiac ossicle (I). The very small pectinal ossicle (VIII) has a triangular shape with four accessory teeth. An anteriorly directed spine extends from the middle of the subdentate ossicle (XIV). Ossicles XVII and XXII are not recognisable.

Paradynomene tuberculata Sakai, 1963 (Fig. 3C–F)

The very small pectinal ossicle (VIII) has a triangular shape with five accessory teeth. The lateral mesopyloric ossicle (XIXa) and the preampullary ossicles (XXII) are only present in this species in contrast to the above described dynomenid species. The infra-uropyloric fragment (XXIa) is short and comma-shaped. The middle pleuropyloric ossicle (XXXII), as in the other species of dynomenids, is more extensive.

Homolidae de Haan, 1839

The membrane of the stomach-sac is comparatively thick compared to all other examined brachyuran species.

Dagnaudus petterdi (Grant, 1905) (Fig. 4A, B)

The mesocardiac ossicle (I) has several posteriorly directed spines. The striped prepterocardiac ossicle (IIa) is more stronger than in Dromiidae and Dynomenidae, and does not reach the midline. A postpterocardiac ossicle (IIb) is not recognisable. The pectinal ossicle (VIII) has a triangular shape with seven accessory teeth.

Homola ranunculus Guinot and Richer de Forges, 1995 (Fig. 4C–F) and *Homola barbata* (Fabricius, 1793)

The very thin, extensive, paired prepterocardiac ossicles (IIa) join at the midline of the antero dorsal gastric mill. The very small pectinal ossicle (VIII) has a triangular shape with seven accessory teeth. The middle pleuropyloric ossicle (XXXII) has a pointed shape.

Paramola cuvieri (Risso, 1816)

The pectinal ossicle (VIII) has a triangular shape with 11 accessory teeth. The ventral keel of the anterior ossicle of the cardio-pyloric valve (XVI) is V-shaped. The posterior mesopyloric ossicle (XX) has on its ventral side an anterior as well as a posterior directed spine.

Latreilliidae de Haan, 1840

The foreguts of *Latreillia valida* und *Latreillia metanesa* share two remarkable autapomorphic characters that distinguish them from all other brachyuran species examined here. First, the foreguts are laterally flattened and secondly, the oesophagus is anteriorly-directed.

Latreillia valida de Haan, 1839 (Fig. 5) and *Latreillia metanesa* Williams, 1982

The paired oval prepterocardiac ossicles (IIa) are joined at the midline. The unpaired propyloric ossicle (VI) is inclined some 10–20° in the posterior direction. The pectinal ossicle (VIII) is horseshoe-shaped with 11 accessory teeth. Ossicle (XXIa) is not recognisable.

Majoidea Samouelle, 1819

Inachus dorsettensis (Pennant, 1777) (Fig. 6)

The unpaired propyloric ossicle (VI) is inclined a few degrees in the anterior direction; and its dorsal margin is sharp. The pectinal ossicle (VIII) is horseshoe-shaped with seven accessory teeth. Ossicles “XVII–

XXIII” are observed as mixed ossicles. The anterior lateral cardiac plate (XI) and the infra-uropylic fragment (XXIa) are not present.

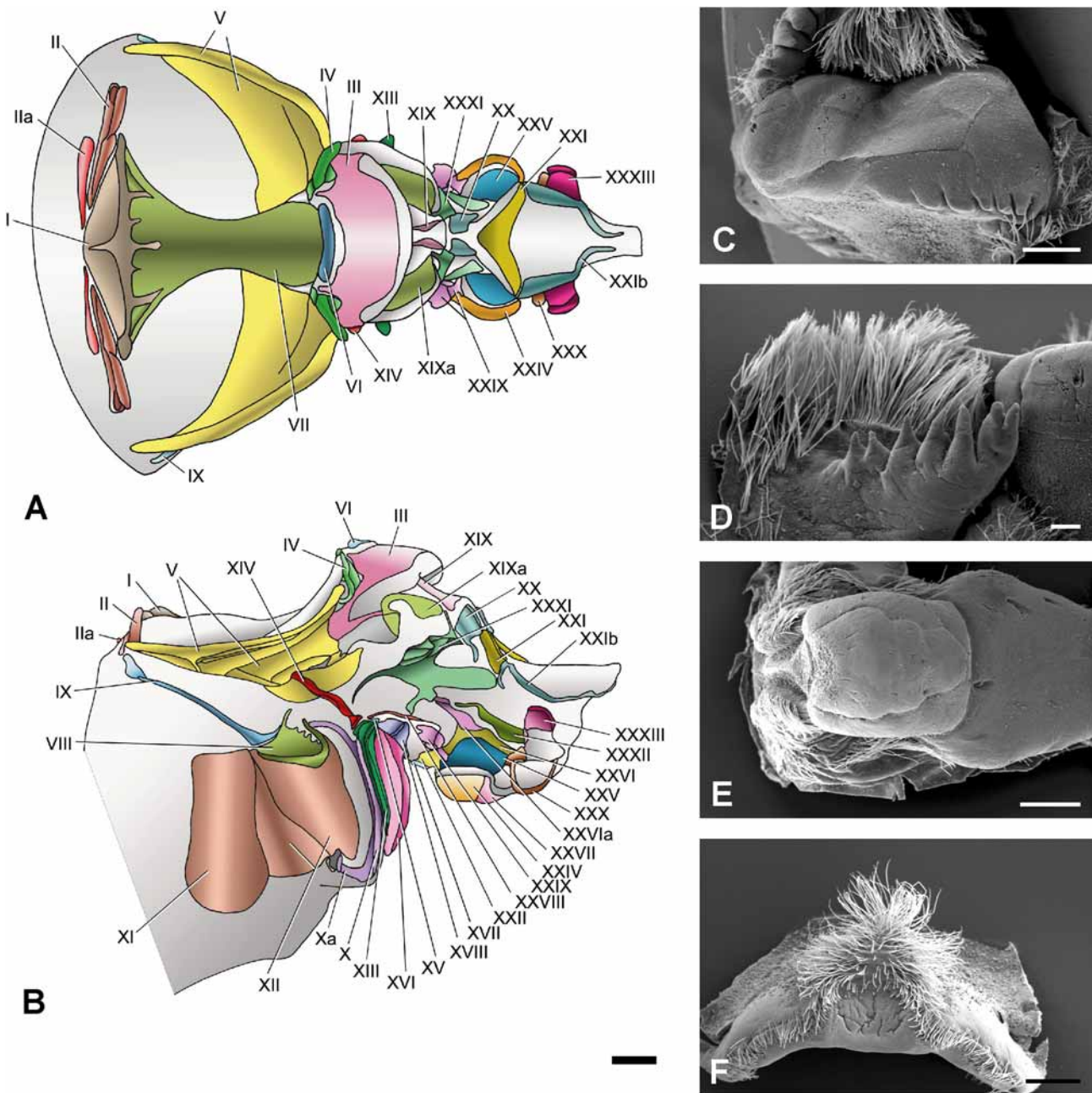


FIGURE 4. Foregut ossicles of *Dagnaudus petterdi* (Grant, 1905), A. dorsal view, B. lateral view; gastric teeth of *Homola ranunculus* Guinot & Richer de Forges, 1995, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F cardio-pyloric valve scales: A. & B. 2mm, C. 500µm, D. 200µm, E. & F. 500µm.

Hyas araneus (Linnaeus, 1758) and *Hyas coarctatus* Leach, 1815

The paired pyloric ossicle (III) is weakly calcified and has an oval shape. The exopyloric ossicle (IV) and the zygo-cardiac ossicle (V) are inseparable from one other. They are observed as mixed ossicles. The anterior end of the mixed ossicle “VI–V” (zygo-cardiac part) has an additional antero ventral spine which is directed toward the prepectinal ossicle (IX). The propyloric ossicle (VI), in contrast to that of *Inachus dorsettensis*, in a nearly vertical position. The pectinal ossicle (VIII) is horseshoe-shaped with three accessory teeth. The lateral mesopyloric ossicle (XIXa) is recognisable.

Libinia dubia H. Milne Edwards, 1834

The zygo-cardiac ossicle (V) has an additional antero ventral an additional spine which is directed to the prepectinal ossicle (IX). The pectinal ossicle (VIII) is horseshoe-shaped with four accessory teeth. Ossicles XIXa and XXII are not recognisable. An infra-uropylic fragment (XXIa) is present.

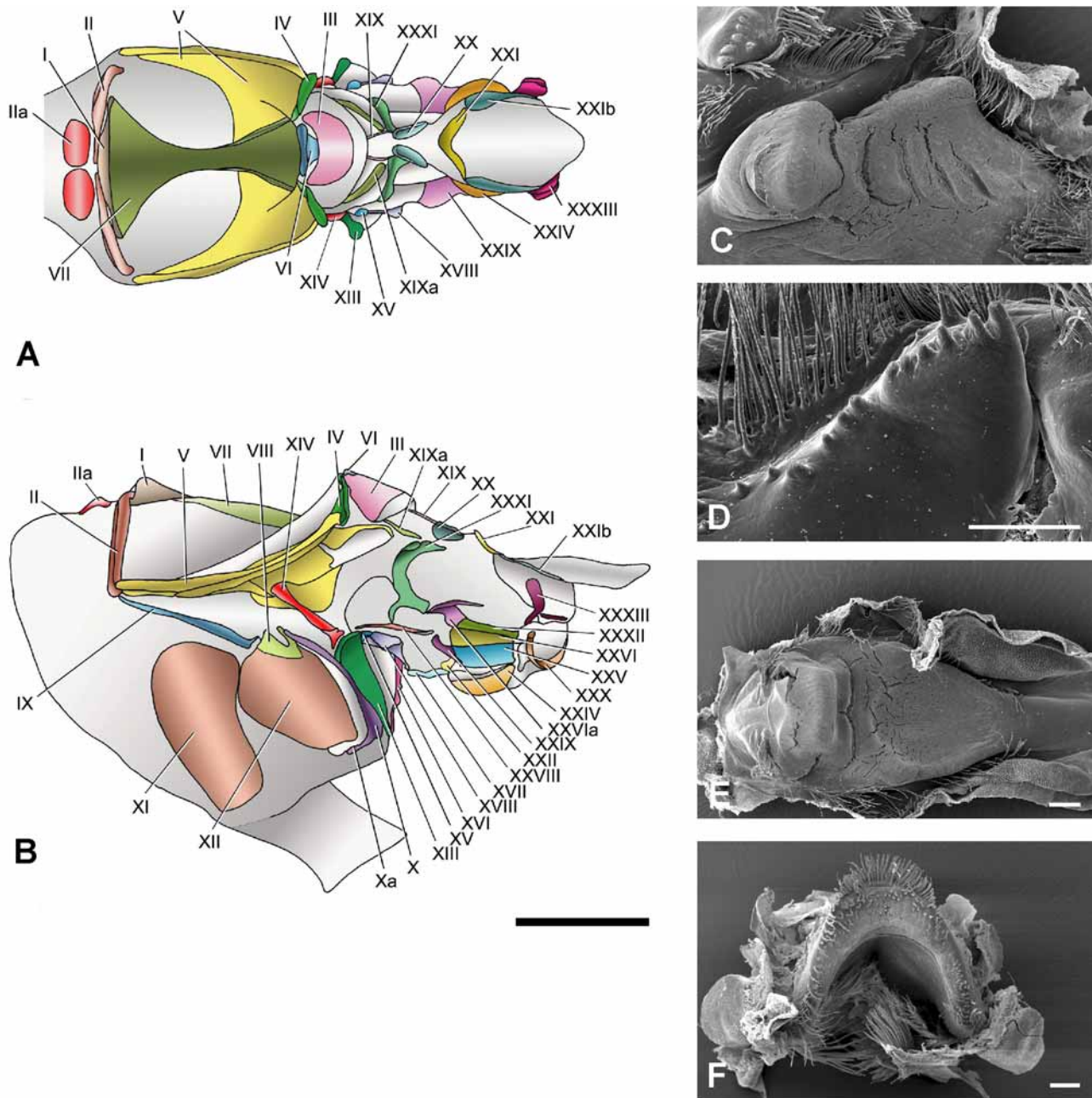


FIGURE 5. Foregut ossicles and gastric teeth of *Latreillia valida* De Haan, 1839, A. dorsal view, B. lateral view, C lateral tooth, D accessory teeth, E dorso-median tooth, F cardio-pyloric valve; scales: A. & B. 1mm, C. – F. 100µm.

Calappidae de Haan, 1833

Calappa granulata (Linnaeus, 1758) (Fig. 7)

The pyloric ossicle (III) is paired. The zygo-cardiac ossicle (V) has a semicircular impression antero ventral. The propyloric ossicle (VI) is nearly vertical, and its dorsal margin is U-shaped and has a sharp margin. The pectinal ossicle (VIII) is horseshoe-shaped with three accessory teeth. The inferior lateral cardiac

ossicle (XIII) has a clearly antero lateral connection to the subdentate ossicle (XIV). On the subdentate ossicle (XIV) there is a circular ventral impression.

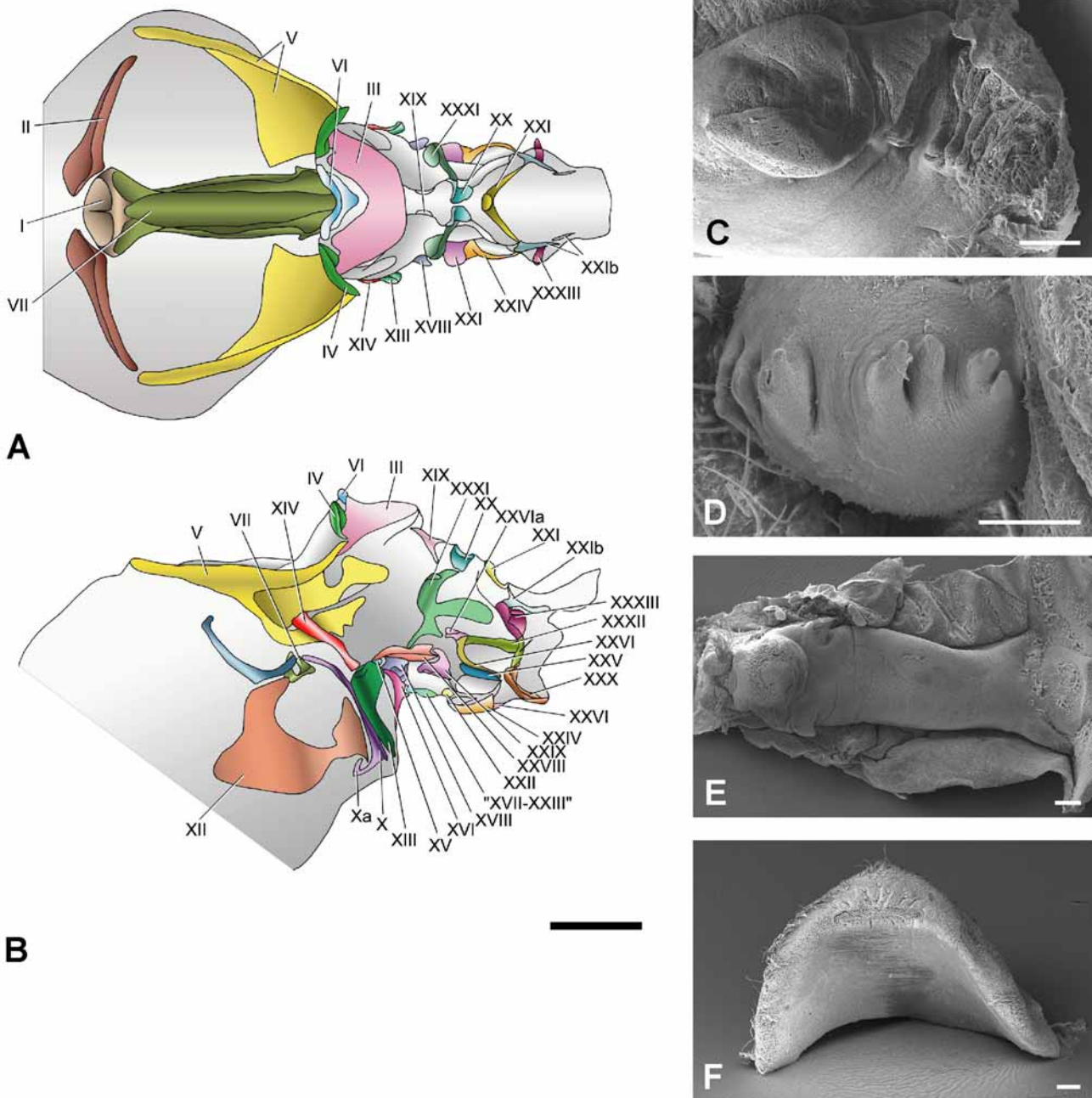


FIGURE 6. Foregut ossicles and gastric teeth of *Inachus dorsettensis* (Pennant, 1777), A. dorsal view, B. lateral, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 200µm, D. 100µm, E. 200µm, F. 100µm.

Parthenopidae MacLeay, 1838

Parthenope notialis Manning and Holthuis, 1981 (Fig. 8)

The propyloric ossicle (VI) is nearly vertical. The zygo-cardiac ossicle (V) has a semicircular impression antero ventral. The pectinal ossicle (VIII) is horseshoe-shaped with two accessory teeth. On the subdentate ossicle (XIV) there is a circular impression.

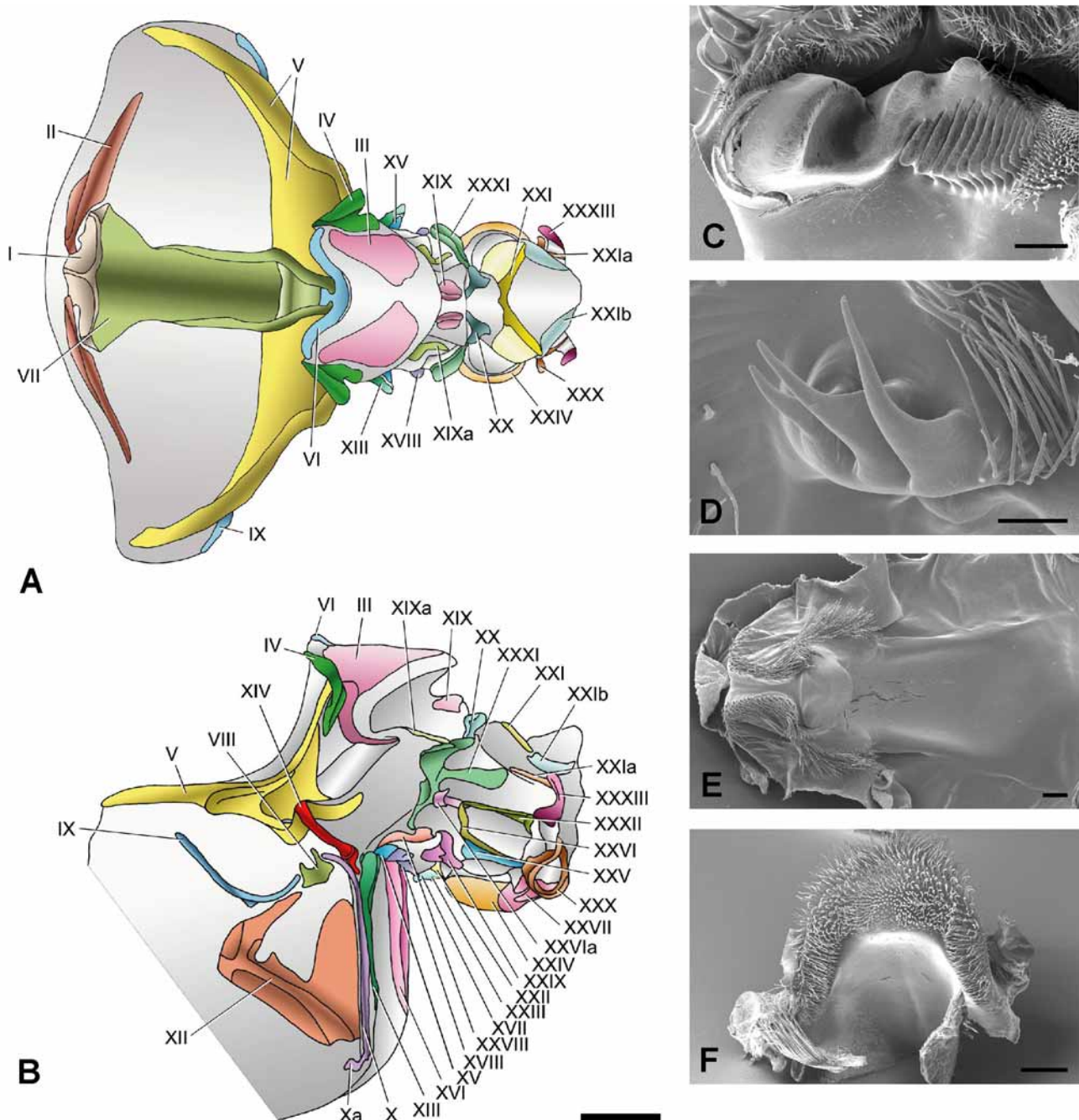


FIGURE 7. Foregut ossicles and gastric teeth of *Calappa granulata* (Linnaeus, 1758), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-medial tooth, F. cardio-pyloric valve; scales: A. & B. 2mm, C. 200µm, D. 100µm, E. & F. 300µm.

Dorippidae MacLeay, 1838

Dorippe sinica Chen, 1980 (Fig. 9A–E) and *Medorippe lanata* (Linnaeus, 1767) (Fig. 9F)

The very small, paired pyloric ossicle (III) has an oval shape. The unpaired propyloric ossicle (VI) is inclined some 10–20° in the posterior direction, its U-shaped dorsal margin is sharp-edged. The pectinal ossicle (VIII) is horseshoe-shaped with one accessory tooth. The ossicles (XI and XIXa) are not recognisable.

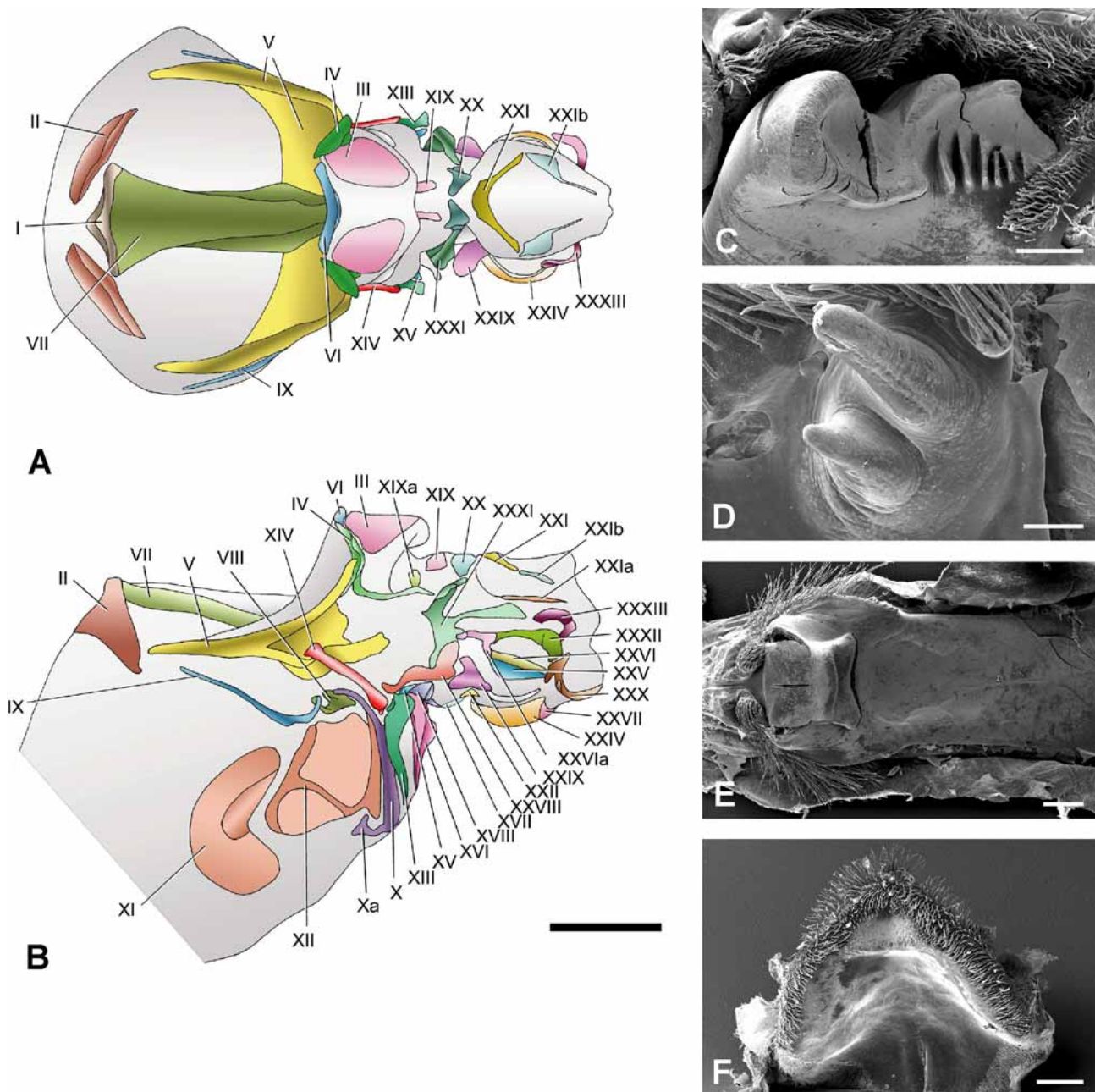


FIGURE 8. Foregut ossicles and gastric teeth of *Spinolambrus notialis* (Manning & Holthuis, 1981), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 200µm, D. 50µm, E. & F. 200µm.

Cyonomidae Bouvier, 1898

Cyonomus granulatus (Thomson, 1873) (Fig. 10)

Antero lateral to the zygo-cardiac ossicle (V) extends the prezygo-cardiac ossicle (Va), only recognised in Cyonomidae. Ossicles VIII, XI, XV, XIX, XIXa, XXIa and XXIb are not recognisable. The inferior lateral cardiac ossicle (XIII) has a clearly lateral connection to the subdentate ossicle (XIV). The subdentate ossicle (XIV) has postero-ventral a small rounded spine. Ossicles “IV–V”, “XVII–XXIII”, “XX–XXXI” and “XXV–XXVI–XXXII” are observed as mixed ossicles.

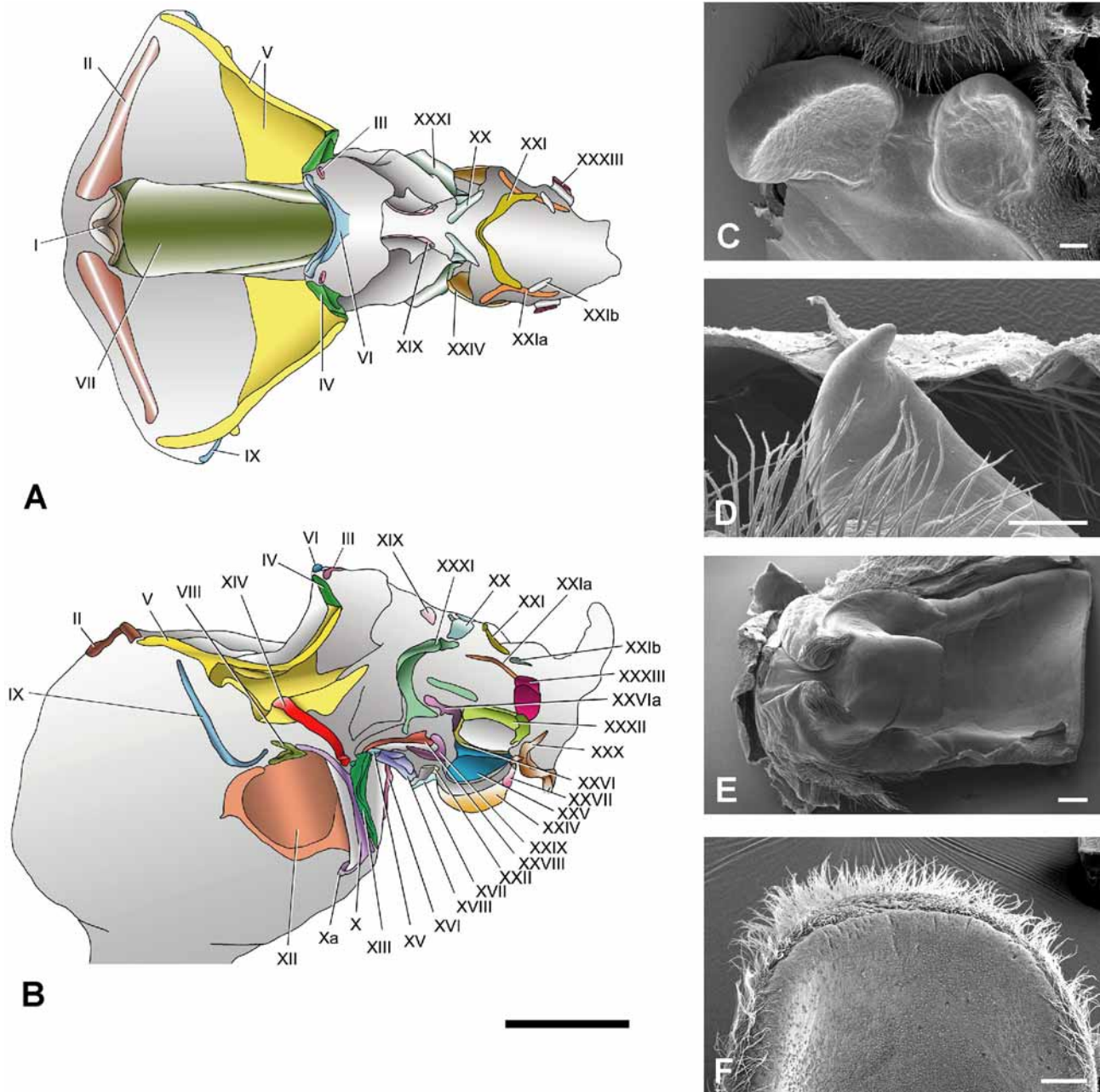


FIGURE 9. Foregut ossicles and gastric teeth of *Dorippe sinica* Chen, 1980, A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve, scales: A. & B. 2mm; C. 200µm; *Medorippe lanata* (Linnaeus, 1767) D. 100µm; E. 200µm; F. 200µm.

Raninidae de Haan, 1839

Ranina ranina (Linnaeus, 1758) (Fig. 11); *Raninoides hendersoni* Chopra, 1933; *Raninoides bouvieri* Capart, 1951; *Raninoides personatus* Henderson, 1888; *Lyreidus tridentatus* de Haan, 1841 and *Lysirude channeri* (Wood-Mason, 1887)

For the description of the foregut structures I am using *Ranina ranina* as the example for all of these species.

The pectinal ossicle (VIII) is horseshoe-shaped with one accessory tooth. The inferior lateral cardiac ossicle (XIII) has a clearly lateral connection to the subdentate ossicle (XIV). The ossicle ("XVII–XXIII") is observed as a mixed ossicle. Ossicles XIX and XIXa are not recognisable.

Lyreidus brevifrons Sakai, 1937

The unpaired propyloric ossicle (VI) is inclined about 45° in the posterior direction.

Notopoides latus Henderson, 1888

The anterior pleuropyloric ossicle (XXXI) is elongated and weakly calcified. The posterior pleuropyloric ossicle (XXXIII) is reduced to a vertical spine.

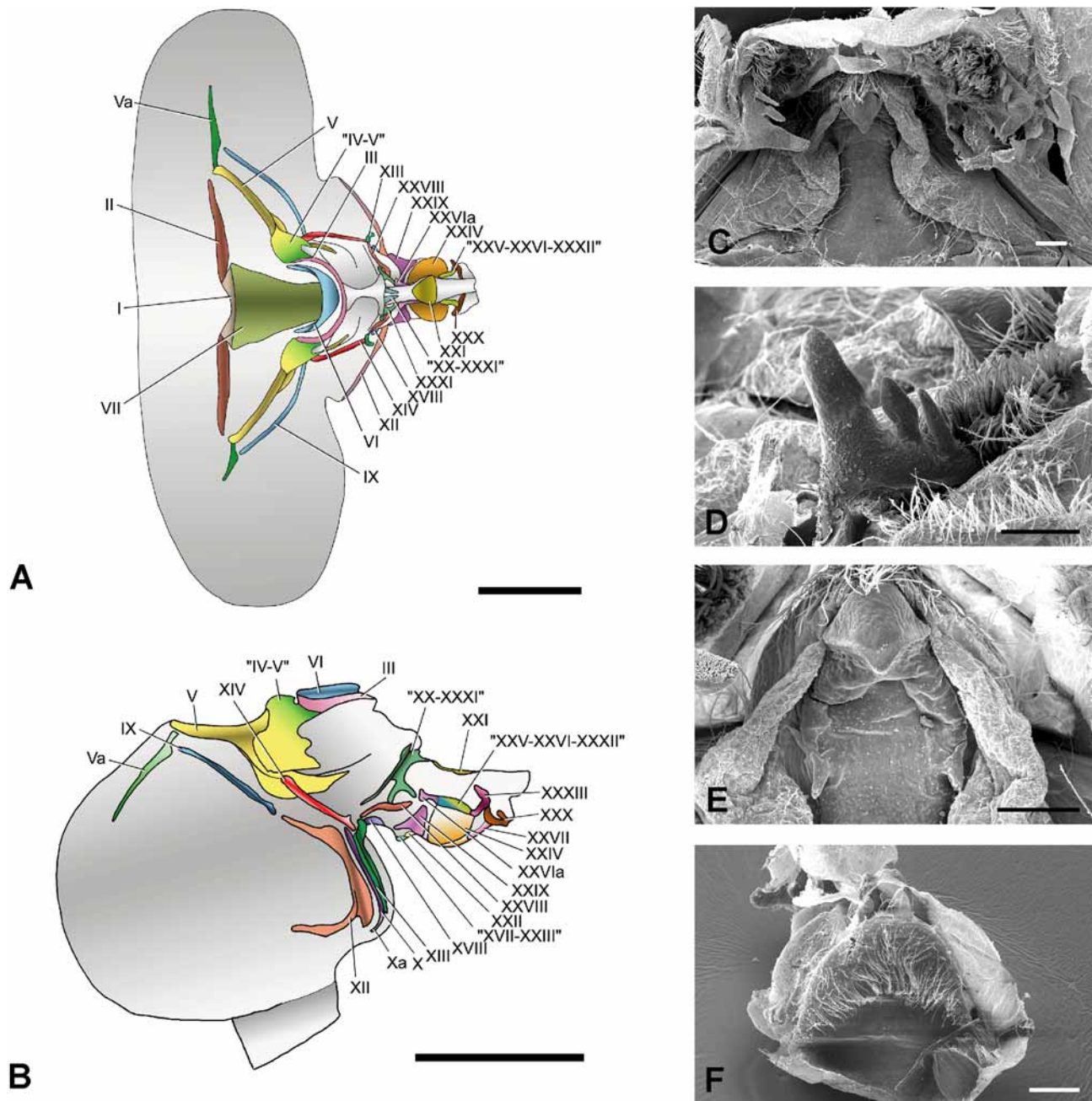


FIGURE 10. Foregut ossicles and gastric teeth of *Cymonomus granulatus* (Norman, in Wyville Thomson, 1873), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. – F. 100µm.

Leucosiidae Samouelle, 1819

Philyra variegata (Rüpell, 1830) (Fig. 12) and *Philyra laevis* (Bell, 1855)

Ossicles “IV–V” is observed as a mixed ossicle. The zygo-cardiac ossicle (V) has a semicircular impression antero ventral. The pectinal ossicle (VIII) is conical and has one accessory tooth. The ossicles (XI and XIXa) are not recognisable. The inferior lateral cardiac ossicle (XIII) has a clear antero lateral connection with the subdentate ossicle (XIV).

Ilia spinosa Miers, 1881

The pyloric ossicle (III) is paired. Ossicles “XVII–XXIII” occur as a mixed ossicle. A lateral mesopyloric ossicle (XIXa) is recognisable.

Leucosia anatum Herbst, 1783

The urocardiac ossicle (VII) has a convex bulge antero dorsally.

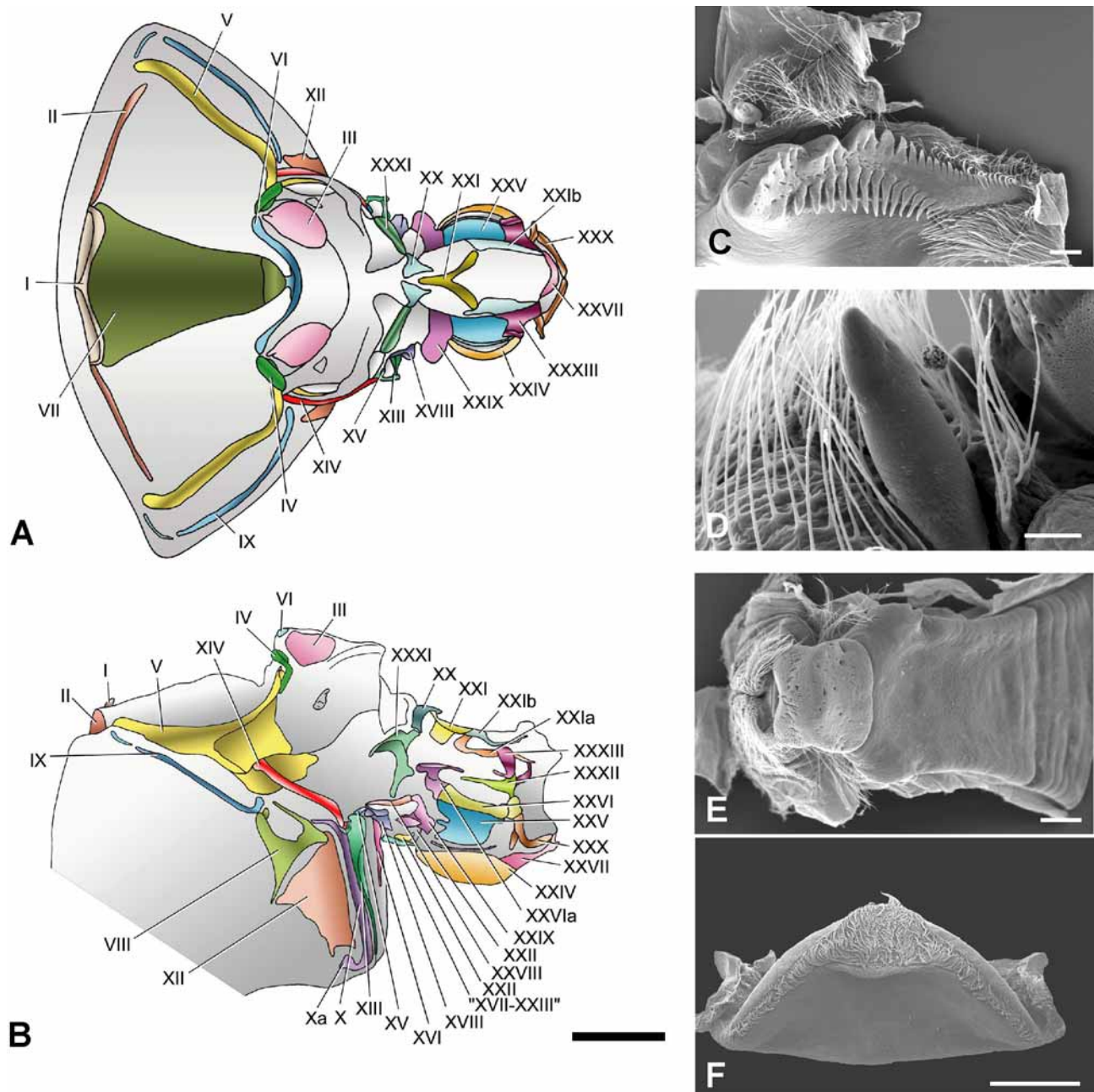


FIGURE 11. Foregut ossicles of *Ranina ranina* (Linnaeus, 1758), A. dorsal view, B. lateral view; gastric teeth of *Raninoides hendersoni* Chopra, 1933 (C.–E.) and *Ranina ranina* (F), C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 2mm, C. 200µm, D. 100µm, E. 200µm, F. 1mm.

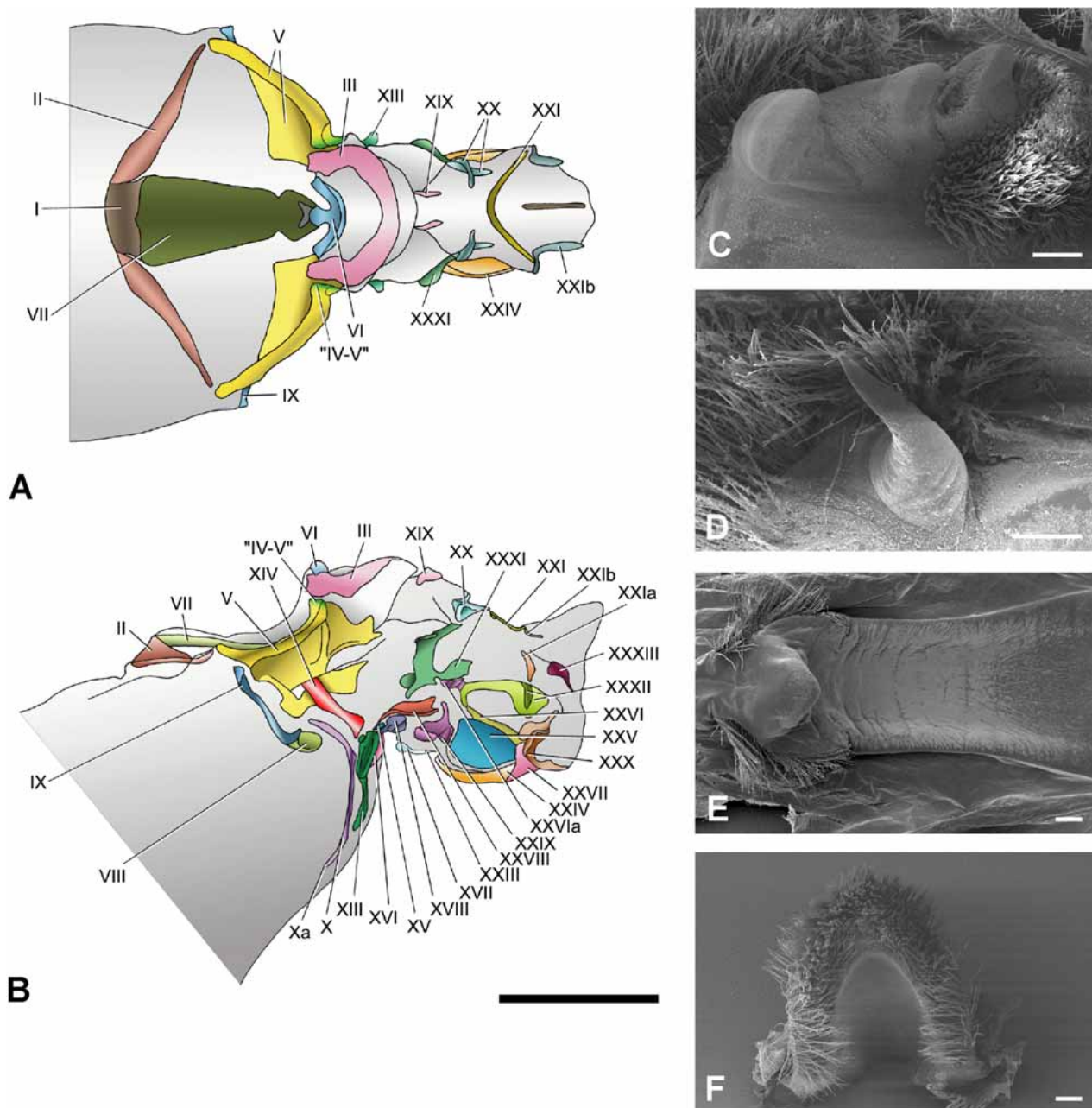


FIGURE 12. Foregut ossicles and gastric teeth of *Philyra variegata* (Rüppell, 1830), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. – F. 100µm.

Portunidae Rafinesque, 1815

Liocarcinus depurator (Linnaeus, 1758) (Fig. 13A, B); *Callinectes sapidus* Rathbun, 1896 (Fig. 13C–F);
Portunus (Portunus) pelagicus (Linnaeus, 1758)

The zygocardiac ossicle (V) has a semicircular impression antero ventral. The unpaired propyloric ossicle (VI) is inclined about 45° in the posterior direction; its dorso median margin has a short sharp point. The pectinal ossicle (VIII) is horseshoe-shaped with eight accessory teeth.

Carcinus maenas (Linnaeus, 1758)

The pyloric ossicle (III) is paired. The propyloric ossicle (VI) is nearly vertical. The pectinal ossicle (VIII) is horseshoe-shaped with three accessory teeth.

Cancridae Latreille, 1802

Cancer pagurus Linnaeus, 1758 (Fig. 14)

The zygo-cardiac ossicle (V) has a semicircular impression antero ventral. The unpaired propyloric ossicle (VI) is nearly vertical. The pectinal ossicle (VIII) is horseshoe-shaped with three accessory teeth. The inferior lateral cardiac ossicle (XIII) has a process connecting it with the subdentate ossicle (XIV) antero dorsal. The ossicle (XXIa) is not recognisable.

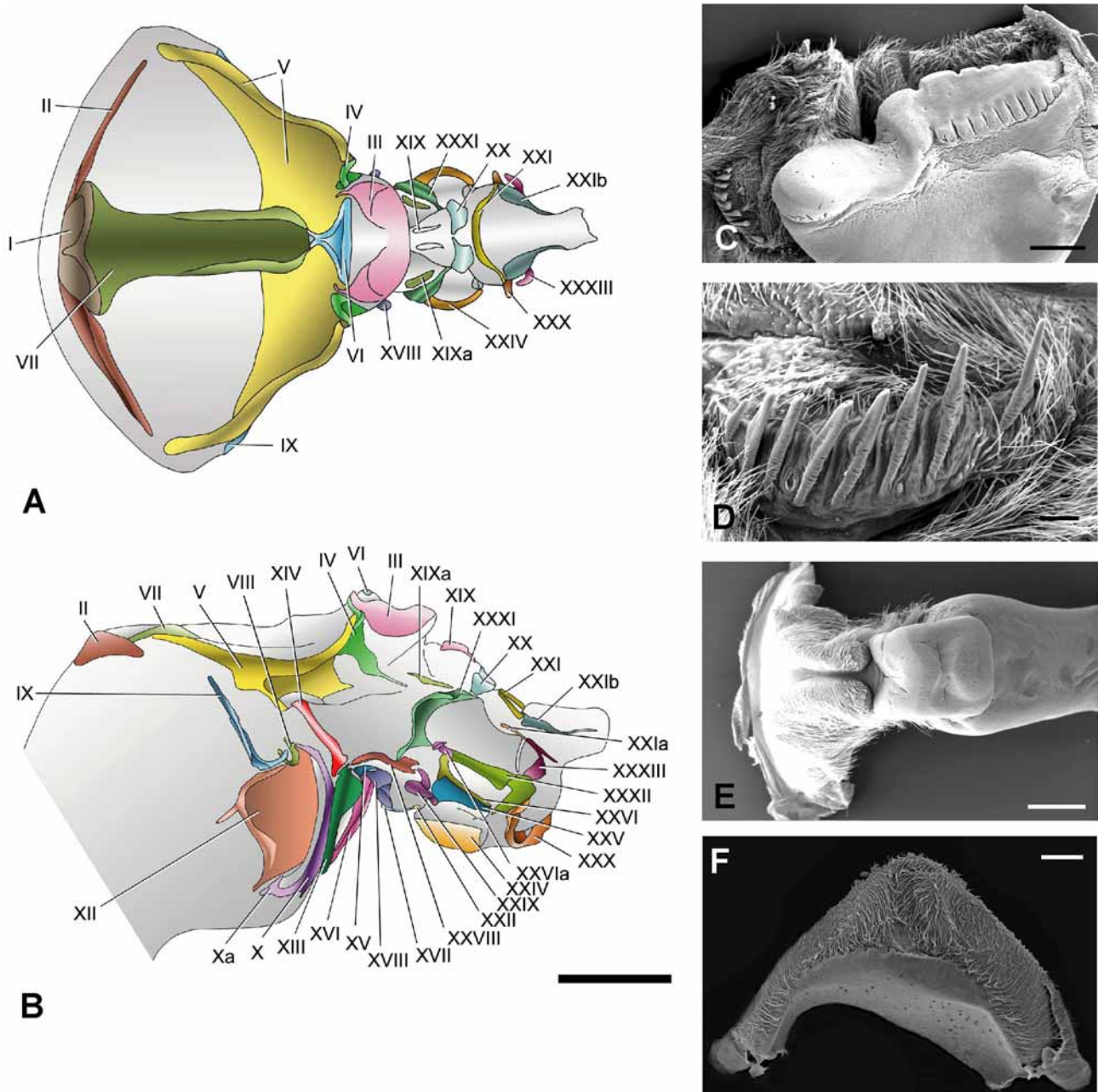


FIGURE 13. Foregut ossicles of *Liocarcinus depurator* (Linnaeus, 1758), A. dorsal view, B. lateral view; gastric teeth of *Callinectes sapidus* Rathbun, 1896, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 2mm, C. 1mm, D. 200µm, E. 1mm, F. 300µm.

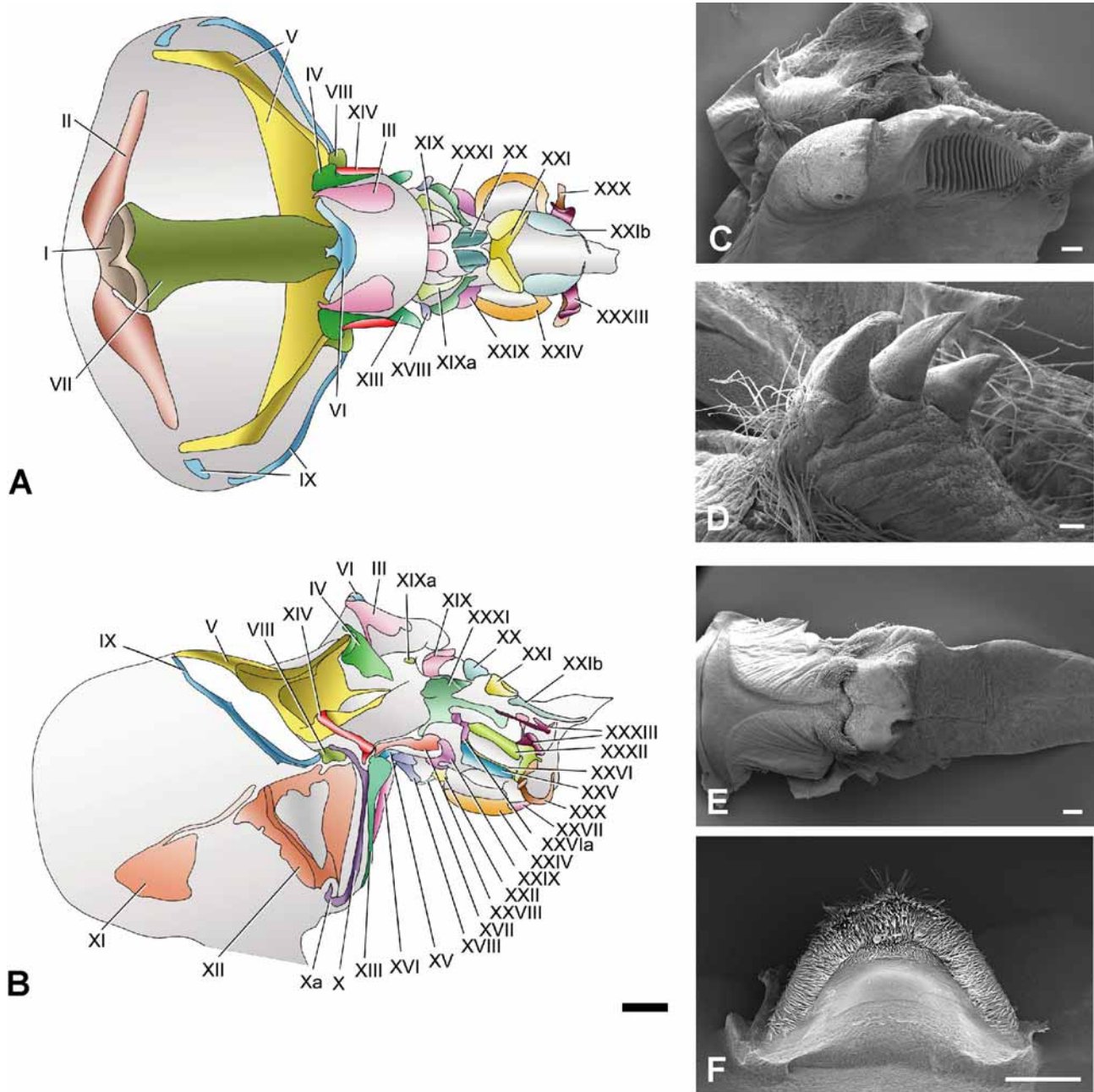


FIGURE 14. Foregut ossicles and gastric teeth of *Cancer pagurus* Linnaeus, 1758, A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-medial tooth; scales: A. & B. 1mm, C. 300µm, D. 100µm, E. 300µm, F. 1mm.

Carpiliidae Ortman, 1893

Carpilius convexus (Forskål, 1775) (Fig. 15)

The pectinal ossicle (VIII) is horseshoe-shaped with four accessory teeth.

Bythograeidae Williams, 1980

Segonzacia mesatlantica (Williams, 1988) (Fig. 16A, B) and *Austinograea alayseae* Guinot, 1989 (Fig. 16C–F)

Ossicles I and II are inclined about 45° in the antero-ventral direction. The zygo-cardiac ossicle (V) has a semicircular impression antero ventral. The unpaired propyloric ossicle (VI) is nearly vertical. The pectinal ossicle (VIII) is horseshoe-shaped with eight accessory teeth. The inferior lateral cardiac ossicle (XIII) has a connection-piece to the subdentate ossicle (XIV) antero dorsal. Ossicles “XVII–XXIII” are observed as a mixed ossicle. Ossicle XXII is not recognisable.

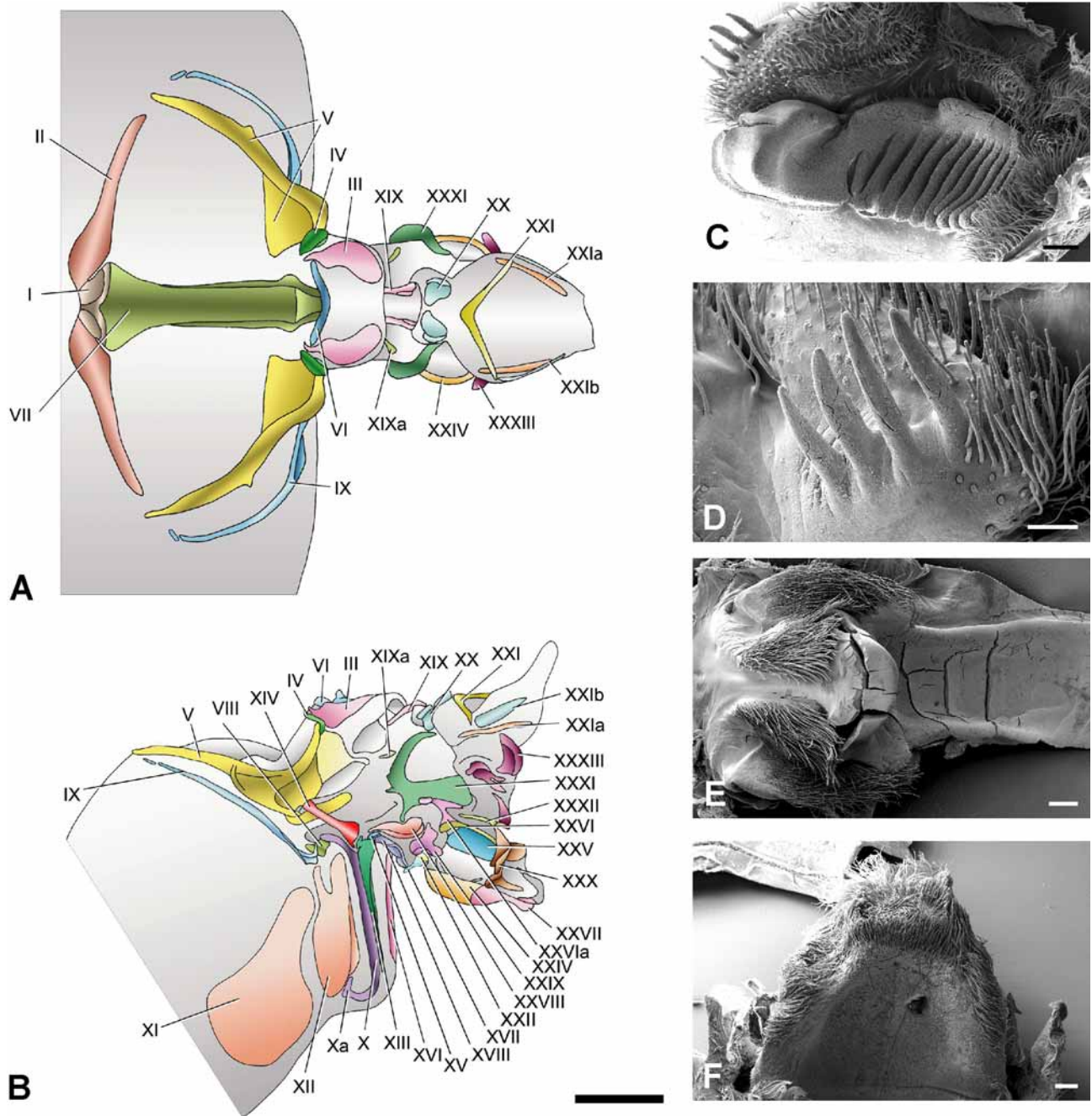


FIGURE 15. Foregut ossicles and gastric teeth of *Carpilus convexus* (Forskål, 1775), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 200µm, D. 100µm, E. & F. 200µm.

Hexapodidae Miers, 1886

Hexaplex megalops Doflein, 1904 (Fig. 17)

Ossicles I and II are inclined about 45° in the antero ventral direction. The zygo-cardiac ossicle (V) has a remarkable impression antero ventral. The unpaired propyloric ossicle (VI) is nearly vertical. The pectinal ossicle (VIII) is horseshoe-shaped with five accessory teeth. The inferior lateral cardiac ossicle (XIII) has a connection-piece to the subdentate ossicle (XIV) antero dorsal. The ossicle (XI) is sickle-shaped. Ossicles “XVII–XXIII” are observed as a mixed ossicle. Ossicles XIXa and XXII are not recognisable.

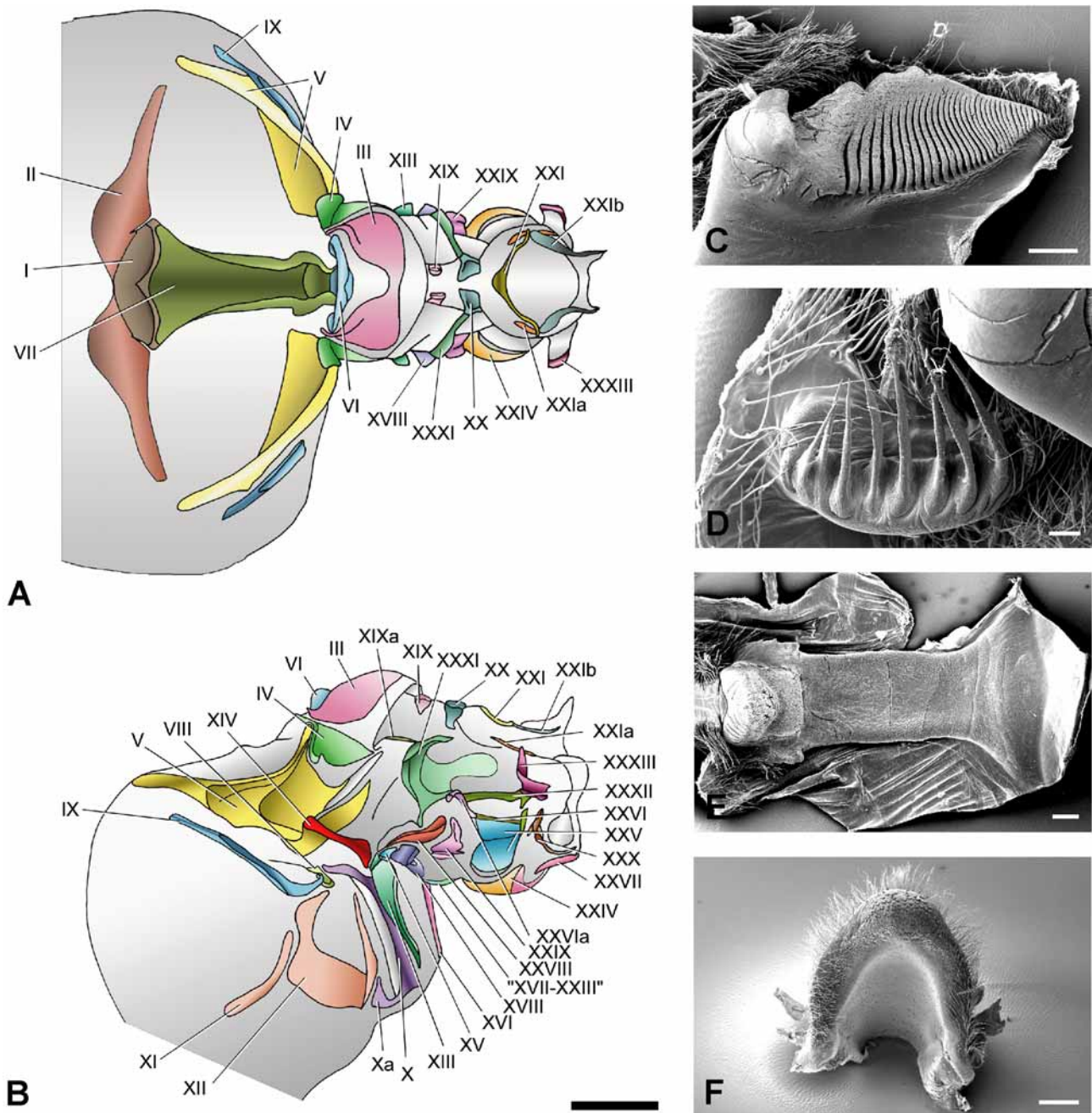


FIGURE 16. Foregut ossicles of *Segonzacia mesatlantica* (Williams, 1988), A. dorsal view, B. lateral view; gastric teeth of *Austinograea alayseae* Guinot, 1990, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 300µm, D. 100 µm, E. & F. 300µm.

Trapeziidae Miers, 1886

Trapezia lutea Castro, 1997 (Fig. 18A, B); *Trapezia cymodoce* (Herbst, 1801) (Fig. 18C–F) and *Tetralia glaberrima* (Herbst, 1790)

The ossicles (I and II) are inclined about 45° in the antero ventral direction. The unpaired propyloric ossicle (VI) is nearly vertical. The pectinal ossicle (VIII) is horseshoe-shaped with four accessory teeth. The inferior lateral cardiac ossicle (XIII) has a connection-piece to the subdentate ossicle (XIV) antero dorsal. Ossicle XIXa is not recognisable.

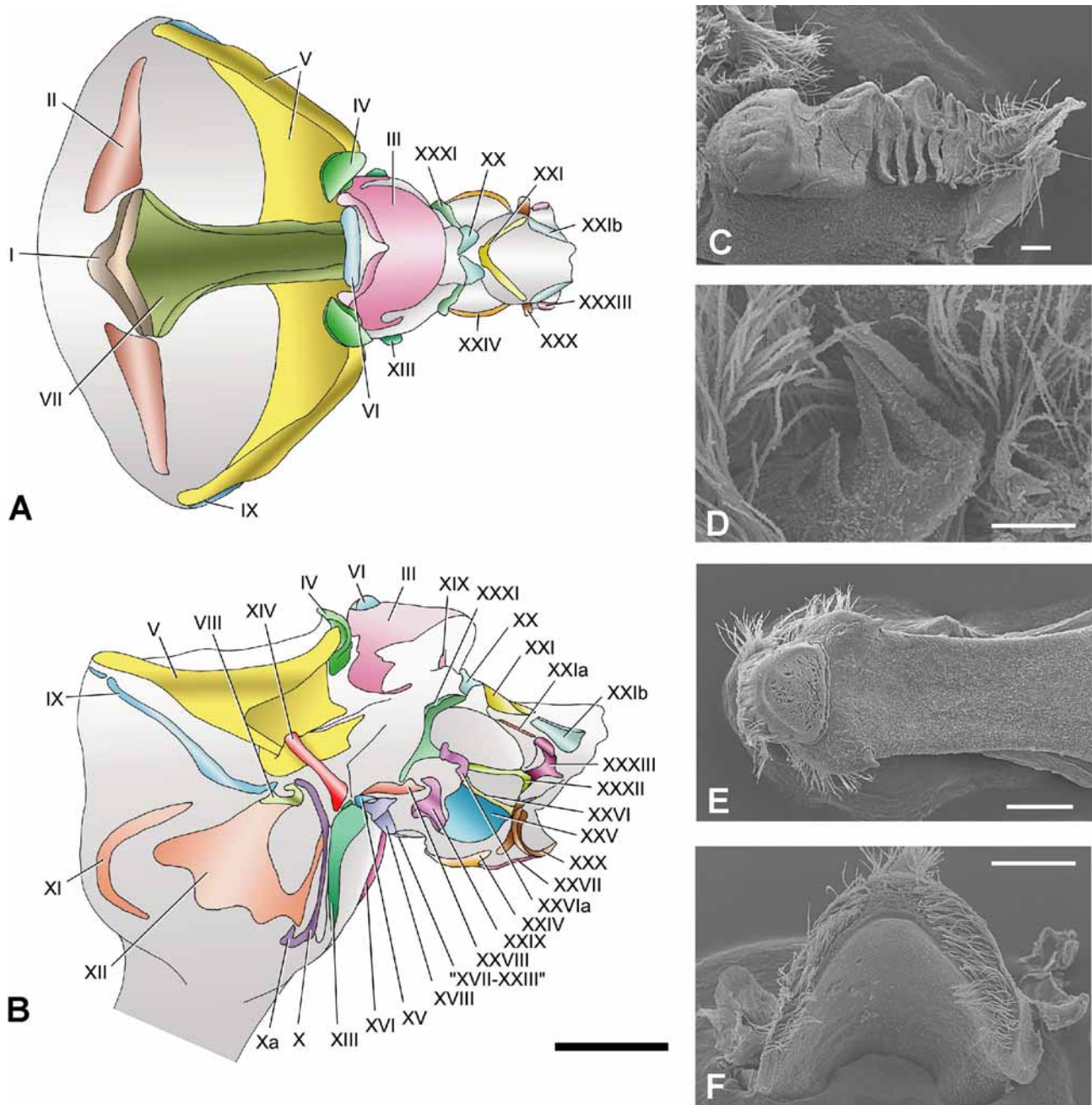


FIGURE 17. Foregut ossicles and gastric teeth of *Hexaplax megalops* Doflein, 1904, A. dorsal view, B. lateral view; C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 100µm, D. 100µm, E. & F. 300µm.

Xanthidae Dana, 1851

Leptodius sanguineus (H. Milne Edwards, 1834) (Fig. 19)

The cardiac sac is comparatively very small. Ossicles I, II and VI are nearly vertical. The pectinal ossicle

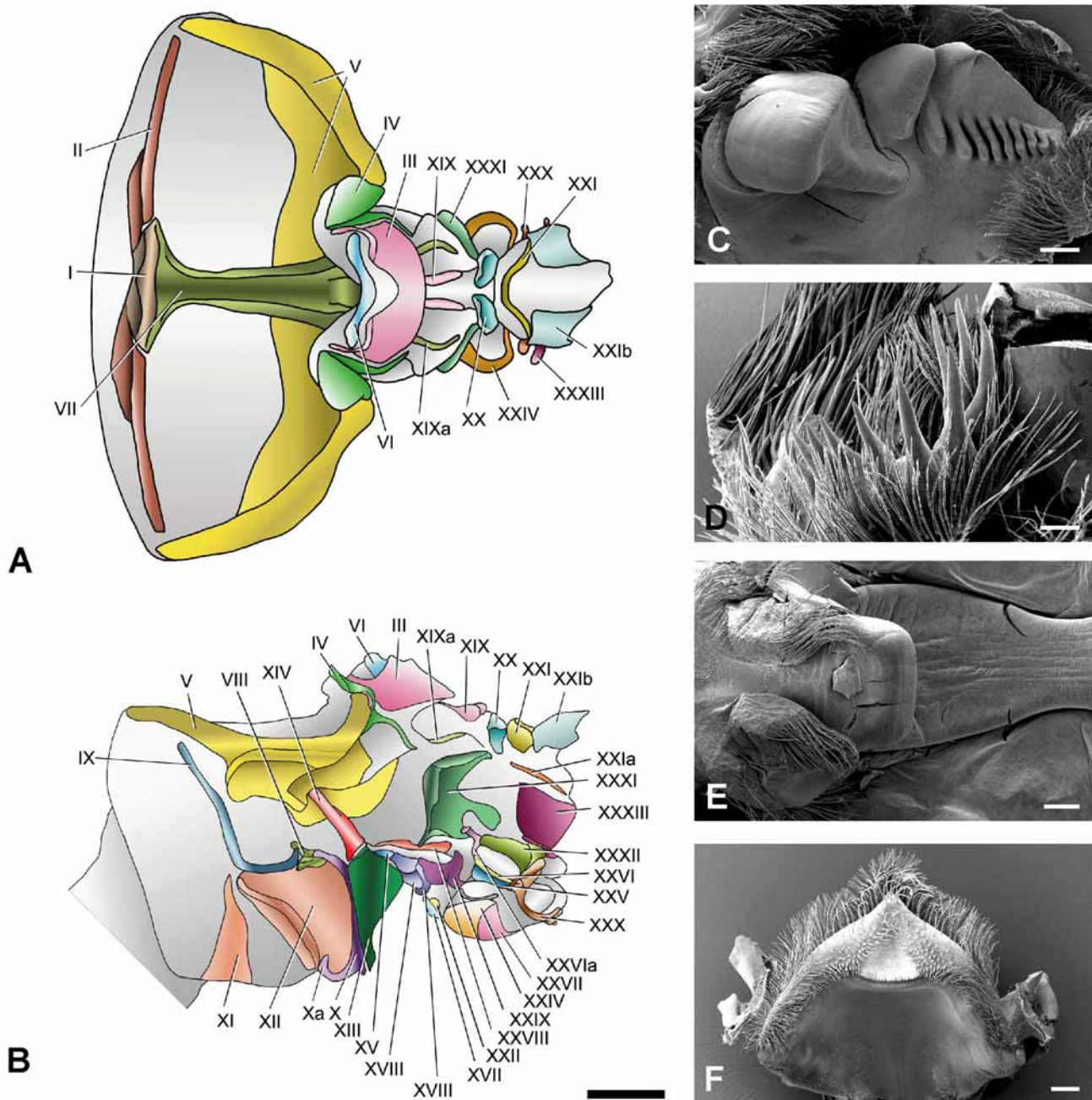


FIGURE 19. Foregut ossicles and gastric teeth of *Leptodius sanguineus* (H. Milne Edwards, 1834), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-medial tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 200µm, D. 100µm, E. & F. 200µm.

Potamonautidae Bott, 1970

Potamonautes lirrangensis (Rathbun, 1904) (Fig. 21)

Ossicles I and II are inclined about 45° in the antero ventral direction. Ossicles “IV–V” are observed as mixed ossicle. The zygocardiac ossicle (V) has a small semicircular impression antero ventral. The pectinal ossicle (VIII) is horseshoe-shaped with five accessory teeth. The inferior lateral cardiac ossicle (XIII) has a connection pice to the subdentate ossicle (XIV) antero dorsal. The subdentate ossicle (XIV) has postero ventral a remarkable spine, which is posteriorly directed. The ossicle (XXIa) is not recognisable.

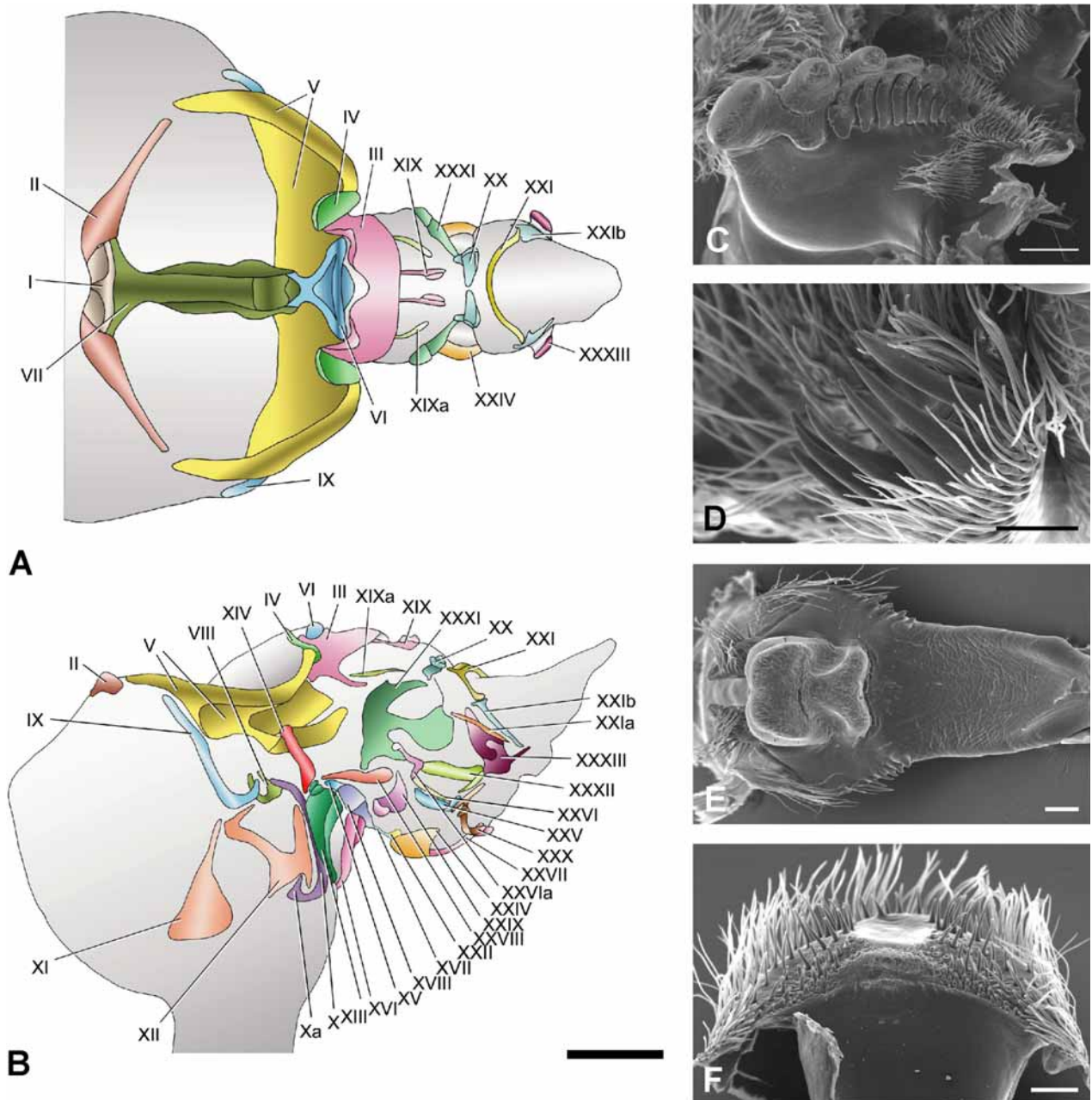


FIGURE 20. Foregut ossicles and gastric teeth of *Rhithropanopeus harrisii* (Gould, 1841), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 200µm, D. – F. 100µm.

Pinnotheridae de Haan, 1833

Nepinnotheres villosulus (Guerin-Meneville, 1830) (Fig. 22)

Ossicles I and II are inclined about 45° in the antero ventral direction. The unpaired propyloric ossicle (VI) is inclined 45° in the posterior direction; its dorsal margin is straight and dorsally rounded. The pectinal ossicle (VIII) is ring-shaped with eight accessory teeth. An anterior directed spine extends from the middle of the subdentate ossicle (XIV). The postpectinal ossicle (X) is at the posterior end circular rolled about 320°. Ossicles “XVII–XXIII” and “XXI–XXIb” are observed as mixed ossicles. It has a remarkable median narrowed strip. Ossicle XVIII has a comparatively greatly increased surface. Ossicle XXVIa is not recognisable.

Retroplumidae Gill, 1894

Retropluma quadrata de Saint Laurent, 1989 (Fig. 23)

Ossicles I and II are inclined about 45° in the antero ventral direction. The zygo-cardiac ossicle (V) has a clear semicircular impression antero ventral. The unpaired propyloric ossicle (VI) is nearly vertical. The pectinal ossicle (VIII) is horseshoe-shaped with six accessory teeth. The ossicle XIXa is not recognisable.

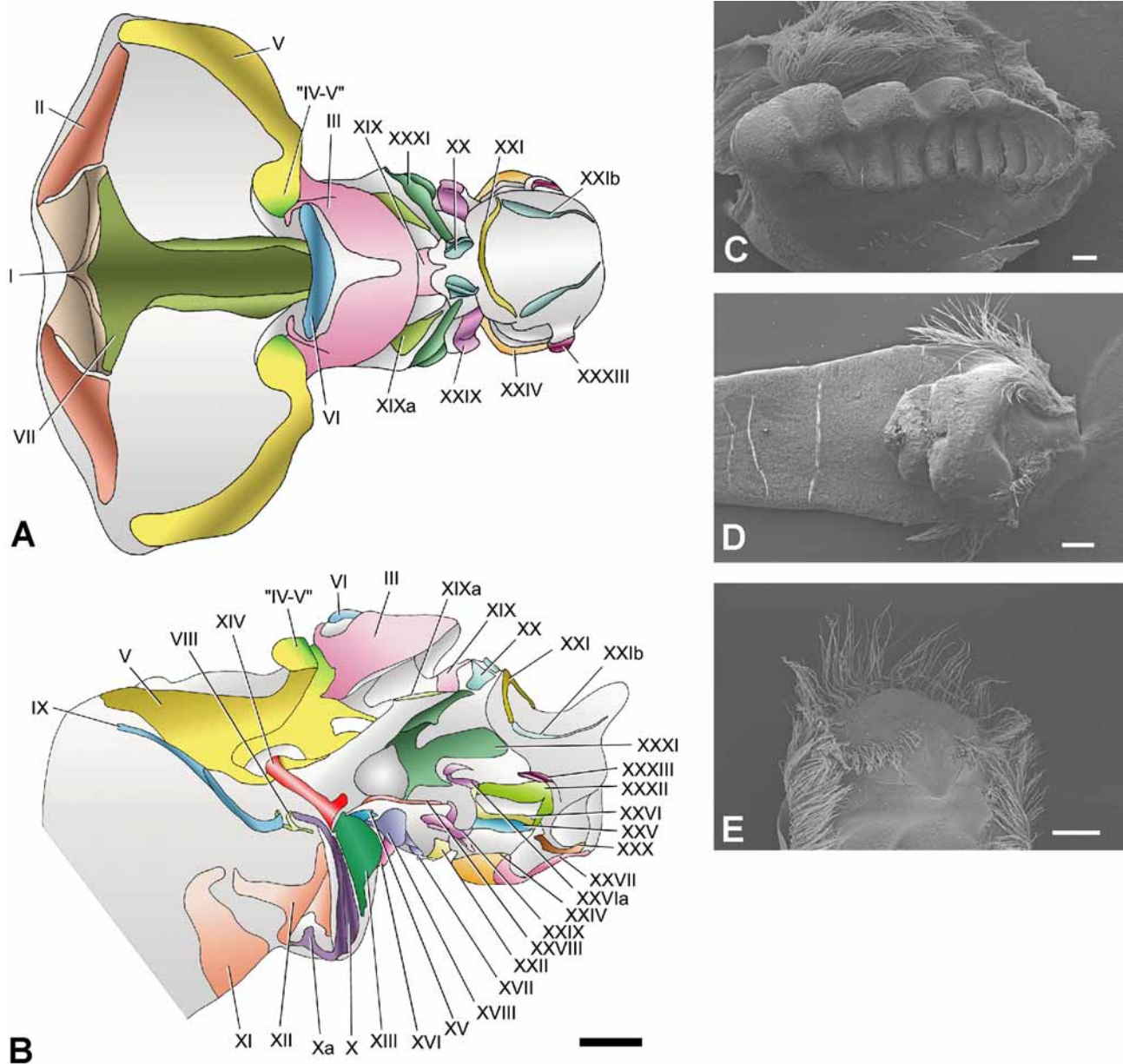


FIGURE 21. Foregut ossicles and gastric teeth of *Potamonautes lirrangensis* (Rathbun, 1904), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth; scales: A. & B. 1mm, C. 300µm, D. 400µm.

Crossotonotidae Moosa & Serène, 1981 and Palicidae Bouvier, 1898

Based on nearly identical foregut characters, species of both families are described here together. *Crossotonotus spinipes* (De Man, 1888) (Crossotonotidae) (Fig. 24A, B); *Pseudopalicus declivis* Castro, 2000 (Fig. 24C-F); *Parapalicus clinodontatus* Castro, 2000 and *Micropalicus vietnamensis* (Zarenkov, 1968) (last three species = Palicidae)

Ossicles I and II are inclined about 45° in the antero ventral direction. The unpaired propyloric ossicle (VI) is inclined about 10° in the posterior direction. The pectinal ossicle (VIII) is horseshoe-shaped with five accessory teeth. Ossicles “XVII–XXIII” are observed as a mixed ossicle. Ossicle XVIII has a comparatively large surface.

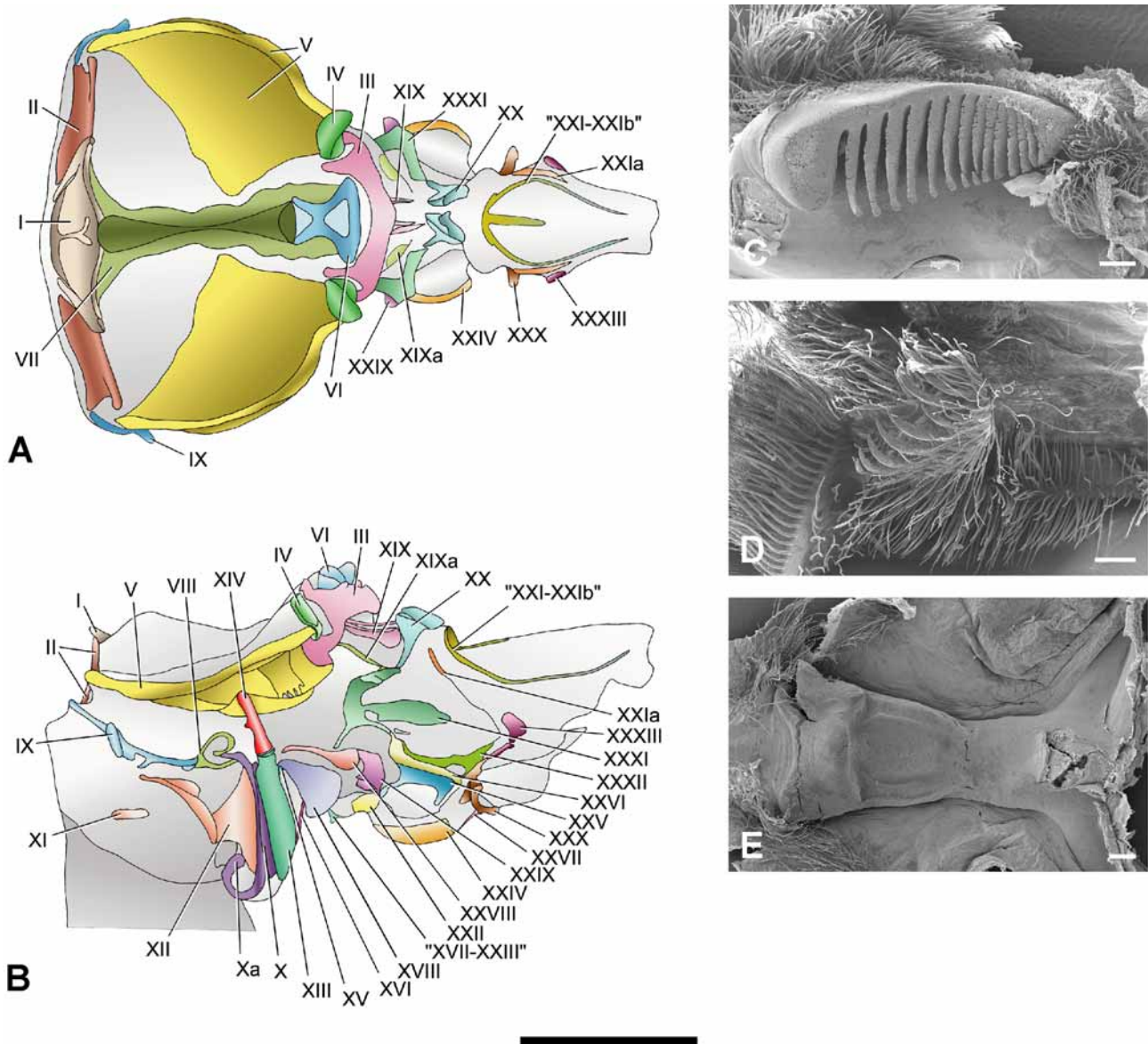


FIGURE 22. Foregut ossicles and gastric teeth of *Nepinnotheres villosulus* (Guérin, 1831), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-medial tooth; scales: A. & B. 1mm, C. – E. 100µm.

Ocypodidae Rafinesque, 1815

Ocypode gaudichaudi Milne Edwards & Lucas, 1843 (Fig. 25A, B) and *Ocypode cursor* (Linnaeus, 1758) (Fig. 25C–F)

Ossicles I and II are inclined about 45° in the antero ventral direction. The unpaired propyloric ossicle (VI) is inclined a few degrees in the posterior direction. The urocardiac ossicle (VII) has an oval non-calcified area antero median. The pectinal ossicle (VIII) is ring-shaped with 13 accessory teeth. The dorsal part of the prepectinal ossicle (IX) is elongate and curves towards the post-pterocardiac ossicle (IIb); its ventral part is significantly widened and has postero ventral a hook-shaped structure. The inferior lateral cardiac ossicle

(XIII) has the shape of an elongate oval shape. Postero dorsal it has a triangular, posteriorly directed connection-piece to the subdentate ossicle (XIV). Ossicles XIXa and XXIa are not recognisable.

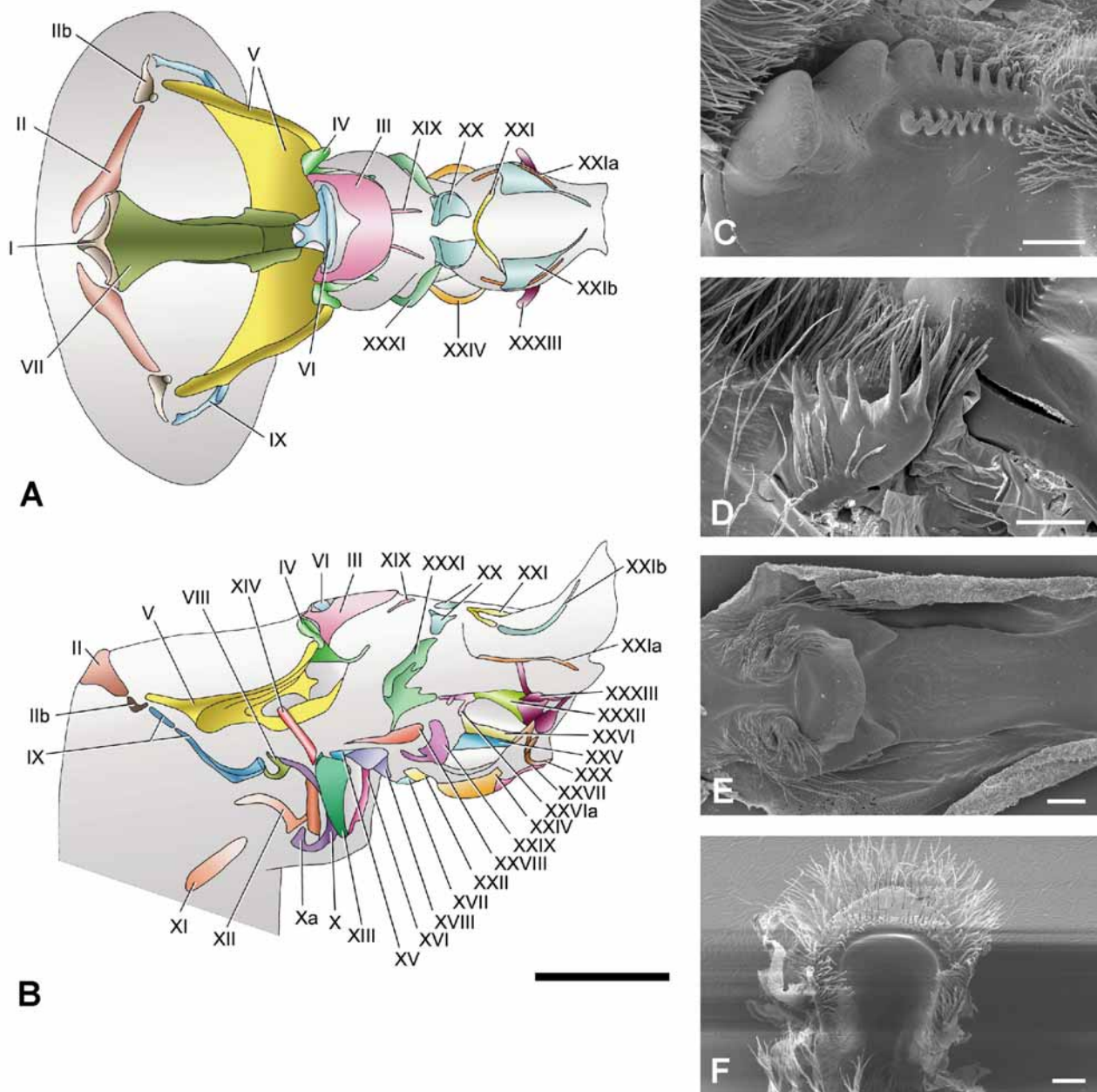


FIGURE 23. Foregut ossicles and gastric teeth of *Retropiluma quadrata* Saint Laurent, 1989, A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-medial tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. – F. 100µm.

Uca (Minuca) rapax (Smith, 1870) (Fig. 26A, B) and *Uca (Gelasimus) tetragonon* (Herbst, 1790) (Fig. 26C–F)

Ossicles I and II are inclined about 45° in the antero ventral direction. The pterocardiac ossicle (II) is nearly completely connected with the entire antero lateral margin of the mesocardiac ossicle (I); laterally it extends in the form of two projections to the ossicles V and IX. The unpaired propyloric ossicle (VI) is nearly vertical. The pectinal ossicle (VIII) is ring-shaped with 11 accessory teeth. The median and postero ventral parts of the prepectinal ossicle (IX) are enlarged. The inferior lateral cardiac ossicle (XIII) has a long oval shape and two ventrally crossed, rounded tips; the ossicle has a clear connection-piece to the subdentate ossicle (XIV). The lateral ossicle of the cardio-pyloric valve (XVIII) is greatly increased in size and covers the lateral side of the cardio-pyloric valve. Ossicles “XXI–XXIa” are observed as a mixed ossicle.

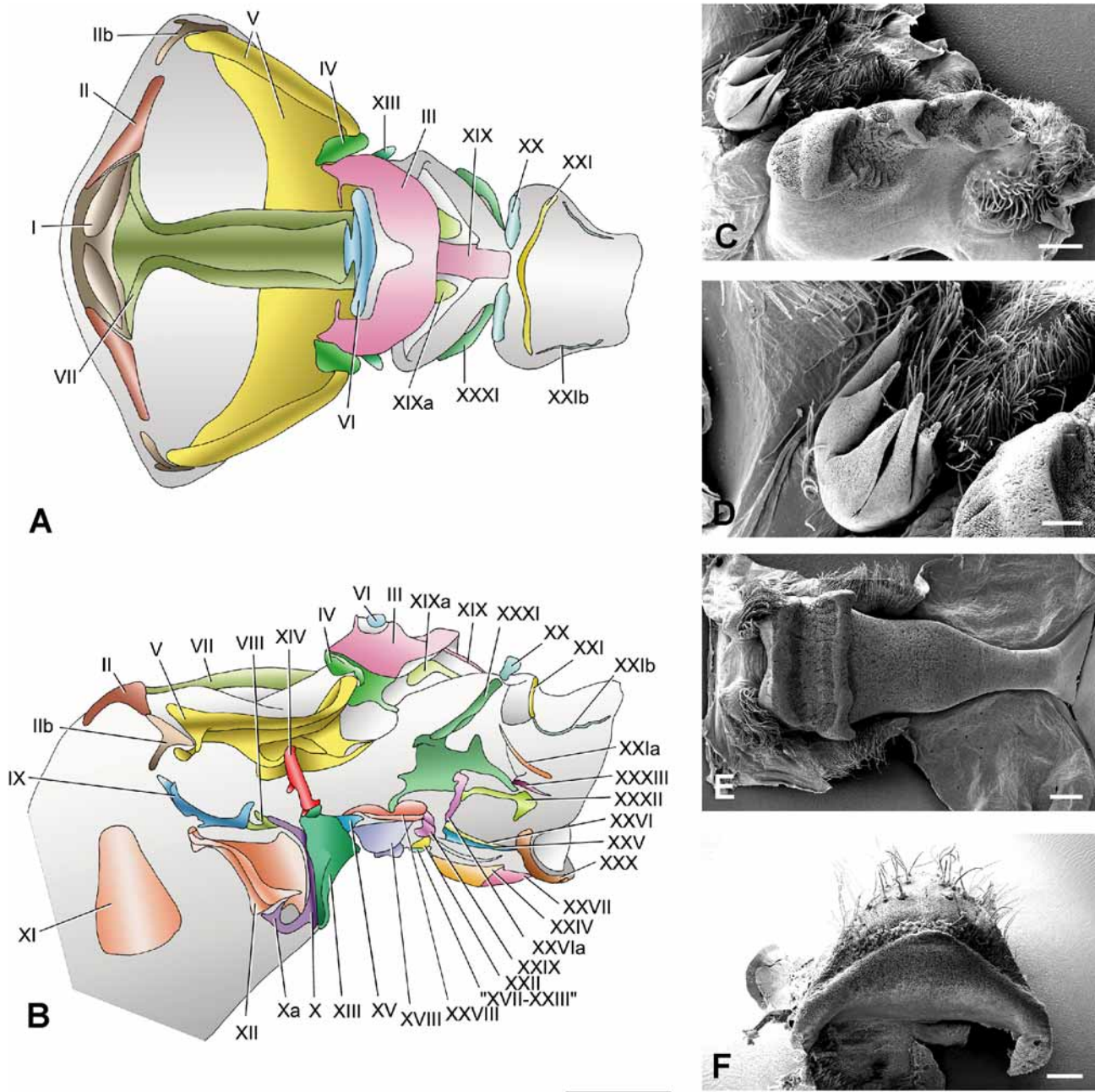


FIGURE 24. Foregut ossicles of *Crossotonotus spinipes* (De Man, 1888), A. dorsal view, B. lateral view; gastric teeth of *Pseudopalicus declivis* Castro, 2000, C. lateral tooth, D. accessory teeth, E. dorso-medial tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 200 μ m, D. 100 μ m, E. & F. 200 μ m.

Mictyridae Dana, 1851

Mictyris longicarpus Latreille, 1806 (Fig. 27) and *Mictyris platycheles* H. Milne Edwards, 1852

Ossicles I and II are inclined about 45° in the antero ventral direction. The pterocardiac ossicle (II) is nearly completely connected with the antero lateral margin of the mesocardiac ossicle (I); laterally it extends in the form of two tips to the prepectinal ossicle (IX) as well as to the zygo-cardiac ossicle (V). The exopyloric ossicle (IV) is comparatively large. The unpaired propyloric ossicle (VI) is inclined about 45° in the posterior direction. The pectinal ossicle (VIII) is ring-shaped with 19 accessory teeth. The median and postero ventral parts of the prepectinal ossicle (IX) are enlarged. The inferior lateral cardiac ossicle (XIII) has a long oval

shape and two ventrally directed crossed tips; postero dorsally it has a posteriorly directed connection-piece. The lateral ossicle of the cardio-pyloric valve (XVIII) is greatly enlarged and covers the lateral side of the cardio-pyloric valve. Ossicle XVII is not recognisable.

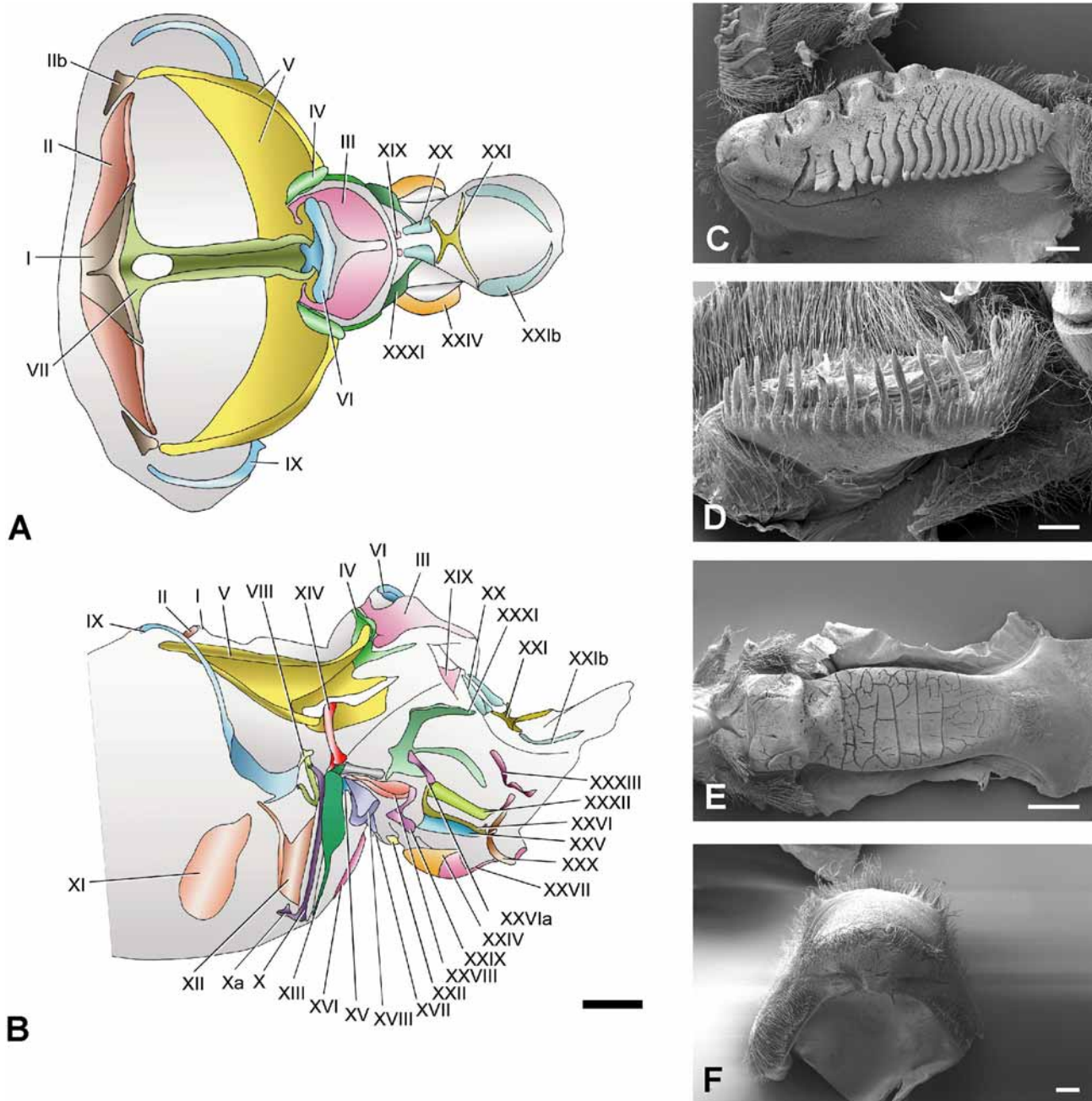


FIGURE 25. Foregut ossicles of *Ocypode gaudichaudi* H. Milne Edwards & Lucas, 1843, A. dorsal view, B. lateral view; gastric teeth of *Ocypode cursor* (Linnaeus, 1758), C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 400µm, D. 100µm, E. 1mm, F. 300µm.

Gecarcinidae MacLeay, 1838

Cardisoma armatum Herklots, 1851 (Fig. 28) and *Dicoplax hirtipes* (Dana, 1851)

Ossicles I, II and IIb are inclined about 45° in the antero ventral direction. The exopyloric ossicle (IV) is enlarged. The unpaired propyloric ossicle (VI) is nearly vertical. The pectinal ossicle (VIII) is ring-shaped with 13 accessory teeth. The inferior lateral cardiac ossicle (XIII) has a long oval shape and two ventrally

directed crossed tips; on its dorsal part it has a posterior directed connection-piece to the subdentate ossicle (XIV). The posterior area of the prepectinal ossicle (IX) is remarkably extended. The ossicle (XIV) has a flattened postero ventral expansion. The lateral ossicle of the cardio-pyloric valve (XVIII) is extremely increased in size and covers the lateral side of the cardio-pyloric valve. Ossicles XXIa and XXIII are not recognisable.

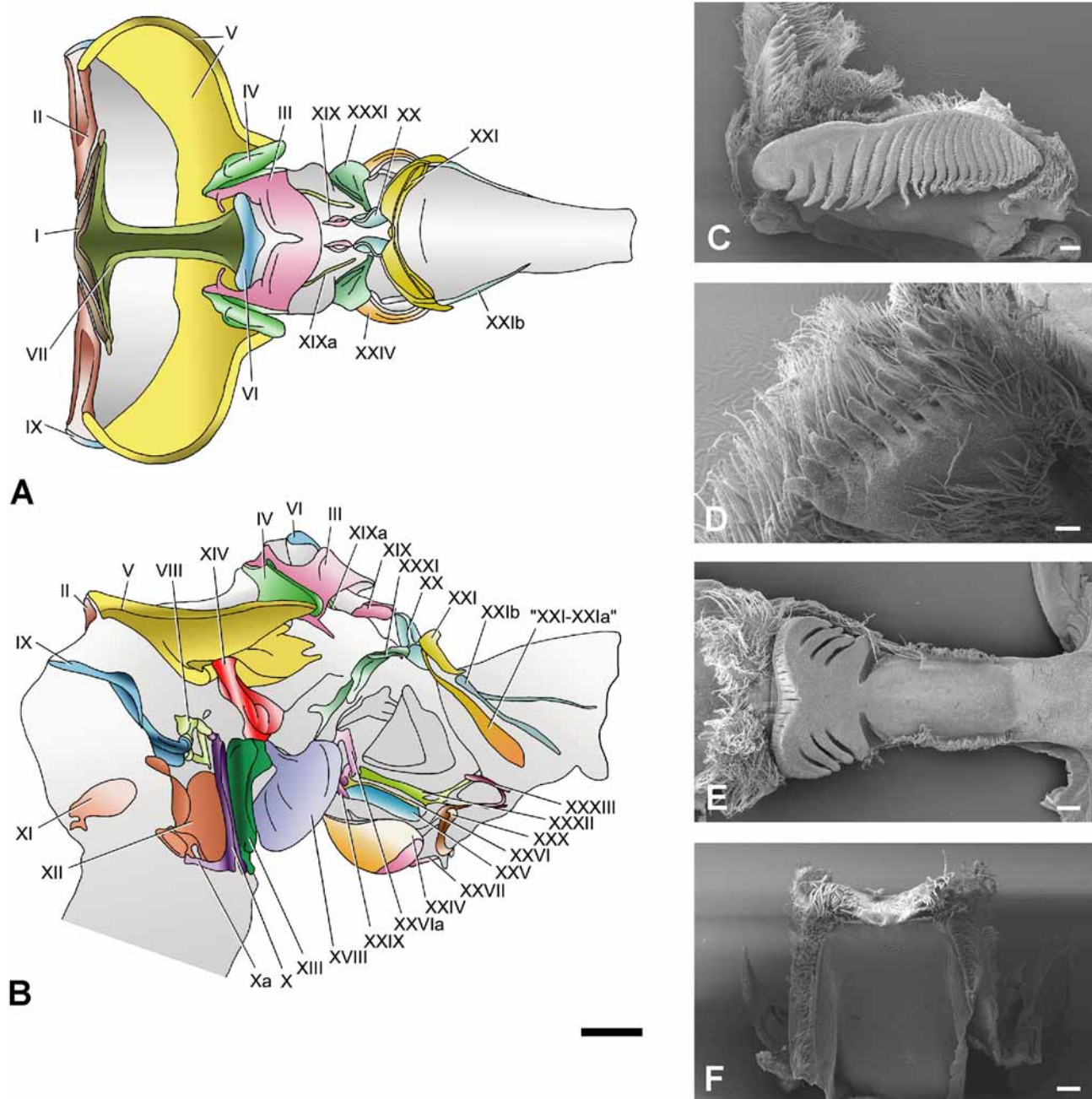


FIGURE 26. Foregut ossicles of *Uca (Minuca) rapax* (Smith, 1870), A. dorsal view, B. lateral view; gastric teeth of *Uca (Gelasimus) tetragonon* (Herbst, 1790), C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 200µm, D. 100µm, E. & F. 200µm.

Sesarmidae Dana, 1851 and Varunidae H. Milne Edwards, 1853

Based on nearly identical foregut characters, species of both families are described here together.

Pseudosesarma moeschi de Man, 1888 (Sesarmidae) (Fig. 29) and *Eriocheir sinensis* H. Milne Edwards, 1853 (Varunidae)

Ossicles I, II and IIb are inclined about 45° in the antero ventral direction. The oval exopyloric ossicle (IV) is enlarged. The pectinal ossicle (VIII) is ring-shaped with 11 accessory teeth. The posterior area of the prepectinal ossicle (IX) is remarkably extended and has a clearly ventrally directed hook at the middle of the ossicle. The inferior lateral cardiac ossicle (XIII) has a long oval shape and two ventrally directed crossed tips; on its dorsal part it has a posterior directed connection-piece to the subdentate ossicle (XIV). The lateral ossicle of the cardio-pyloric valve (XVIII) is greatly enlarged in size and covers the lateral side of the cardio-pyloric valve. Ossicle XXIa is not recognisable.

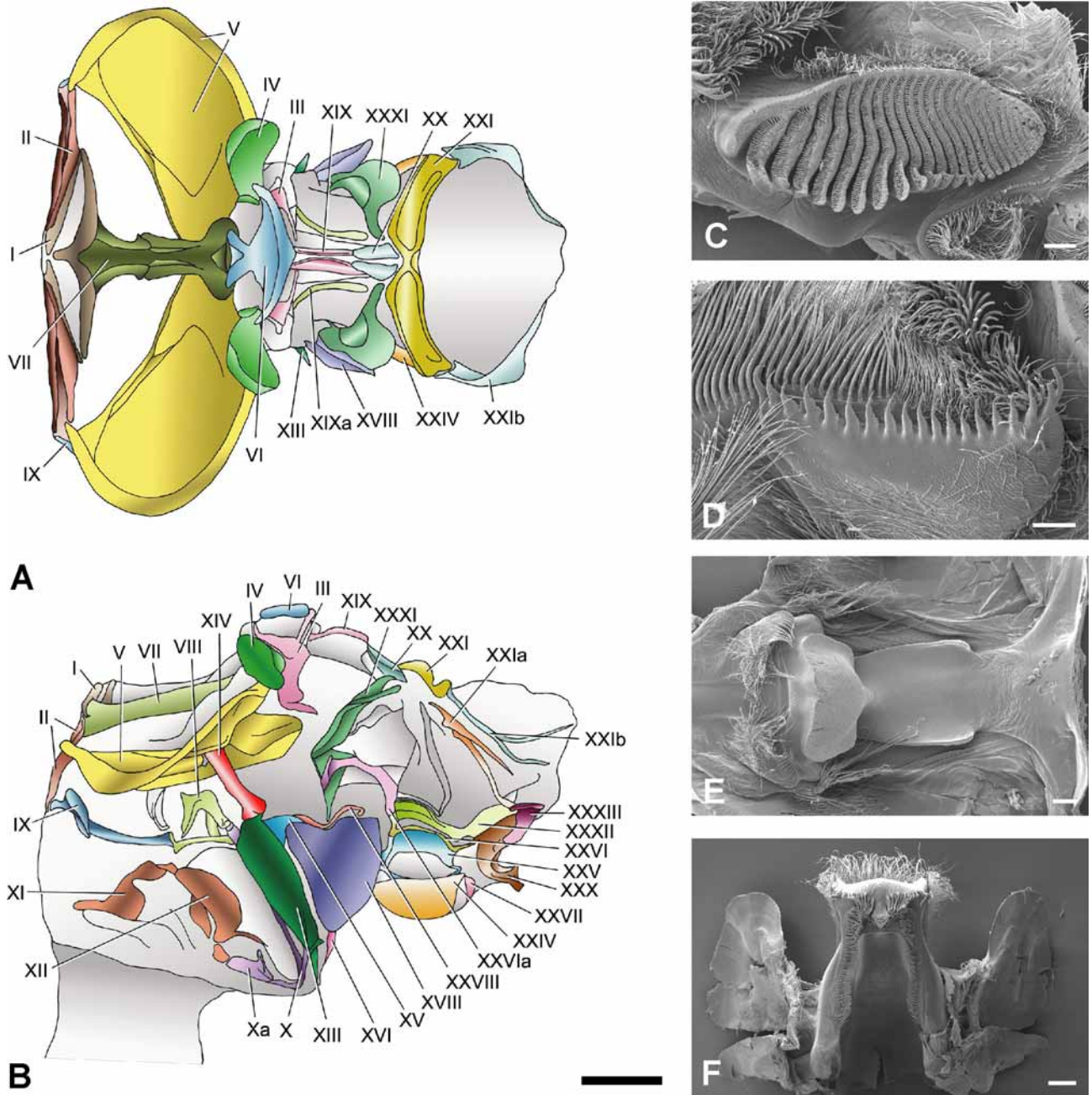


FIGURE 27. Foregut ossicles and gastric teeth of *Mictyris longicarpus* Latreille, 1806, A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. & D. 100µm, E. 200µm, F. 300µm.

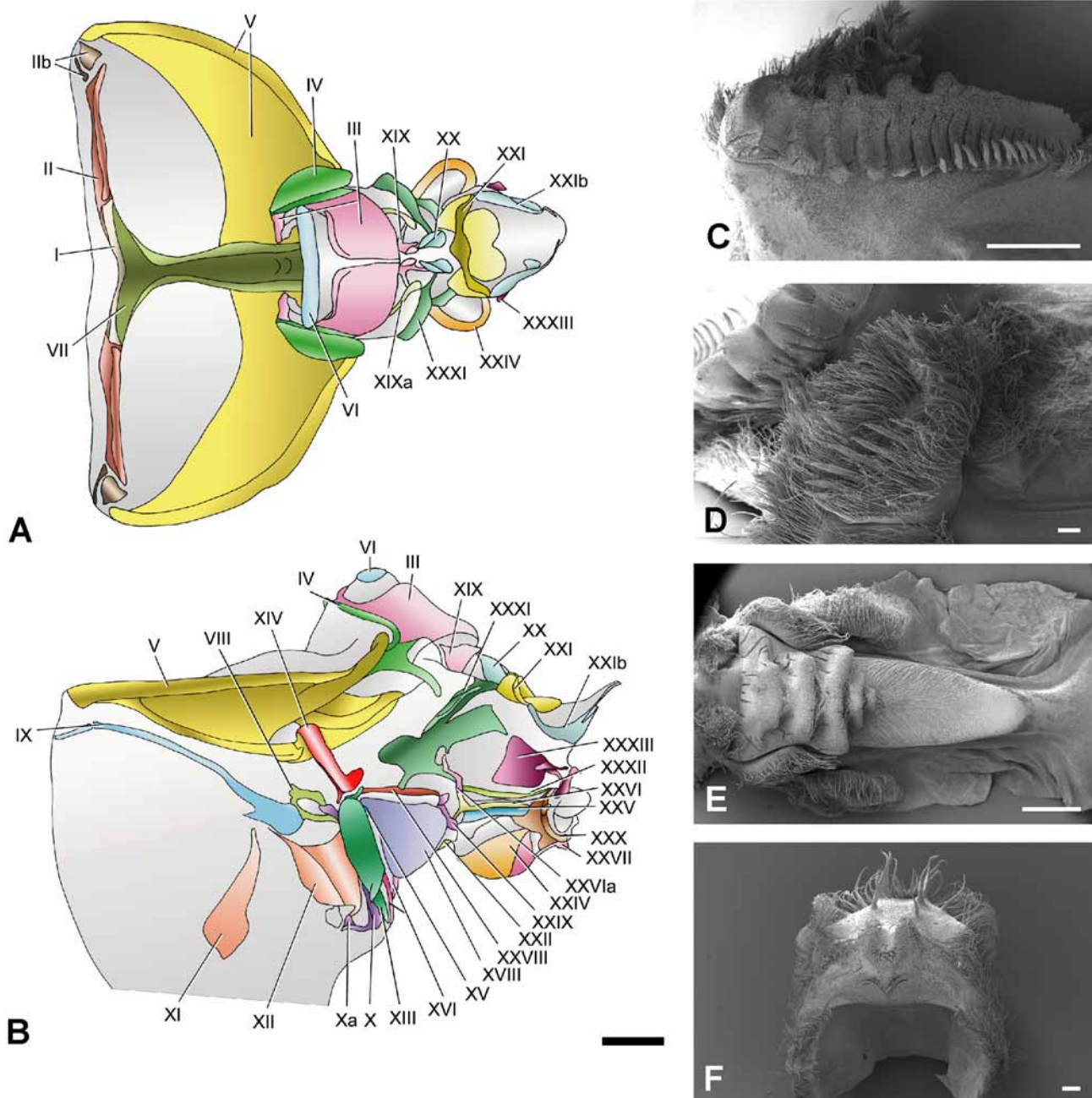


FIGURE 28. Foregut ossicles and gastric teeth of *Cardisoma armatum* Herklots, 1851, A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve, scales: A. – C. & E. 1mm, D. 200µm, F. 200µm.

Cambaridae Hobbs, 1942

Orconectes limosus (Rafinesque, 1817) (Fig. 30)

The pterocardiac ossicle (II) is more or less completely connected with the antero-lateral margin of the mesocardiac ossicle (I) and is inclined about 45° in the lateral direction. The unpaired propyloric ossicle (VI) is nearly horizontally oriented underneath the pyloric ossicle (III). The pectinal ossicle (VIII) consists of two calcified plates and has a number of irregularly shaped accessory teeth. The post-pterocardiac ossicle (IIb) is present. Ossicles Xa, XIX, XIXa, XX, XXI and XXIa are not recognisable. Ossicles “XIX-XX-XXI” and “XXV-XXVI-XXXII” are observed as mixed ossicles.

Lithodidae Samouelle, 1819

Lithodes maja (Linnaeus, 1758) (Fig. 31)

The unpaired, triangular mesocardiac ossicle (I) covers nearly the whole width of the antero dorsal gastric mill. Ossicles “XXI-XXIa” and “XVII-XXII-XXIII” are observed as mixed ossicles. The unpaired propyloric ossicle (VI) is inclined a few degrees in the posterior direction.

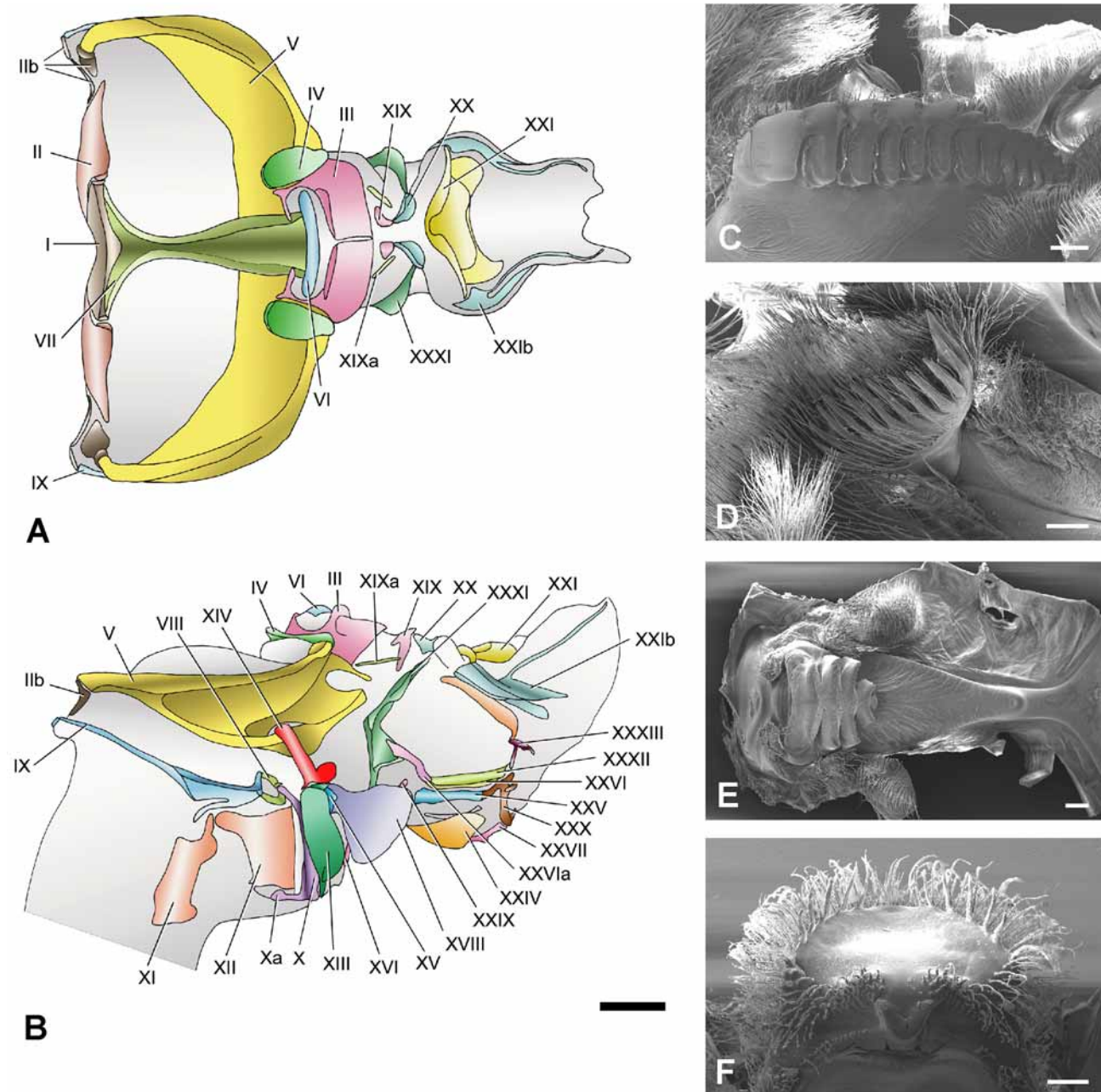


FIGURE 29. Foregut ossicles and gastric teeth of *Pseudosesarma moeschi* (De Man, 1888), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. – F. 200µm.

Discussion

New aspects of the brachyuran foregut morphology

In the present paper, the foregut ossicles and gastric teeth of 66 species of the Brachyura, together with the

outgroup taxa *Orconectes limosus* and *Lithodes maja*; were studied comparatively and described according to the different regions of the stomach (Fig. 1). The description of six new ossicles from the anterior gastric mill (IIa, IIb und Va) as well as from the dorsal and lateral pyloric filter (XIXa, XXIIb and XXVIa) underscores the importance and also the benefits of staining with Alizarin Red (Brösing 2002, Brösing *et al.* 2002). With the staining it becomes possible to clarify the three-dimensional form of each ossicle for more precisely. In addition, the foregut ossicles and gastric teeth of 30 species (including the out-group representatives) were documented by drawings and SEM-investigations. Furthermore the ossicle nomenclature used by Maynard & Dando (1974) was revised and new ossicles recognized.

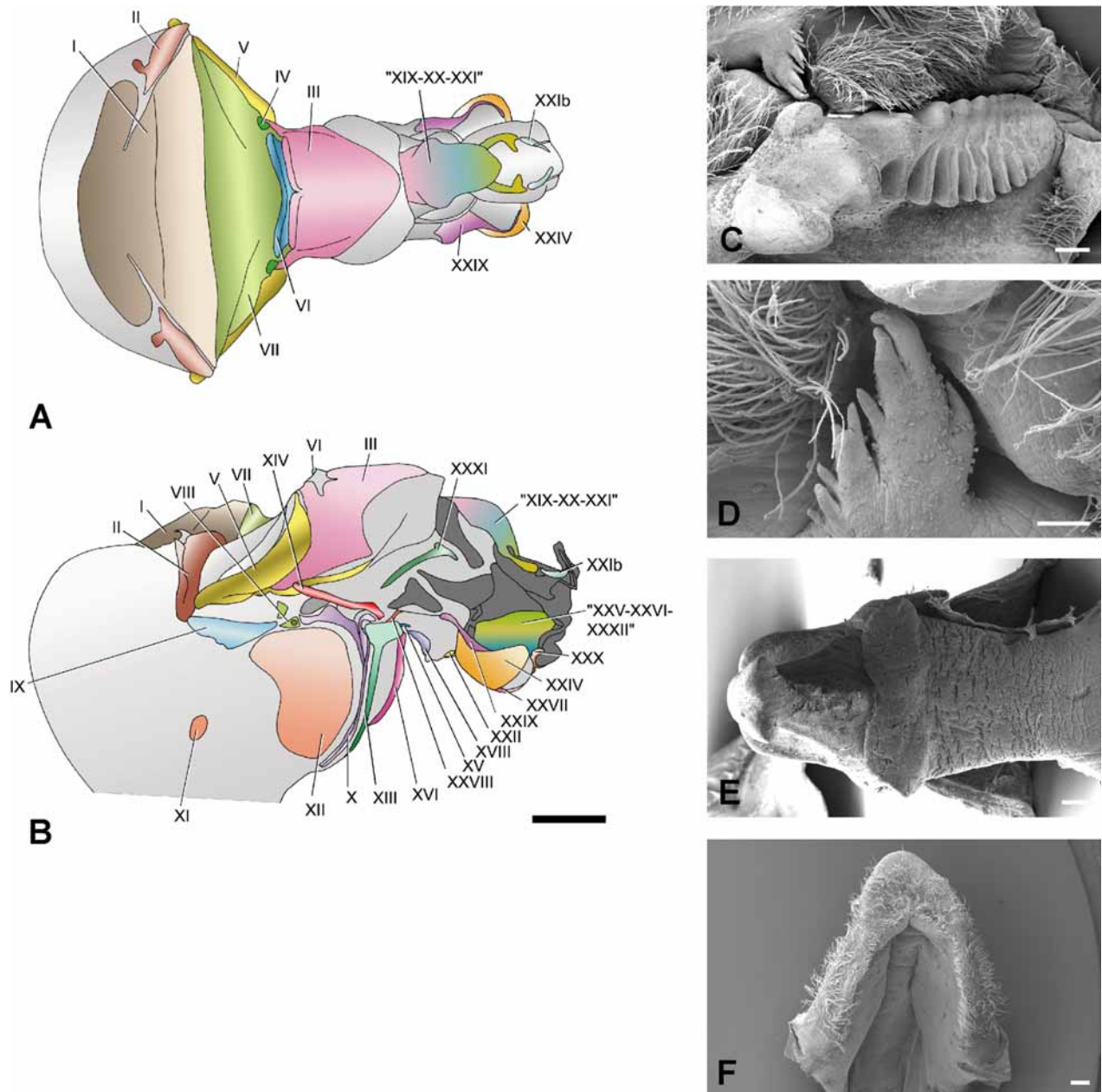


FIGURE 30. Foregut ossicles and gastric teeth of *Orconectes limosus* (Rafinesque, 1817), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 200µm, D. 100µm, E. & F. 200µm.

The results presented here largely confirm the basic findings of previous morphological studies of the stomachs of decapods crustaceans (Milne-Edwards 1837, Parker 1876, Huxley 1880; Nauck 1880; Mocquard 1883; Ringel 1924; Balss 1944; Patwardhan, 1934, 1935a-e; Cochran 1935, Maynard & Dando 1974; Meiss & Norman, 1977; Kunze & Anderson 1979).

However, none of these authors used a specific staining method for the ossicles. A commonly used method was the maceration of the stomachs in a potassium-solution to remove remnants of muscles and nerve fibers, and the midgut gland (Nauck, 1880; Patwardhan 1935b–e; Maynard & Dando 1974).

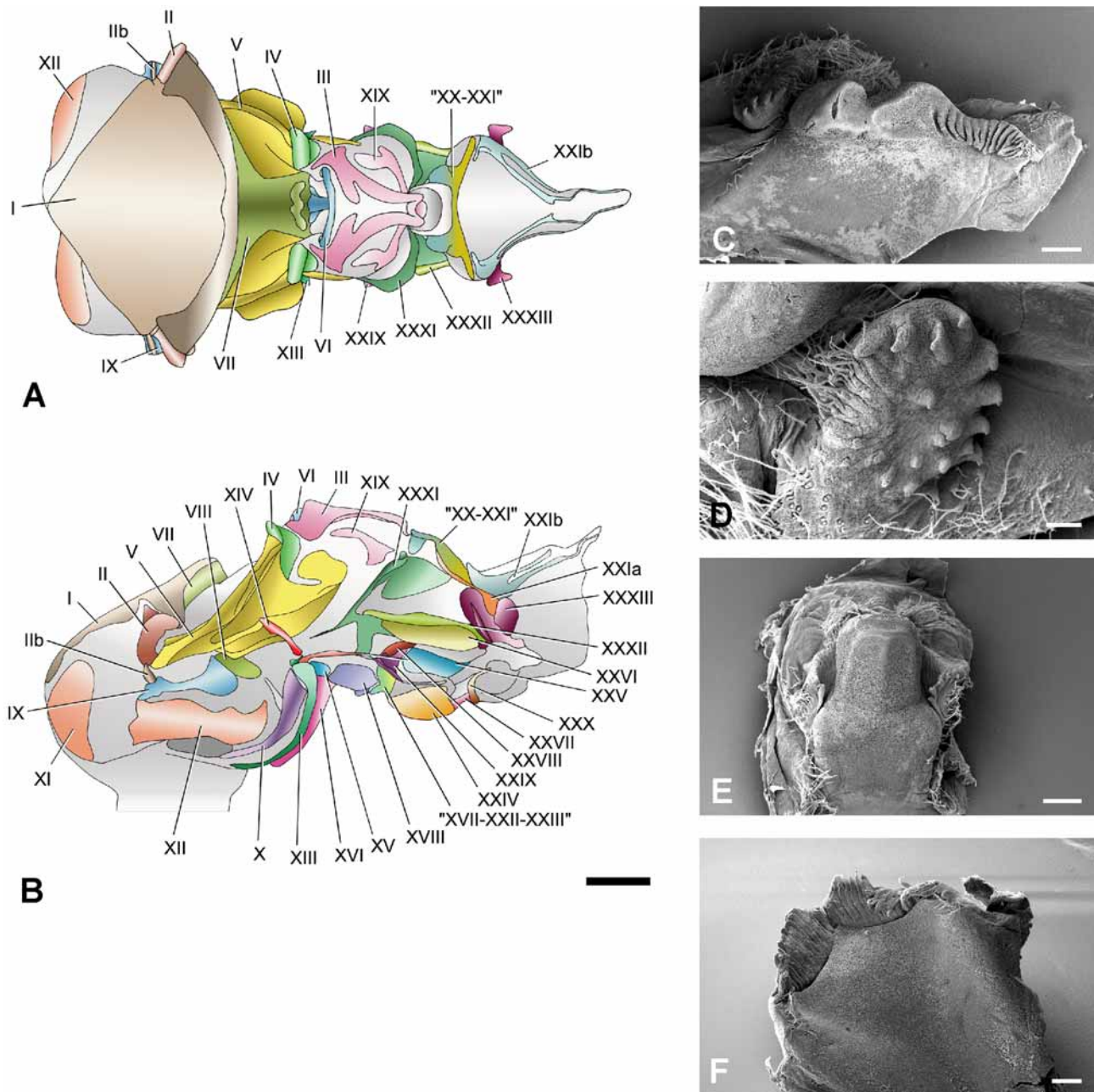


FIGURE 31. Foregut ossicles and gastric teeth of *Lithodes maja* (Linnaeus, 1758), A. dorsal view, B. lateral view, C. lateral tooth, D. accessory teeth, E. dorso-median tooth, F. cardio-pyloric valve; scales: A. & B. 1mm, C. 300µm, D. 100µm, E. 300µm, F. 200µm.

In an unstained state the three-dimensional form of the ossicles and connections between the ossicles are difficult or impossible to see. These include the preptero-cardiac ossicles (IIa) and the postptero-cardiac ossicles (IIb). Both ossicles occur as narrow strips anterior and lateral to the unpaired mesocardiac ossicle (I) and the pterocardiac ossicle (II). Only within representatives of the Dromiidae and Dynomenidae are both ossicles present. In previous studies of the foreguts of Dromiidae (Nauck 1880, Patwardhan 1935a), these ossicles were not described or illustrated by the authors. Their basic findings on the morphology of the stomach, however, were confirmed by this study. Within the Homolidae and Latreillidae the preptero-cardiac ossicle (IIa) has now been described for the first time. Furthermore, a prezygocardiac ossicle (Va) was

detected only in two representatives of the Cymonomidae. The lateral mesopyloric ossicle (XIXa) is very slightly calcified, in all species in which it occurs, but is clearly visible in the stained condition. Also, the uropyloric ossicle (XXI) was often contradictorily described, because of its often poor separation from the posterior uropyloric ossicle (XXIb). Cochran (1935) interpreted the uropyloric ossicle (XXI) of *Callinectes sapidus* incorrectly as a paired structure, which forms the poster-dorsal end of the pyloric foregut. She did not recognise the separation of uropyloric ossicle (XXI) from the posterior uropyloric ossicle (XXIb).

Maynard & Dando (1974) illustrated the ossicles (XXI and XXIb) as a single ossicle (XXI) and referred to the description by Cochran (1935). The posterior uropyloric ossicles (XXIb) were described for all examined species, with the exception of *Nepinnotheres villosulus*. Within *N. villosulus* it is not clear whether the ossicles XXI and XXIb are fused or one of them does not exist.

On the lateral pyloric filter it was possible to detect another detail: there exists a clear separation between the ampullary-roof-ossicle, upper portion (XXVI) and an anterior hook-like structure. For this reason, this hook-shaped structure was given its own name: the anterior process of the ampullary-roof-ossicles, upper portion (XXVIa). This extension has so far been identified only among representatives of the Brachyura.

In addition to the six newly described ossicles, further remarkable characteristics of different ossicles shall be discussed in the following section:

Within the examined species the pyloric ossicle (III) on the postero dorsal part of the gastric mill shows an enormous variety of shapes. Various interpretations of this ossicle as paired or an unpaired structure are often attributed to a lower level of calcification in the median section of the ossicle. Meiss & Norman (1977) described this ossicle as an unpaired structure in *Calappa sulcata*. In contrast in *Calappa granulata* this ossicle is paired. On the transition from the gastric mill to the pyloric filter, a paired lateral ossicle of the cardio-pyloric valve (XVIII) as well as the unpaired posterior ossicle of the cardio-pyloric valve (XVII) are illustrated in the literature (Maynard & Dando 1974; Meiss & Norman 1977, Kunze & Anderson 1979).

The lateral ossicle of the cardio-pyloric valve (XVIII) is unpaired in all species of the Brachyura examined here. A central division of the ossicle (XVIII) is only visible in *Orconectes limosus*.

In most of the present species the posterior ossicle of the cardio-pyloric valve (XVII) is connected with the ossicle of the cardio-pyloric valve (XVIII) (Maynard & Dando 1974; Meiss & Norman, 1977). Balss (1944) illustrated in his contribution to the stomach morphology of *Cancer pagurus* an ossicle-structure, which is similar to ossicle (XVIII). However, he did not explain it.

Summary of the functions of the ossicles:

- 1.) stabilisation of the entire stomach and specially the very thin anterior membranous part
- 2.) a firm anchorage of the stomach within the antero-dorsal carapace
- 3.) ossicles serve
- 4.) as points of insertion of the extensive stomach-musculature
- 5.) ossicles support the function and movement of the gastric teeth

Homology of the foregut-structures

Fundamental to the use of foregut structures for phylogenetic reconstructions is knowledge about their homology-probability. Most of 41 described ossicles of all species presented here are arranged in a uniform pattern. One exception is the prezygocardiac ossicle (Va), which was observed only in two specimens of *Cymonomus granulatus*. Further ossicles, like the anterior mesopyloric ossicle (XIX) as well as the lateral mesopyloric ossicle (XIXa) were not recognisable in some species (e.g. *C. granulatus*, *Ranina ranina*). The evaluation of a possible homology becomes more difficult, if two or more ossicles are fused. In this case only one big ossicle-structure is recognisable in the original position. Within the antero lateral part of the gastric mill of *Potamonautes lirrangensis* there is only one structure recognisable in the position of ossicles IV and V. It is difficult to decide whether the ossicle IV is not present or fused with the zygocardiac ossicle (V). But, posteriorly the zygocardiac ossicle joins the exopyloric ossicle (IV) in most of the species examined here. Therefore this structure is observed as a "mixed ossicle".

Based on a constant position of the ossicles within the complex stomach, a homology-probability of the

ossicles can be justified by using the criterion of the position (Remane 1961; Sudhaus & Rehfeld 1992; Wägele 2000). The same can be postulated for the gastric teeth, which are regularly arranged within the gastric mill.

Foregut structures and its phylogenetic significance

Numerous studies on decapod crustaceans suggest a food-specific modification of the anatomy of the foregut (Patwardhan 1935a–e; Reddy 1935; Powell 1974; Caine 1975; Fryer 1977; Ngoc Ho 1984). Icely & Jones (1978) showed on four species of the genus *Uca* (all from the same locality with similar food strategies) that the stomachs reflect differences in the size and composition of the food particles. Furthermore investigations on the gastric mills of 15 ‘astacid’ crayfishes (Caine 1975; Grouns & Richardson 1990) showed only small structural differences in comparison to the respective food spectrum. Also Felgenhauer and Abele (1983, 1985, and 1989) described many examples of close-related decapods with a similar stomach anatomy, but a different food spectrum.

The present study of 66 species of the Brachyura as well as two out group taxa confirm that the stomachs and especially the foregut ossicles exhibit a relatively constant pattern within species of one family or within species of close-related families, respectively. This opinion is supported by an observation of the variability of the ossicles and gastric teeth of samples of the same species-, generic- and family-level. This test showed nearly identical character states at the species-level, but also remarkable differences at the family-level. The fact that structures of the foregut, and specially foregut ossicles and gastric teeth, are useable for phylogenetic reconstructions within the Crustacea as well as the Malacostraca were indicated by former phylogenetic analysis of Isopoda (Wägele 1989), Amphipoda (Coleman 1994), Peracarida (Kobusch 1999) and Brachyura (Brösing *et al.* 2007, Brösing 2008).

Nauck’s Heterodontea-Cyclodontea concept

In 1880, Nauck established a new classification of brachyuran crabs based on a comparative study of foregut ossicle- and gastric mill-structures of about 70 species of the Brachyura (see tab. 3). He placed representatives of the Pinnotheridae and the Gelasimidae (=Heterodontea) in opposition to the Cyclodontea (all other brachyuran taxa investigated by Nauck).

His classification was justified by two arguments:

1. He described a position of the “cardiacalen vorderen Superolateralia” (ptero-cardiac ossicles (II)) frontal to the “Superomedianum” (mesocardiac ossicle (I)).

2. According to Nauck, transverse lamellas on the dorso median tooth of the Pinnotheridae and “Gelasimiden” never exists. He did not explained, what he understood by simple transverse lamellas. For *Disoplax hirtipes* he described: “The dorso median tooth consisting of six lamellas (five within *C. carnifex*)”.

Within the present study, the pterocardiac ossicle (II) is situated on both sides of the mesocardiac ossicle (I), either laterally or antero-laterally. An excluding anterior position of pterocardiac ossicle (II) within the Pinnotheridae or “Gelasimidae” is not confirmed.

Furthermore, representatives of the Gecarcinidae (*Disoplax hirtipes* and *Cardisoma armatum*) as well as the Sesarmidae and Varuidae (*Pseudosesarma moeschi* and *Eriocheir sinensis*) show such lamellas on the median tooth. Therefore, both arguments by Nauck find no support by the results described here.

In addition, the dorso median tooth of *Uca (Gelasimus) tetragonon* has three deep cuts, separating the lateral margin into rip-like structures. This character is not analogous to the transverse lamellas in the Gecarcinidae and Sesarmidae.

Within the suggested Cyclodontea, Nauck postulated furthermore the Coelostylidea (with the Catometopa and the Oxyrhyncha) and the Platystylidea (with the Oxystomata and the Cyclometopa). The basis for this separation was the “Superomedianum” (urocardiac ossicle (VII)). Within the Coelostylidea, Nauck observed vaulted lateral margins, in contrast to flattened lateral margins in the Platystylidea. With his separation of brachyuran crabs into Catometopa, Oxyrhyncha, Oxystomata and Cyclometopa, Nauck used an already existing classification (see Milne-Edwards & Lucas 1843). Vaulted lateral margins at the “middle Superomedianum” (urocardiac ossicle (VII)) were also observed in representatives of the Gecarcinidae, the

Sesarmidae and the Ocypodidae (all among the Catometopa). Within the Oxyrhyncha, especially in *Inachus dorsettensis* and *Parthenope notialis* there are similar vaulted margins in contrast to a weakly vaulted margin in *Hyas araneus* and *Hyas coarctatus*.

TABLE. 3 Nauck’s classification scheme (changed after Nauck, 1880) (species names examined by Nauck were changed according Ng *et al.* 2008 and marked with *)

Heterodontea (Dorso median tooth never consisting of ordinary transverse lamellae, “cardiacale Superlateralia” (ossicles II, IV, V) in front of “Supero-medianum (ossicles I, VI, VII)	Cyclodontea (Dorso median tooth consisting of hemicircular transverse lamellae (with one exception), “vorderen Superlateralia” = part of pterocardiac ossicles (II) placed beside to the mesocardiac ossicle))			
	Coelostylidea (dorsal side of ossicle VII narrow and with increased lateral margins)		Platystylidea (dorsal side of ossicle VII broad and whitout or with small increased lateral margin)	
	Catometopa <i>Discoplax hirtipes</i> * <i>Gecarcinus ruricola</i> <i>Sesarmops intermedium</i> * <i>Pseudohelice quadrata</i> * <i>Gaetice depressus</i> * <i>Varuna litterata</i> <i>Ptychognathus pilipes</i> * <i>Pseudograpsus albus</i> * <i>Percnon planissimum</i> * <i>Metopograpsus latifrons</i> <i>Grapsus albolineatus</i> * <i>Somanniathelphusa sinensis</i> * <i>Oziotelphusa aurantia</i> * <i>Ocypode kuhlii</i> *	Oxyrhyncha <i>Micippe cristata</i> <i>Doclea muricata</i> <i>Camposcia retusa</i> <i>Maja crispata</i> <i>Hyas araneus</i> * <i>Phalangipus indicus</i> * <i>Hyastenus aries</i> * <i>Inachus thoracicus</i> <i>Naxia sp.</i> <i>Cryptopodia fornicate</i> <i>Daldorfia horrida</i> *	Oxystomata <i>Calappa lophos</i> <i>Calappa tuberculata</i> <i>Ashtoret picta</i> * <i>Ranina ranina</i> * <i>Myra fugax</i> <i>Leucosia craniolaris</i> * <i>Soceulia marmorea</i> * <i>Philyra platycheir</i> * <i>Persephona guaia</i> <i>Dorippe quadridens</i> *	Cyclometopa <i>Lophozozymus pictor</i> * <i>Leptodius sanguineus</i> * <i>Ozius lobatus</i> <i>Pilumnus vespertilio</i> <i>Menippe rumphii</i> * <i>Actaea areolata</i> <i>Halimede ochtodes</i> * <i>Cancer pagurus</i> * <i>Carcinus maenas</i> <i>Carpilius convexus</i> <i>Atergatis dilatatus</i> <i>Etisus utilis</i> <i>Scylla serrata</i> <i>Thalamitoides tridens tridens</i> * <i>Lissocarcinus boholensis</i> <i>Podophthalmus vigil</i> <i>Thalamita sima</i> <i>Ovalipes punctatus</i> * <i>Charybdis (Charybdis) feriata</i> * <i>Portunus (Portunus) pelagicus</i> * <i>Lupocyclus philippinensis</i> <i>Trapezia digitalis</i> * <i>Tetralia glaberrima</i> *

The results observed here of the “Platystylidea” as well as the Oxystomata correspond to the descriptions of Nauck; i.e. representatives of the Calappidae, the Raninidae, the Leucosiidae and the Dorippidae show no increased lateral margin of the urocardiac ossicle (VII). A strongly increased lateral margin was found within the “Cyclometopa” (the Portunidae, the Carpilidae, the Xanthidae and the Trapeziidae).

Additionally, some of Nauck’s taxonomical placements make a recent understanding of his classification more difficult. He arranged *Mictyris longicarpus*, *Macrophthalmus (Mareotis) definitus* (former *Macrophthalamus definitus*), *Heloecius cordatus* (former *Heloecius signatus*) and *Uca (Australuca) bellator* (former *Gelasimus bellator*) within the “Gelasimidae”. According to the recent taxonomic literature (Ng *et al.* 2008) *Heloecius cordatus* is placed within its own family Heloeciidae (H. Milne Edwards, 1852). Furthermore *Uca (Australuca) bellator* is placed within the Ucinæ Dana, 1851 (e.g. Ng *et al.* 2008). *Mictyris longicarpus* and *Macrophthalmus (Mareotis) definitus* are assigned to their own families (Mictyridae and Macrophthalmidae).

Therefore *Heloecius cordatus*, *Uca (Australuca) bellator* and *Macrophthalmus (Mareotis) definitus* would be more related with the Catometopa within the Coelostylidea (Nauck 1880).

The suggested classification by Nauck (1880) including the separation into Heterodontea and Cyclodontea finds no support from the present study. Instead, the present study further supports the phylogenetic conclusion published by Brösing *et al.* (2007).

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