Possible Homologies in the Proventriculi
of Dicondylia (Hexapoda) and Malacostraca (Crustacea)

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Abstract. Striking similarities were found between the armarial part of the proventriculus of Lepismatidae (Hexapoda: Dicondylia: Zygentoma) and the cardia of Decapoda (Crustacea: Malacostraca: Eucarida). These include a similar shape and arrangement of the sclerites and denticles, a similar pattern of apodemes, and similar symmetry relations. The armarium of Dicondylia and the cardia of Malacostraca may, therefore, be homologous, and the similarities between Lepismatidae and Decapoda may belong to the ground-plan of Mandibulata. On the other hand, the distribution of the structural features of these organs within Tracheata and within Crustacea is inconsistent with this assumption and may indicate that this similar morphology was developed independently in Dicondylia and in Malacostraca. The homology question cannot yet be definitely resolved.

Key words. Zygentoma, Decapoda, Mandibulata, gizzard, stomach, armarium, cardia, phylogeny, homoplasy, ground-plan, symmetry.

1. INTRODUCTION

Many Hexapoda Dicondylia (Zygentoma + Pterygota) have the posterior part of the ectodermal, cuticle-lined foregut differentiated into a strongly muscular proventriculus (gizzard). Its morphology and function are very diverse in the individual orders. The proventricular wall usually has longitudinal folds (plicae), which often form sclerotised structures in the anterior part (armarium). Based on a comparison of Lepismatidae (Zygentoma), Blattidae (Dictyoptera), and nymphs of Corduliidae (Odonata), the ground-plan of the proventriculus of Dicondylia was reconstructed (KLASS 1998). This ground-plan is very similar to the proventricular morphology of Lepismatidae. In the armarium, six large sclerites, each with a strong denticle, are present in an essentially hexaradial arrangement. Hexaradial symmetry is overlain by a distinct bilateral symmetry established by individual differentiation of the sclerites and denticles: A dorsal and a ventral sclerite/denticle lying in the plane of bilateral symmetry are single (unpaired elements) and have an intrinsic bilateral symmetry. Two dorsolateral sclerites/denticles are a pair of mirror-images, and the same is true for two ventrolateral sclerites/denticles; these paired elements have an intrinsic asymmetry. The primary function of this armature is certainly mastication.

Many Crustacea Malacostraca also have the posterior part of the foregut differentiated into a masticatory- and filtering organ called stomach or proventriculus. It has a bilateral symmetry, and it is composed of an anterior cardia and a posterior pylorus, both of which may have a complicated cuticular morphology with many sclerites. Some cardia sclerites bear denticles. As in Dicondylia, the morphology of this organ varies strongly within the Malacostraca. Morphological descriptions are numerous. SIEWING (1952, 1954, 1956) gives a comparative account throughout the Malacostraca; PATWARDHAN (1934, 1935a–e) and SCHAEFER (1970) survey the Decapoda; HAFFER (1965) surveys mainly the Peracarida. So far, no detailed comparison was made between the proventriculi of Dicondylia and Malacostraca, and, to my knowledge, no homology relations have been suspected. The organs are generally regarded as having developed independently in Dicondylia and Malacostraca (e.g. SIEWING 1956; GRUNER et al. 1993).

2. MATERIAL AND METHODS

2.1. Species investigated and preparation

The cuticular elements of the armarium of *Ctenolepisma lineata* (Fabricius, 1775) (Hexapoda: Zygentoma: Lepismatidae) and those of the cardia of *Carcinus maenas* (Linnaeus, 1758) (Crustacea: Decapoda: Brachyura: Portunidae) were investigated. Hereafter, these species are referred to by the generic name alone. The specimens were stored in 4% formaldehyde. The soft tissues were removed by treatment with 10% KOH, and the remaining cuticle was washed in distilled water and stored in 70% isopropanol.

When data from previous studies are referred to, the names of the respective taxa, mostly species, are specified as completely as in the original papers (specification often incomplete).

2.2. Abbreviations

(Single small letters: compare in chapter 3)

acp anterolateral cardiac plate
ap apodeme on primary armarial sclerite (numbered 1–6)
at tooth/denticle bearing "lateral accessory teeth"
ca apodeme on posterolateral cardiac plate
cl lobe formed by posterior part of cardiopyloric valve
cpv cardiopyloric valve
D   position of dorsal side of whole animal
da apodeme anterior to denticle mt
dcp dorsal cardiac plate
dp primary armarial denticle (numbered 1–6)
ea apodeme along anterior margin of exopyloric ossicle
epo exopyloric ossicle
fp primary armarial plica (numbered 1–6)
ia plate-like posterior part of apodeme on inferolateral cardiac ossicle
ico inferolateral cardiac ossicle
ip primary interplicium = interspace between two neighboring primary plicae fp: ip2-3 between fp2 and fp3; ip5-6 between fp5 and fp6
la anterior apodeme of prepectineal ossicle
lt lateral tooth/denticle
mco mesocardiac ossicle
mt median tooth/denticle
pa posterior apodeme of prepectineal ossicle, extending onto pectineal ossicle
pco pterocardiac ossicle
pcp posterolateral cardiac plate
peo pectineal ossicle
poo postpectineal ossicle
ppo propyloric ossicle
pro prepectineal ossicle
pyo pyloric ossicle
sdo subdentary ossicle
sp primary armarial sclerite (numbered 1–6)
ta apodeme along ventral and posterior margins of pectineal ossicle
ua U-shaped apodeme on zygocardiac ossicle
uco urocardiac ossicle
V   position of ventral side of whole animal
va median apodeme of cardiopyloric valve
za apodeme along dorsomedian margin of zygocardiac ossicle
zco zygocardiac ossicle

3. CARDIAC/ARMARIAL MORPHOLOGY OF *CARCINUS* AND *CTENOLEPISMA*

3.1. *Carcinus maenas*

The cuticular morphology and the muscles of the proventriculus are described in COCHRAN (1935) for the closely related Blue Crab, *Callinectes sapidus* Rathbun (Decapoda: Brachyura: Portunidae), and in PATWARDHAN (1934) for the freshwater crab *Paratelphusa guerini* Milne-Edwards (Decapoda: Brachyura: Telphusidae). The cuticular morphology of the crab *Cyclograpsus punctatus* Milne-Edwards (Decapoda: Brachyura: Grapsidae) is described by SCHAEFER (1970). The cardiac morphology of *Carcinus*, *Callinectes*, *Paratelphusa*, and *Cyclograpsus* is very similar.

The terminology of COCHRAN (1935) and PATWARDHAN (1934, 1935a–e) is largely adopted here; additionally, abbreviations are used. As a general difference from *Ctenolepisma*, most cardiac sclerites are encrusted with calcite. COCHRAN and PATWARDHAN refer to them as "ossicles" or "plates". Some sclerites form bulges projecting into the cardiac lumen. COCHRAN and PATWARDHAN call these bulges "teeth"; I call them, as in *Ctenlepisma*, "denticles". Many sclerites form apodemes, which are in most cases low, massive ridges along the sclerite's epidermal face, and which are usually seen as shallow grooves on the opposite face of the cuticle. These apodemes are not named in COCHRAN or in PATWARDHAN. The abbreviations used here for the sclerites comprise three lower case letters; those for the denticles comprise two lower case letters, with "t" in the second position; those for the apodemes comprise two lower case letters, with "a" in the second position. (Only some apodemes are named; in Fig. 1 the line along which the apodeme infolds, i.e. the apodeme base, is labeled with the abbreviation of the apodeme.) Some further conspicuous elements are designated by single lower case letters. Two elements forming a pair (see below) have the same name. Setae, very important for the function of the cardia but not for the scope of this comparison, are omitted from the figures although some are mentioned in the description. The heaviness of sclerotisation or calcification is, with some exceptions, not represented in the figures. The following description proceeds mainly from dorsal to ventral.

Cardiac symmetry is purely bilateral (Fig. 1). The plane of symmetry coincides with that of the whole animal (dorsal side = **D**, ventral side = **V** in Fig. 1). Most elements are paired, i.e. represented by two mirror-image counterparts in the left and the right half of the cardia.

Some elements in the dorsal or ventral midline lie in the plane of symmetry and are unpaired.

The dorsal wall of the cardia is occupied by a T-shaped group of sclerites (Fig. 1). The transverse T-bar is formed by the pair of pterocardiac ossicles **pco**, with the unpaired mesocardiac ossicle **mco** (sensu PATWARD-HAN) between them. The **pco** are only posteriorly sepa-rated from **mco** by a deep membranous cleft **a**. Each **pco** has an apodeme **aa** along its posterior margin. The longitudinal T-bar is composed of the urocardiac ossi-cle **uco** (its anterior part, **(mco)** in Fig. 1, is the meso-cardiac ossicle sensu COCHRAN, which is by no means demarcated from the posterior part) and the roughly tri-angular propyloric ossicle **ppo** – both unpaired. The
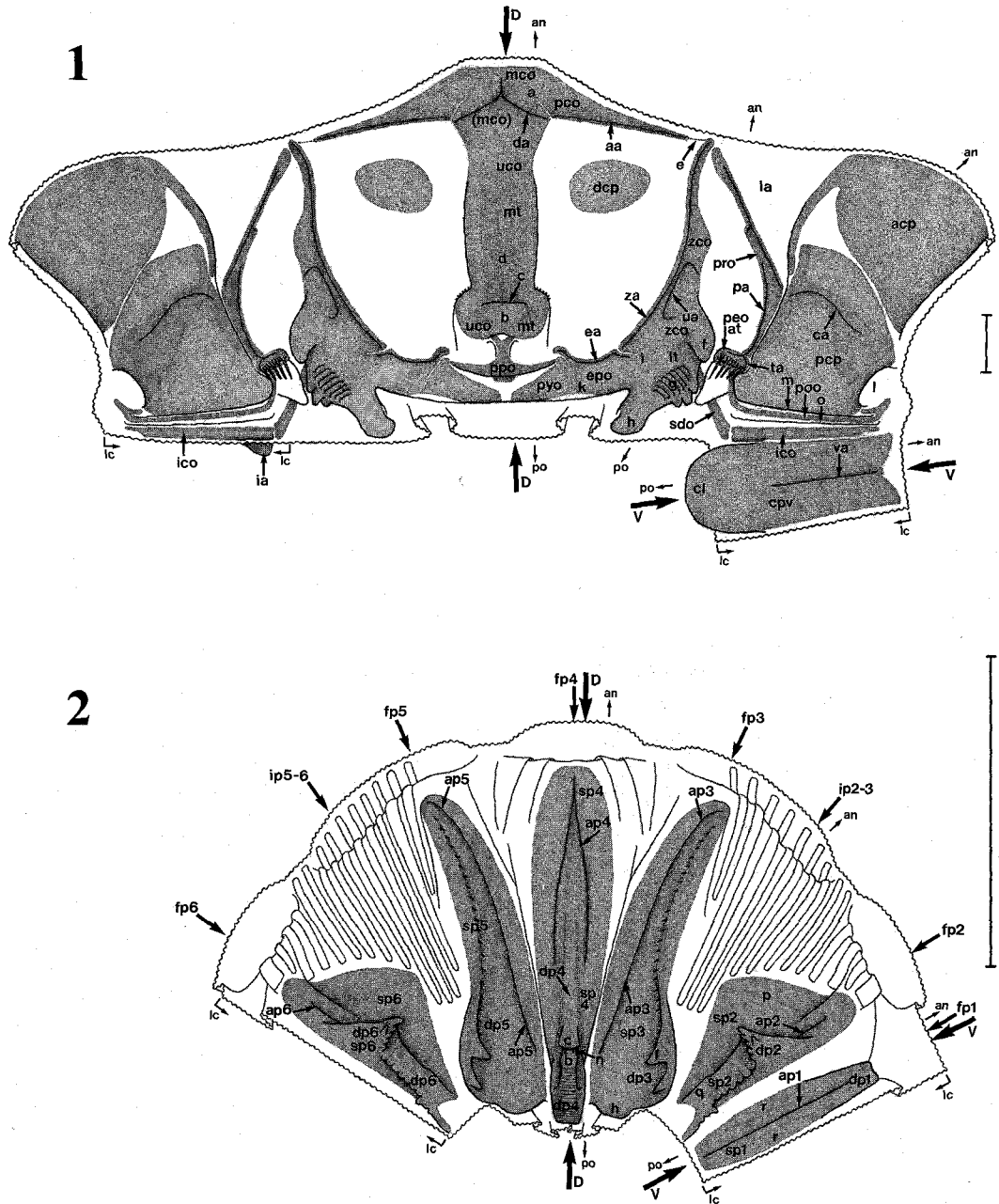
Figs. 1, 2. Entire internal view of cardia/armarium. The cardia (*Carcinus*) or armarium (*Ctenolepisma*) is shown, cut longitu-dinally and spread out. Undulate lines are cutting lines. Longitudinal cut in *Carcinus* between sclerites **cpv** (right side) and **ico** (left side), in *Ctenolepisma* between primary plicae **fp1** (right side) and **fp6** (left side) – along the undulate line in between the ar-rows **lc**. All elements seen from center of proventriculus. Sclerotisations dark. **D** = dorsal, **V** = ventral midline of whole animal. Arrows **an** and **po** give the directions anterior and posterior. Scale 1mm. **Fig. 1.** *Carcinus maenas.* **Fig. 2.** *Ctenolepisma lineata.*

uco is firmly connected with the mco anterior to it; the border is the invertedly Y-shaped apodeme da. The ppo has a forked anterior part, and the two tips support the uco from the posterior and articulate with it. The articulations are concealed beneath the posterior margin of uco. The cuticle between the posterior margin of uco and the ppo-branches is strongly thickened. The ppo has apodemal ridges all along its margins (not represented in Figs. 1, 3).

The sclerotisations uco and ppo lie upon a massive denticle, the median tooth mt, which as a whole sags posteriad. The mt has its main tip b far posteriorly (Figs. 1, 3fp4) and a transverse ridge c immediately anterior to it. The posteriormost part of mt is strongly convex in profile (Fig. 3fp4). Anterior to ridge c, mt has a broad, shallow median groove d. Lateral to mt there is, on each side, a wide and mostly membranous area (Fig. 1). Its central part has a weak sclerotisation named here the dorsal cardiac plate dcp (not mentioned in COCHRAN or in PATWARDHAN).

The dorsolateral cardiac wall is occupied by a sclerite group comprising the large zygocardiac ossicle zco, the exopyloric ossicle epo, and the pyloric ossicle pyo – all paired elements. The anterior end of zco is connected with the adjacent lateral end of sclerite pco by a strip of thickened cuticle e. The posterior half of zco lies upon a large, broadly shovel-shaped denticle, the lateral tooth lt. The crest of lt is highly differentiated: 4 distinct tips lie one behind the other; the anteriormost and largest tip f is slightly inclined dorsomedially, towards denticle mt. On its median surface near the 3 smaller tips, lt has a series of transverse ridges g. The posteriormost part of the denticle is a weaker sclerotised, bristled lobe h. Along the entire dorsomedian margin of zco runs an apodemal ridge za. Another apodeme ua, with the shape of a broad U, is present centrally on zco. The small sclerite epo is only partly separated from zco by a short membranous cleft i, and the mobility between the two sclerites is low. The epo has an apodeme ea, which begins at the posterior margin of the cleft i and extends along the anterior margin of epo – like a posteromedian continuation of the apodeme za on zco. The plate-like sclerite pyo is almost completely separated from epo by a long membranous cleft k. Its anterior end articulates with the lateral end of sclerite ppo. The median ends of the two pyo are close to each other.

The prepectineal ossicle pro in the lateral wall of the cardia is an L-shaped, rod-like sclerite. It has two ridge-like apodemes: pa runs along the posterior arm of the L, la runs along the anterior arm. The anterodorsal end of the L either approaches or reaches (both conditions found) the anterior end of sclerite zco. The posterior end of the L articulates with the pectineal ossicle peo. This peo lies on a small bulge-shaped denticle at. 5 or 6 spines (the lateral accessory teeth sensu COCHRAN)

originate from the crest of this denticle. The spine bases are arranged in a dorsoventral row whose ventral section curves slightly posteriad (Fig. 7). The spines become gradually shorter from dorsal to ventral. The apodemal ridge pa of sclerite pro bridges the articulation between pro and peo, bends dorsad, and continues along the anterior margin of peo (Figs. 1, 3fp2, 7). (At the articulation, pa consists of strongly thickened but not sclerotised cuticle.) The ventral and posterior margins of peo are strengthened by another apodemal ridge ta, which begins at the articulation between pro and peo but is distinctly separated from apodeme pa. The dorsal and central parts of peo, where the spines originate, are weakly sclerotised, and the spines are mobile at their bases. The postpectineal ossicle poo supports sclerite peo from the posterior and articulates with it (further data on poo below).

The ventrolateral cardiac wall is occupied by two large sclerite plates, the anterolateral cardiac plate acp and the posterolateral cardiac plate pcp. Their sclerotisation is mostly weak, and they have rather indistinct borders. Some parts are stronger, mainly the center of pcp along the apodemal ridge ca. Anteroventral to plate pcp there is a densely setose membranous cushion l; in the undamaged proventriculus it is close to the opening of the oesophagus into the cardia.

The ventral cardiac wall forms the unpaired cardiopyloric valve cpv, a longitudinal plate whose median part may be calcified (various degrees of calcification were observed). The anterior part of cpv has an apodemal ridge va along its median line. Apodeme va is also visible as a shallow groove along the internal face. Posteriorly cpv forms a broad lobe cl overlying the entrance to the pylorus.

The ventral margin of plate pcp folds over the dorsolateral margin of cpv. The narrow area beneath this fold (the paired ventral groove sensu PATWARDHAN; it is unfolded in Fig. 1) has a complex morphology: The ventral margin m of pcp bears a comb of setae, which are directed ventromesad and cover the lateral parts of cpv. Beneath these setae the rod-like sclerite poo extends anteroposteriad. The posterior part of poo bends dorsad and, as mentioned above, articulates with sclerite peo. The anterior part of poo also bends dorsad and then forks, with the branches embracing the base of cushion l. Ventromedian to poo, and parallel to it, there is another fold o armed with a comb of setae similar to that on the pcp-margin m. Ventromedian to fold o extends the inferolateral cardiac ossicle ico; both its dorsal and ventral margins form an apodemal ridge (not represented in Fig. 1). The ventral apodeme becomes excessively deep in its posteriormost part to form a plate-like apodeme ia (Fig. 1, left side). The posterior end of sclerite ico articulates with another stout rod-like sclerite, the subdentary ossicle sdo, which runs to

the ventrolateral base of denticle **lt** to articulate with sclerite **zco**.

3.2. *Ctenolepisma lineata*

The cuticular morphology of the proventriculus of *Ctenolepisma* is completely described in KLASS (1998). A description restricted to the armarium and aimed at facilitating comparison with *Carcinus* is given here. The terminology of the main elements remains the same. In Figs. 2, 4, setae and the heaviness of the sclerotisation are not represented.

The symmetry of the armarium has a distinct bilateral component but, in contrast to *Carcinus*, also a slight hexaradial component (Fig. 2). Hexaradiality is established by the presence of 6 major longitudinal folds or primary plicae (**fp1–6**). In the armarium each plica forms a primary sclerite (**sp1–6**), a primary denticle (**dp1–6**), and a primary apodeme (**ap1–6** in Figs. 2, 4; in Fig. 2 **ap1–6** are the lines along which the apodemes infold, i.e. the apodeme bases). The bilateral component is established by an individual differentiation of these plicae and their sclerites, denticles,

and apodemes. Plica **fp1** and its elements as well as plica **fp4** and its elements are unpaired and lie in the plane of bilateral symmetry. They have an intrinsic bilateral symmetry. The plicae **fp2** and **fp6** and their elements are mirror-images of each other, i.e. they are paired structures; the same is true for the plicae **fp3** and **fp5** and their elements. (A pair of elements, e.g. **sp2** and **sp6**, is designated **sp2/sp6**.) These paired plicae and their elements have an intrinsic asymmetry. The bilateral symmetry of the proventriculus coincides with that of the whole animal (dorsal side = **D**, ventral side = **V** in Fig. 2).

The dorsal wall of the armarium is occupied by sclerite **sp4**, whose peripheral parts are rather weak. Anteriorly **sp4** forms an invertedly Y-shaped apodeme **ap4**. More posteriorly **sp4** forms denticle **dp4**, which as a whole strongly sags posteriad. Far to the posterior **dp4** has two distinct tips, **b** and **c**, with a notch **n** between them (Fig. 4). The notch **n** extends onto the flanks of **dp4** (Figs. 2, 4). In some specimens tip **c** is represented by a transverse ridge only, and the notch **n** is less distinct. The convex posteriormost part of the denticle has 30–40 fine transverse ridges. Anterior to the tip **c** the
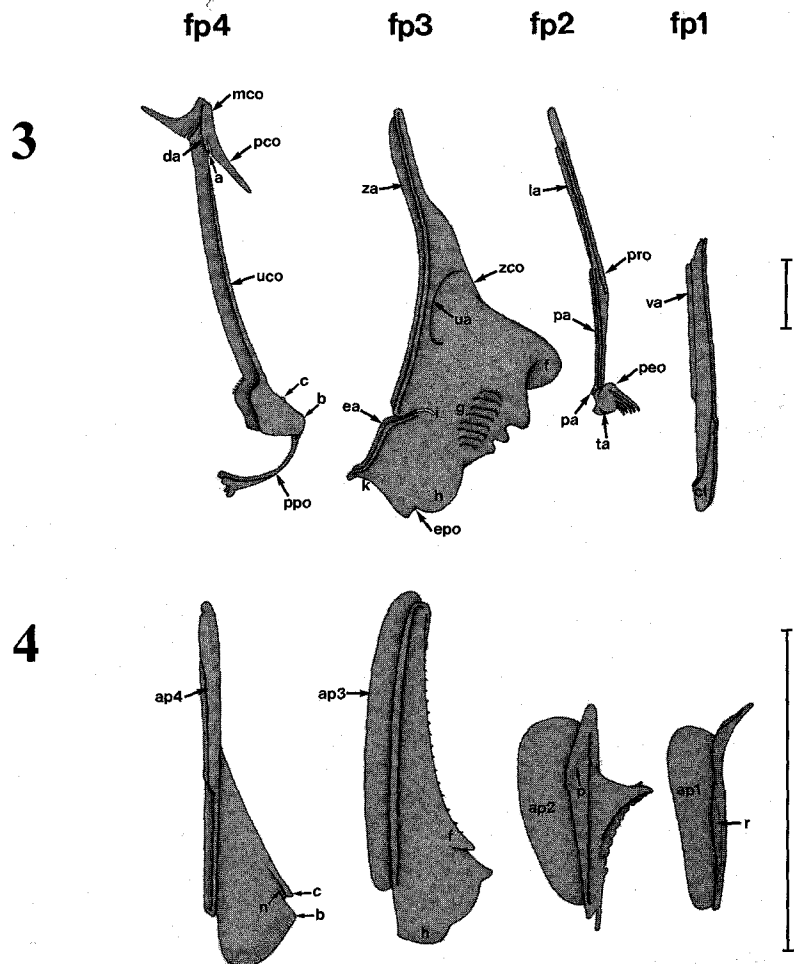
Figs. 3, 4. **Main sclerites, denticles, and apodemes in profile.** The primary sclerites, denticles, and apodemes of *Ctenolepisma* and their possible homologues in *Carcinus* are shown in profile. Of the paired elements, those of the left half of the cardia/armarium (= right side in Figs. 1, 2) are shown. Anterior ↑; proventriculus center →. Scale 1mm. Column fp4: denticle **dp4** and sclerite **sp4** of *Ctenolepisma*; denticle **mt** and sclerites **pco**, **mco**, **uco**, and **ppo** of *Carcinus*. Column fp3: denticle **dp3** and sclerite **sp3** of *Ctenolepisma* (**dp5** and **sp5** are the same but mirror-images); denticle **lt** and sclerites **zco** and **epo** of *Carcinus*. Column fp2: denticle **dp2** and sclerite **sp2** of *Ctenolepisma* (**dp6** and **sp6** are the same but mirror-images); denticle **at** and sclerites **pro** and **peo** of *Carcinus*. Column fp1: denticle **dp1** and sclerite **sp1** of *Ctenolepisma*; sclerite **cpv** of *Carcinus*. **Fig. 3.** *Carcinus maenas.* **Fig. 4.** *Ctenolepisma lineata.*

crest of **dp4** is even; *Eurycotis floridana* (Walker, 1868) (Blattaria: Blattidae), whose **dp4** is very similar to that of *Ctenolepisma*, has a shallow median longitudinal groove along the anterior crest of this denticle (KLASS 1998, fig. 4).

The dorsolateral armarial walls are occupied by the sclerite pair **sp3/sp5**. The major posterior part of **sp3/sp5** lies upon a large, broadly shovel-shaped denticle **dp3/dp5**, which has two distinct tips (the anterior one is labeled **f**) strongly inclined towards denticle **dp4**. The posteriormost part **h** of **dp3/dp5** is lobe-like and less strongly sclerotised. **sp3/sp5** has a longitudinal apodeme **ap3/ap5** which folds in along most of the sclerite's dorsomedian margin. Ventral to **sp3/sp5**, in the area designated **ip2-3/ip5-6**, the anterior part of the armarial wall has a cluster of membranous longitudinal folds.

The ventrolateral armarial walls are occupied by the sclerite pair **sp2/sp6**. **sp2/sp6** has a weak dorsal part expanded towards **sp3/sp5** and traversed by a shallow groove **p** (groove indistinct or absent in many specimens). The ventral part of **sp2/sp6** forms a denticle **dp2/dp6** whose anterior part is most prominent. The arch-shaped, uniformly serrate or tuberculate crest of this denticle has a dorsoventral orientation anteriorly but curves, becoming lower, far posteriad in its ventral part (Figs. 2, 8). Far posteriorly **sp2/sp6** has an area **q** with a polished appearance. **sp2/sp6** forms a longitudinal plate-like apodeme **ap2/ap6**, which infolds along the dorsal flank of **dp2/dp6** but extends anteriorly beyond the denticle base.

The ventral armarial wall is occupied by sclerite **sp1**. Most anteriorly **sp1** forms a spatulate, anteriad-directed process **dp1**. (This **dp1** is the anterior, strongly projecting part of denticle **dp1** as defined in KLASS 1998.) Posterior to **dp1**, **sp1** forms a longitudinal apodeme plate **ap1**, which folds inwards along the sclerite's median line. On each side **sp1** has a distinctly bordered area **r** with a polished appearance.

4. POSSIBLE HOMOLOGIES BETWEEN *CARCINUS* AND *CTENOLEPISMA*

In this chapter the similarities between *Carcinus* and *Ctenolepisma* are analysed. The cardiac morphology of *Carcinus* is more complicated than the armarial morphology of *Ctenolepisma*, mainly in the higher number of separate sclerites and apodemes. However, nearly each armarial element of *Ctenolepisma* – sclerites, denticles, and apodemes – has in the cardia of *Carcinus* a structurally similar counterpart in the same position. Figs. 5, 6 give a survey of these similarities. (In Fig. 5 the cardia of *Carcinus* is labelled according to the *Ctenolepisma* terminology; compare Fig. 1 for the original *Carcinus* terminology.)

4.1. Analysis of similarities

Primary plica fp4: The following elements take a dorsal position and are mostly unpaired (single) with an intrinsic bilateral symmetry. Denticle **dp4** and denticle **mt** have a similar shape: The anterior part of the denticle ascends straightly and gradually (Figs. 3, 4); in *Carcinus* and *Eurycotis*, but not in *Ctenolepisma*, this part has a shallow median groove **d**. The main tip **b** has a far posterior position. Just anterior to **b** there is another tip or ridge **c**, which is more elaborate in *Ctenolepisma*. The part posterior to tip **b** is short and convex in profile. The apodemes **ap4** and **da** are similar in their invertedly Y-like shape and in their position anterolateral to the base of denticle **dp4** or **mt**. (In *Ctenolepisma* the arms of **ap4** extend farther to the posterior.) Regarding the sclerotisations occupying these denticles and apodemes, **sp4** corresponds to the sclerites **pco + mco + uco**, all firmly connected, and **ppo**; the additional inclusion of **dcp** is conceivable. (Only *Carcinus* has the posterior sclerotisation **ppo** of denticle **mt** articulated with the anterior sclerotisation.)

Primary plicae fp3/fp5: The following elements take a dorsolateral position, are paired (two mirror-image counterparts in the left and the right half of the cardia/armarium), and have an intrinsic asymmetry. Denticle **dp3/dp5** and denticle **lt** arise from the posterior part of their sclerites (**sp3/sp5** or **zco**) and are, as a whole, broad and somewhat shovel-shaped. They have a strong anterior tip **f** and one (*Ctenolepisma*) or more (*Carcinus*) smaller tips behind it. The posteriormost part of the denticle is a weakly sclerotised lobe **h**. The sclerites **sp3/sp5** and **zco** (possibly including the exopyloric ossicle **epo** and the pyloric ossicle **pyo**) have a rather similar shape. The apodemes **ap3/ap5** and **za** (possibly including **ea**) take the same position along the dorsomedian margin of their sclerites.

Primary plicae fp2/fp6: The following elements take a ventrolateral (*Ctenolepisma*) or lateral (*Carcinus*) position, are paired, and have an intrinsic asymmetry. Denticle **dp2/dp6** as well as denticle **at** are bulges with a row of short tubercles (*Ctenolepisma*) or long spines (*Carcinus*) along the crest. The tubercle/spine bases are in an arch-like arrangement (Figs. 7, 8), with the arch spanning from anterodorsally to posteroventrally. In *Ctenolepisma*, the curvature of the arch to the posterior is stronger, the tubercles are shorter and stouter than the spines of *Carcinus*, and the number of tubercles/spines is much higher. The crab *Cyclograpsus punctatus* (SCHAEFER 1970, Figs. 4, 5), however, closely resembles *Ctenolepisma* in these features: The curvature of the arch is stronger than in *Carcinus*, and the spines are stouter and numerous. The anterodorsal part of **sp2/sp6** and the prepectineal ossicle **pro** are in a similar position and extend towards sclerite **sp3/sp5** or the zygocardiac ossicle

zco. (This sclerotisation is much narrower and separated from the denticle sclerotisation in *Carcinus*.) Apodeme **ap2/ap6** of *Ctenolepisma* is entirely straight and infolds anterior and dorsal to denticle **dp2/dp6**. Apodeme **pa** of *Carcinus* resembles it in lying anterior to the denticle and extending posteriorly towards the dorsal denticle flank (Figs. 7, 8); however, its sclerotisation – but not the ridge-like thickening of the cuticle – has a gap at the articulation between **peo** and **pro**, and behind this articulation

apodeme **pa** sharply bends dorsad. The groove **p** on the weak dorsal part of **sp2/sp6** of *Ctenolepisma* and apodeme **la** of *Carcinus* are similar in their transverse course directed towards **sp3/sp5** or the zygocardiac ossicle **zco.** Since groove **p** is mostly indistinct, the indication of homology with **la** is weak. When the proventriculus is constricted, the main body of denticle **dp2/dp6** or **at** (the anterior part in *Ctenolepisma*) rests upon the crest of denticle **dp3/dp5** or **lt** (upon the part shortly anterior to tip **f**).
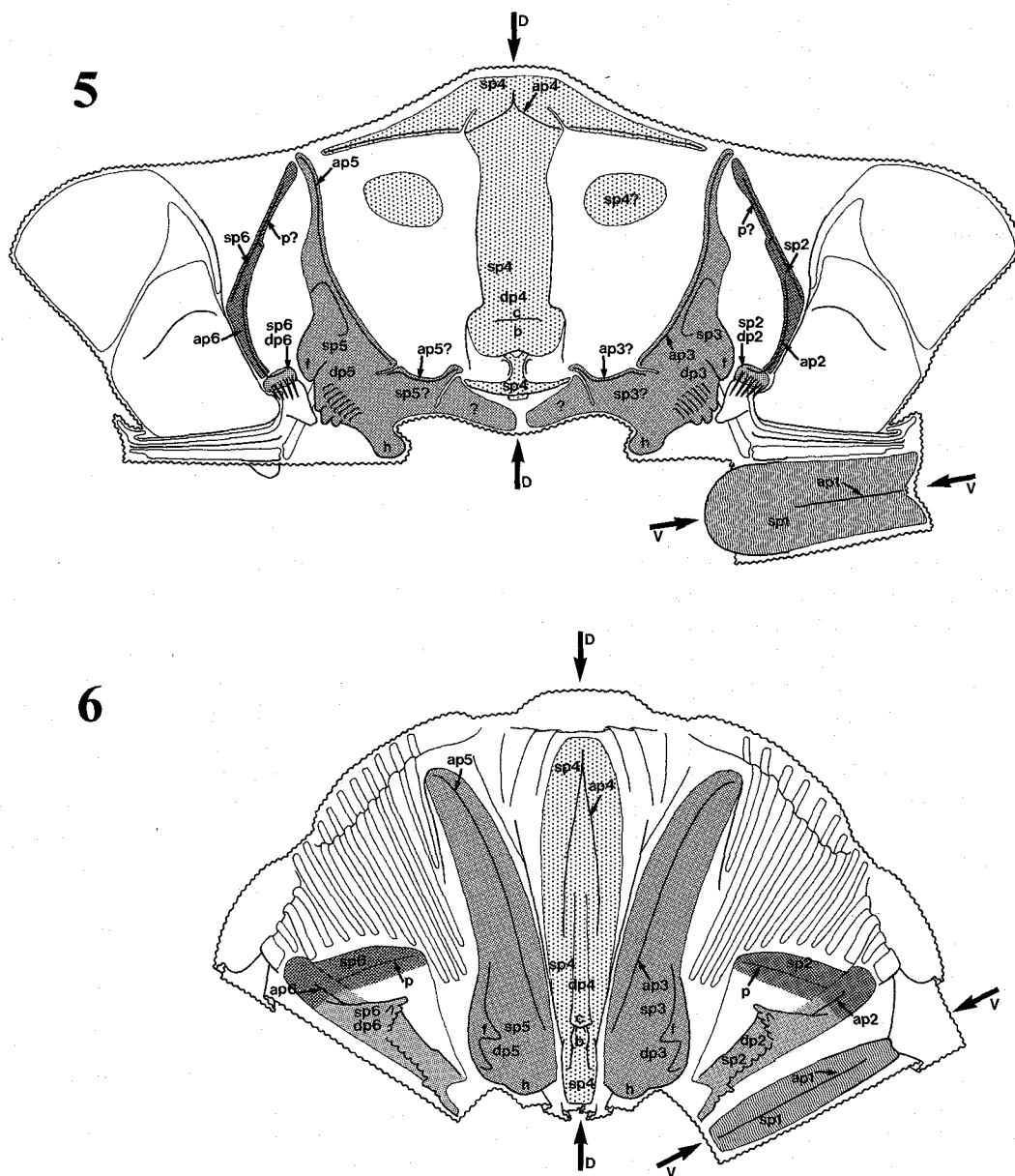
Figs. 5, 6. Possible homology relations between cardia and armarium. Cardia and armarium shown as in Figs. 1, 2. Sclerotisations present in both species differently patterned according to possible homology relations. Terminology of *Ctenolepisma* used for *Carcinus*, too. Only suspectedly homologous elements labeled. **Fig. 5.** *Carcinus maenas.* **Fig. 6.** *Ctenolepisma lineata.*

Primary plica fp1: The following elements take a ventral position, are unpaired, and have an intrinsic bilateral symmetry. Sclerite **sp1** as well as the cardiopyloric valve **cpv** are longitudinal and roughly plate-like. Both have a median longitudinal apodeme **ap1** or **va**. (Only in *Ctenolepisma* the anterior part of **sp1** forms a process **dp1**. Only in *Carcinus* the posterior part of **cpv** forms a lobe **cl**. **cpv** of *Carcinus* has the shape of a shallow groove; **sp1** of *Ctenolepisma* has the shape of a low longitudinal bulge; Figs. 3, 4.)

Symmetry: *Carcinus* and *Ctenolepisma* show the same kind of bilateral symmetry: The plane of symmetry coincides with that of the whole animal (**D**, **V** in Figs. 5, 6). The similar denticles **dp4** and **mt** and their sclerotisations and apodemes are in a dorsomedian position, the similar sclerites **sp1** and **cpv** and their apodemes are in a ventromedian position (Figs. 1, 2); these elements are unpaired and show an intrinsic bilateral symmetry. The elements in the lateral cardiac wall are paired and show an intrinsic asymmetry. The impression of a hexaradial symmetry component in the armarium of *Ctenolepisma* results from the fact that all main elements are concentrated on 6 major plicae **fp1–6**. Moreover, some of the corresponding elements of different plicae show a closer similarity to each other than their counterparts do in *Carcinus*. In *Ctenolepisma* hexaradiality is not very conspicuous. However, in the evolution of Dicondylia this hexaradial component becomes, several times independently, stronger (KLASS 1998). For instance, a gradual increase of hexaradiality, i.e. a structural convergence of all 6 plicae, can be observed in Dictyoptera, and in the most derived conditions, represented by e.g. Isoptera, there is complete hexaradiality (and an additional trend towards dodecaradiality) with the bilateral component completely lost. Hence, the presence of a slight hexaradial component in *Ctenolepisma* is not in strong contrast to the condition in *Carcinus*. It could be easily explained as the beginning of a trend which becomes much stronger in other Dicondylia.

4.2. Conclusion

In the cardia of *Carcinus* and in the armarium of *Ctenolepisma*, elements of similar structure are in similar positions. It is regarded here as important that not only the sclerites and denticles are similar, but that, additionally, the apodemes labeled in Figs. 5, 6 are in a very similar condition and position. All the similarities together form a complex pattern. Therefore, the elements and their features discussed here are, according to the homology criteria I (structure) and II (relative position) of REMANE (1952), clearly suggested to be homologous. It seems thus highly reasonable to ascribe these elements and features to the ground-plan of the

Table 1. List of cardiac/armarial elements possibly homologous in *Carcinus* and *Ctenolepisma*.

| *Ctenolepisma* (and *Eurycotis*):	*Carcinus*:
sp1	cpv
sp2/sp6	pro + peo
sp3/sp5	zco (+ epo + pyo?)
sp4	pco + mco + uco + ppo (+ dcp?)
dp1	–
dp2/dp6	at
dp3/dp5	lt
dp4	mt
ap1	va
ap2/ap6	pa
ap3/ap5	za (+ ea?)
ap4	da
tubercle row on dp2/dp6-crest	spine row on at-crest
tip f of dp3/dp5	tip f of lt
posterior lobe h of dp3/dp5	posterior lobe h of lt
main tip b of dp4	main tip b of mt
tip c of dp4	ridge c of mt
groove d on dp4 of *Eurycotis*	groove d on mt
(groove p on sp2/sp6?	la?)

smallest monophyletic taxon including *Carcinus* and *Ctenolepisma*, which is, according to the presently prevailing hypothesis, the Mandibulata. ("Monophyly" is used in this paper in its strict sense, excluding paraphyly.) The possible homologies are listed in Tab. 1.

5. CARDIAC/ARMARIAL MORPHOLOGY IN OTHER MANDIBULATA

In both Crustacea and Tracheata the morphology of the posterior foregut is highly variable. In taxa having a reasonably complex foregut morphology this is widely used for phylogenetic and taxonomic purposes (e.g. WÄGELE 1989). Descriptions of this gut region are numerous. Only a short survey of the morphological range is given here.

5.1. Crustacea

PATWARDHAN (1934, 1935a–e) compares the cardia throughout the Decapoda. In the probably monophyletic Reptantia, a morphology similar to that of *Carcinus* is prevailing in all subgroups. Of course, there is some variation (compare also SCHAEFER 1970), but all the similarities listed above for *Ctenolepisma* and *Carcinus* are shared with most of the investigated Reptantian species (apodemes not described). In "Natantia" (with the major groups Caridea, Stenopidea = Stenopo-
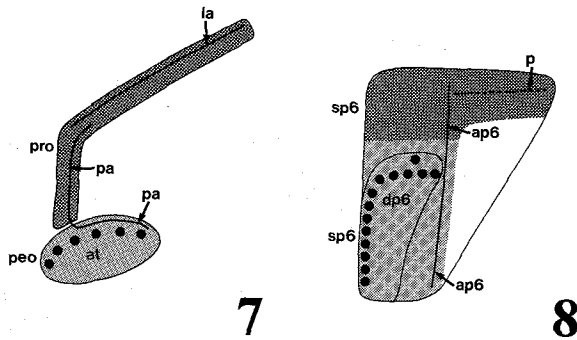
Figs. 7, 8. Denticles dp6 and at and associated structures. Scheme of denticle **at**, sclerites **peo** and **pro**, and apodemes **pa** and **la** of *Carcinus*, and of denticle **dp6**, sclerite **sp6**, apodeme **ap6**, and groove **p** of *Ctenolepisma*. The elements of the right proventricular wall (left side in Figs. 1, 2) are shown as seen from the proventricular center. Black dots are bases of spines or tubercles. Anterior ↑, dorsal →. No scale. **Fig. 7.** *Carcinus maenas.* **Fig. 8.** *Ctenolepisma lineata.*

didea, and Penaeidea = Dendrobranchiata), regarded as a paraphyletic assemblage of more primitive Decapoda (e.g. GRUNER et al. 1993), the cardia is more diverse: In all Caridea, PATWARDHAN found a rather simple morphology. The denticles are represented by folds that are hardly sclerotised or calcified and hardly show any further differentiation. Only some species have distinct median and lateral denticles with sclerotised tips (**mt** and **lt**; best developed in *Caridina brachydactyla* de Mann; Atyidae), but most lack these. The Dendrobranchiata and Stenopodidea have a cardia resembling that of Reptantia. According to PATWARDHAN's descriptions, the dorsal sclerites (**pco, mco, uco, ppo,** and **zco**) and denticles (**mt** and **lt**) are in a similar condition to the Reptantia. The posterior spine-row of the infero-lateral cardiac plate (**ilc** of PATWARDHAN 1935e, fig. 7) of *Stenopus spinosus* Risso. (Stenopodidae) is, regarding its similar shape and position, probably homologous with the spine-row on the pectineal ossicle **peo** of *Carcinus*. Regarding the ventral elements, PATWARDHAN's descriptions are not very detailed, and a comparison with Reptantia is not possible.

Since the Dendrobranchiata are probably the sistergroup of the remaining Decapoda (= Pleocyemata) (e.g. GRUNER et al. 1993), it is reasonable to assume that at least the dorsal sclerites and denticles (and possibly also the ventral ones) are, in the condition found in Dendrobranchiata and Reptantia, ground-plan elements of Decapoda, and that the reduction of this cardiac armature in Caridea is a secondary trait. PATWARDHAN (1935e) also comes to this conclusion.

Decapoda, Euphausiacea, and Amphionidacea together form the Eucarida. The superorders Eucarida, Peracarida, Pancarida, Syncarida, Hoplocarida, and Phyllocarida constitute the Malacostraca, which are generally accepted as a monophyletic taxon. SIEWING (1952, 1954, 1956) surveys the proventricular morphology throughout the Malacostraca and gives a comprehensive hypothesis on the evolution of the organ. His descriptions focus on the geometry of the proventricular folds (the denticles are part of them) and the distribution of setae. Hardly any sclerotisations and no articulations or apodemes are mentioned. Hence, most of the elements discussed above are not considered in SIEWING's descriptions, or they are largely absent in the species he has studied. HAFFER (1965) gives a survey on the proventriculus of Peracarida and Eucarida – including the muscles – and a synonymy list of the terminologies used previously in these taxa. HAFFER describes the overall shape, the position, and the setae or spines of the sclerites and denticles but, unfortunately, not the exact structure of the sclerotisations or any articulations or apodemes. Similar inadequacies in the morphological descriptions are true for most other available contributions (compare also WÄGELE 1989, p. 25). A comparison between Decapoda and other Malacostracan taxa by means of the previous literature is thus only partly possible, and some of the homologies assumed below are tentative.

HAFFER (1965) points out the similarity between the proventriculi of Decapoda, Euphausiacea (Eucarida), and Mysidacea (Peracarida): "Dekapodentyp" of proventriculus. The cardiac elements of *Neomysis vulgaris* (Mysidacea) are, in the frame of HAFFER's data, mostly similar to those of Dendrobranchiata and Reptantia (HAFFER's abbreviations in brackets): sclerite **cpv** (= CV), setal comb on fold **o** (= BG on CLi), sclerites **acp** and **pcp** (= CLa), sclerite **peo** and denticle **at** with their spines (= CLp), sclerite **zco** and denticle **lt** (= CDl; CL according to HAFFER, p. 203), and denticle **mt** with a shallow groove **d** (= CD with concavity KV). For some Euphausiacea, HAFFER reports a similar condition to that in *Neomysis vulgaris*. ZIMMER (1912), however, says that in *Euphausia superba* Dana (Euphausiacea) parts of the cardiac wall epithelium are thickened and bulge into the lumen (denticles; ZIMMER's "Stücke"), but the cuticle has roughly the same thickness in all parts of the cardia. Distinct sclerotisations or calcifications, comparable with the ossicles of Decapoda, are not mentioned. Whether crucial elements such as the apodemes described above are present in Mysidacea and Euphausiacea cannot be decided from these descriptions. The proventriculi of Isopoda and Tanaidacea (both Peracarida) are rather different from those of Eucarida and Mysidacea (HAFFER 1965; LAUTERBACH 1970; SCHELOSKE 1976; WÄGELE 1989). WÄGELE

(1989) describes, for various Isopoda, chitinous ridges ("Chitinleisten = Sklerite") in the anterior part of the proventriculus; these are, regarding their positions, partly comparable to the apodemal ridges of *Carcinus* (Sk1 = **aa**; Sk2 = **za+ua**; Sk4 = **la+pa**). Strong sclerotisations in similar positions are also present in Tanaidacea (LAUTERBACH 1970). However, for a detailed comparison of the apodemes the descriptions are too scarce, and there are probably also some stronger differences between these taxa. As a result, these data on Eucarida and Peracarida altogether show that a morphology **at least** similar to that of *Carcinus* was already present in the common ground-plan of Eucarida and Peracarida. If Pancarida are actually the sister-group of Peracarida (e.g. GRUNER et al. 1993) the cardiac morphology of this taxon (no detailed morphological data available) must also be derived from this ground-plan. Syncarida and Phyllocarida have a much simpler cardiac morphology than Dendrobranchiata and Reptantia (SIEWING 1956; CLAUS 1888). The cardia of Hoplocarida is also quite simple in some respects, but it also shows some peculiar derivations (SIEWING 1956; REDDY 1935).

Hence, no other Malacostracan taxa seem to have a cardiac morphology as similar to that of *Ctenolepisma* as the Reptantia. However, at least some other Eucarida and some Peracarida also show many of the respective similarities, and it is unclear whether the remaining elements and features are actually absent or whether they are just not considered in the descriptions.

For completeness, it may be mentioned here that various Malacostraca share similarities with *Ctenolepisma* that are absent in *Carcinus*: (1) Many Reptantia (PATWARDHAN 1935b,c), Lophogastrida, and Cumacea (SIEWING 1956) have the lateral parts of the cardiopyloric valve **cpv** differentiated as longitudinal bulges distinctly set off from the main median part. These bulges have the same position as the lateral areas **r** of **sp1** of *Ctenolepisma*. (2) At least in some Hoplocarida and Syncarida (*Squilla mantis* and *Anaspides tasmaniae* in SIEWING 1956) the anterior part of **cpv** forms an anteriad-directed process in the same position as **dp1** of *Ctenolepisma*. (3) In some Peracarida, Euphausiacea, and Caridea (HAFFER 1965), sclerite **cpv** does not have the shape of a shallow longitudinal groove as in *Carcinus* (Fig. 3 fp1) but bulges into the proventricular lumen like **sp1** of *Ctenolepisma* (Fig. 4fp1). (4) In *Neomysis vulgaris* (HAFFER 1965, fig. 6) denticle **lt** (= CDl) has two strong tips strongly inclined towards denticle **mt**, like denticle **dp3/dp5** of *Ctenolepisma*. Of course, the assumption of homology would be highly speculative in these cases.

Most Malacostracan superorders include subgroups in which simple cardiac morphology is undoubtedly due to secondary reduction. Within Peracarida, such a re-

duction trend is present in e.g. some Mysidacea (comparison of *Mysis stenolepis* Smith and *Spelaeomysis longipes* in FRIESEN et al. 1986) and Tanaidacea (SIEWING 1954). In Eucarida, as mentioned above, at least Caridea and, according to ZIMMER'S (1912) descriptions, some Euphausiacea show strong secondary reductions. In Syncarida, strong reduction is certainly true for Bathynellacea (GRUNER et al. 1993) and has been suspected also for Anaspidacea (SIEWING 1956, p. 112). In Phyllocarida, *Nebaliopsis typica* has lost most cardiac elaborations (GRUNER et al. 1993). Certain elements of these reduction trends are similar in different taxa (e.g. SIEWING 1956, p. 112).

As regards the remaining Crustacea, sclerotised differentiations of the posterior foregut are, to my knowledge, only reported for some Ostracoda (SIEWING 1956) and Acrothoracica (GRUNER et al. 1993). These structures are regarded as completely different from and evolved independently of the proventriculus of Malacostraca. Many non-Malacostracan Crustacea have a set of 4 simple longitudinal folds running along the foregut (1 dorsal, 1 ventral, 2 lateral; SIEWING 1956).

SIEWING (1956) regards this latter condition as the starting point of proventricular anagenesis in Malacostraca. Some simple subdivisions of the 4 folds lead to the ground-plan of Malacostraca, which includes a still indistinct separation between cardia and pylorus and, in the cardia, a subdivision of the lateral fold pair into lateralia superiores (roughly denticle **lt**) and lateralia inferiores (roughly area of plates **acp** and **pcp** and denticle **at**). According to this hypothesis, the condition in Mysidacea, Dendrobranchiata, and especially Reptantia has to be regarded as highly apomorphic within Malacostraca. Within the range of SIEWING's comparison, which is restricted to Crustacea, this view is certainly conclusive.

5.2. Tracheata

The armarium of *Ctenolepisma* (Zygentoma: Lepismatidae) completely, or at least nearly so, shows the ground-plan condition of Dicondylia (cf. descriptions in KLASS 1998). Of the Dicondylia so far investigated, only further Lepismatidae, some Blattaria (mainly Blattidae), and the nymphs of some Odonatan families (Corduliidae, Libellulidae) have an armarium which is in many respects close to that of *Ctenolepisma*. The remaining Dicondylia have the armarium either strongly modified or strongly reduced. Modifications and reductions also occur within Blattaria and Odonata, and the anagenetic trends are partly similar in these two taxa (details in KLASS 1998).

For Diplopoda, Pauropoda, and Symphyla (together the Progoneata), and for the Hexapoda Parainsecta (= Ellipura = Protura + Collembola), Diplura, Archaeog-

natha, and Lepidotrichidae (Zygentoma; the most primitive taxon of Dicondylia, possibly the sister-group of all other Dicondylia; KRISTENSEN 1995) no cuticular differentiations of the posterior foregut are reported which could be compared with the armarium of *Ctenolepisma*. Many Chilopoda have, according to the survey in LEWIS (1981), longitudinal folds variously armed with small sclerites, spines, or setae in the posterior foregut; these structures, however, bear no resemblance to the armarium of *Ctenolepisma*.

5.3. Other Arthropoda

Of the Chelicerata, I have checked *Limulus polyphemus* (Linnaeus, 1758) (Xiphosura: Limulidae) regarding its foregut morphology. It has a muscular proventriculus with ca. 14 longitudinal folds that are weakly sclerotised and transversely corrugated. No further similarity with the proventriculi of *Carcinus* or *Ctenolepisma* was detected. For the Onychophora, no foregut structures bearing any resemblance to those of *Carcinus* or *Ctenolepisma* are reported.

5.4. Conclusion

Regarding the complex similarities between the armarium of *Ctenolepisma* and the cardia of *Carcinus*, it seems reasonable to assume homology for the elements and features listed above and to ascribe them to the ground-plan of Mandibulata. In this case, the anagenesis of the Malacostracan proventriculus would be the reverse of SIEWING's hypothesis.

On the other hand, the distribution of these elements and features over the Mandibulatan subgroups contradicts this assumption: In Crustacea, a proventriculus is found only in Malacostraca, and a morphology closely similar to *Carcinus* is known only from Decapoda (but may be present in other Eucarida and Peracarida, then being plesiomorphic for these taxa). In Tracheata, an armarium similar to that of *Ctenolepisma* is found only within Dicondylia. Many parallel reductions or losses of the cardia/armarium within the more basal offshoots of Crustacea and Tracheata have to be assumed in the case of homology, and only a highly derived clade of both Crustacea (Decapoda, or possibly Eucarida + Peracarida + Pancarida) and Tracheata (Dicondylia) would have retained the Mandibulatan ground-plan condition. In this respect, the assumption of homology seems very unparsimonious, and it seems more reasonable to assume that the cardiac morphology as found in *Carcinus* is a development within Malacostraca, and that the armarial morphology as found in *Ctenolepisma* is an autapomorphy of Dicondylia (or of Lepismatidae + Pterygota if Zygentoma are paraphyletic with respect to Pterygota as suspected by KRISTENSEN 1995).

6. HYPOTHESES ON THE PHYLOGENY OF MANDIBULATA

To obtain an impression on the extent of non-parsimony inherent in the assumption of cardiac/armarial homology, the present knowledge on the phylogeny of Mandibulata has to be briefly surveyed – focused on the estimation of the phylogenetic distance between Malacostraca and Dicondylia. For detailed information see the cited papers. STYS & ZRZAVY (1994) give a more comprehensive survey on current hypotheses and recent literature.

6.1. Mandibulata

The traditional view, advocated by e.g. WÄGELE (1993), assumes monophyly for Mandibulata. (These probably include Pentastomida, which are not considered here.) The Uniramia hypothesis sensu MANTON (e.g. 1977) is regarded here as discarded because of its incorrect argumentation (compare WEYGOLDT 1986; STYS & ZRZAVY 1994) and because of recent evidence on several organs (compare AVEROF & AKAM 1995b; OSORIO et al. 1995). Mostly, Crustacea and Tracheata are regarded as the two basal sister-groups within Mandibulata (e.g. WEYGOLDT 1986).

6.2. Crustacea

Malacostraca are generally accepted as a monophyletic unit, with their peculiar tagmosis and the characteristic position of the genital openings being their most convincing autapomorphies. The Phyllocarida are regarded as the sister-group of the remaining Malacostraca; the relations between the other superorders are, in part, still subject to debate. The relations between Malacostraca and the other major Crustacean groups are uncertain.

Crustacea as a whole are mostly regarded as monophyletic, but the support is weak. WÄGELE (1993) lists three possible autapomorphies: (1) The nephridia of head-segment V (segment of first maxillae) have been lost (like in Hexapoda). (2) A nauplius eye is present, which, however, is merely a closer grouping of the medial group of the frontal eyes of the Mandibulatan ground-plan. (3) The sinus gland, or some of its properties, may be suspected to be autapomorphic. The implications of the carapace and the stalked eyes are highly uncertain, and there are cases of secondary reduction.

6.3. Tracheata

Dicondylia as well as Insecta (= Ectognatha) are certainly monophyletic taxa. Autapomorphies of the former are, for instance, a derived morphology of the gonangulum and of the mandible. Autapomorphies of the

latter are the ovipositor with gonapophyses, flagellar antennae with Johnston's organ, the subdivision of the tarsus, and many others. The monophyly of Hexapoda is supported by their unique tagmosis and by the tight union of patella and tibia in the legs (complete accounts in KRISTENSEN 1991, 1995).

KRAUS & KRAUS (1994) list some possible synapomorphies of Hexapoda and Progoneata. The coxal vesicles are possibly a good argument. The stylus, however, may be a vestige of the outer limb ramus. (In extant Hexapoda, this feature of KRAUS & KRAUS 1994 concerns only the thoracic styli of Archaeognatha; the abdominal styli are almost certainly the reduced telopodites, compare BIRKET-SMITH 1974.) The formation of a maxillary plate, primarily by the second maxillae, may be a homoplasy due to terrestrial life, but the few structural similarities between Symphyla and Hexapoda may suggest homology within Progoneata + Hexapoda. The dorsal organ and the superlinguae are regarded as doubtful synapomorphies by KRAUS & KRAUS (1994).

The monophyly of Tracheata as a whole is supported by several apomorphies. Some of them are or may be correlated with terrestrial life (tracheae; Malpighian tubules; strong reduction of outer limb ramus; loss of second antennae and of mandibular palpus), but others are probably not (anterior tentorial arms; temporal organs = organs of Tömösvary; loss of pretarsal levator muscles). The "terrestrial" apomorphies all have counterparts in other terrestrial arthropods (e.g. Arachnida, terrestrial Isopoda) and are, therefore, often suspected to have arisen independently also in the Tracheatan subgroups and to be of low value as arguments for Tracheatan monophyly. Wherever tracheae are present in non-Tracheatan Arthropoda, their position is always completely different from that in Tracheata, whereas at least Chilopoda (Scutigeromorpha excluded), Diplopoda, and Hexapoda have segmentally repeated pairs of spiracles in a pleural position (compare, e.g., SNODGRASS 1958). The exact position of the spiracles, however, is often stated to be quite different in these Tracheatan clades, and these clades are now mostly regarded as having developed the tracheal system independently (e.g. GRUNER et al. 1993; KRAUS & KRAUS 1994). The Malpighian tubules of Arachnida arise from the midgut; those of Tracheata arise from the hindgut and may well be regarded as an autapomorphy of this group. Of the "non-terrestrial" features, the temporal organs are suspected to have a homologue in Crustacea, the organs of Bellonci (WÄGELE 1993). The tentorial arms and the absence of pretarsal levators (SNODGRASS 1958; KRISTENSEN 1991) remain, to my knowledge, unchallenged. Also, the fact that all the Tracheatan apomorphies mentioned here form together a complex pattern of similarities not present in any other arthropod

supports the monophyly of Tracheata. As a result, Tracheatan monophyly is not easily discarded.

6.4. Hexapoda + Crustacea

Evidence that Hexapoda alone are the closest relatives of Crustacea, with "Myriapoda" only more distantly related, comes from genetic analyses (FRIEDRICH & TAUTZ 1995, "Myriapoda" represented by Diplopoda and Chilopoda; BALLARD et al. 1992, "Myriapoda" represented by Chilopoda only). AVEROF & AKAM (1995b) point out the probably derived similarities in the ontogeny of the central nervous system that are shared by Hexapoda and Crustacea but not by Chilopoda (remaining "Myriapoda" not investigated). In this context, the similarity in ommatidial structure, the scolopidial sensilla, and the loss of nephridia in head segment V could be synapomorphic for Hexapoda and Crustacea, and the structure of the lateral eyes and the lack of scolopidial sensilla in "Myriapoda" could be plesiomorphic.

There are indications that Crustacea are not monophyletic but paraphyletic with respect to Hexapoda. The presence of three optic neuropiles (lamina, medulla, lobula) and their similar structure (see OSORIO et al. 1995) may be an argument for a close relation between Hexapoda and Malacostraca. On the other hand, similarities in the pattern of *hox* gene expression along the trunk may indicate a closer relation between Hexapoda and branchiopod Crustacea (AKAM 1995; AVEROF & AKAM 1995a).

The implications of most of these data, however, are still unclear since the investigations are only scattered in terms of taxa and characters (e.g. genes). The main obstacle for well-founded conclusions on phylogeny is the scarcity of data on the "myriapod" taxa.

6.5. Conclusion

For obtaining a clearer picture of the phylogeny of Mandibulata, we have to wait for further results on morphology, on genetics, and on the interrelations between these two levels. A sister-group relation between Crustacea and Tracheata still seems to be the most convincing hypothesis, but a sister-group relation between Crustacea and Hexapoda or even between a Crustacean subgroup and Hexapoda cannot be ruled out. Accordingly, in the following discussions the smallest monophyletic taxon comprising both *Carcinus* and *Ctenolepisma* is represented by "Mandibulata". If another hypothesis is preferred, this would have to be replaced by "Crustacea + Hexapoda" or "Malacostraca + Hexapoda".

If homology is accepted for the cardiac/armarial morphology of Decapoda and Dicondylia, the (rather improbable) assumption of a sister-group relation between

Malacostraca and Hexapoda would be most parsimonious in terms of independent losses or reductions of this morphology, but some losses or reductions in "basal offshoots" have still to be assumed: in several Malacostracan subgroups, and in Entognatha (or in Parainsecta **and** Diplura), Archaeognatha, and Lepidotrichidae among the Hexapoda. Therefore, these similarities between Decapoda and Dicondylia certainly yield no argument for close Malacostracan-Hexapodan relationships.

7. HOMOLOGY OR HOMOPLASY OF CARDIAC/ARMARIAL MORPHOLOGY?

7.1. The basic problem

As a result from the foregoing discussions, there is one major problem in the homologisation of the cardiac/armarial structures of Lepismatidae and Decapoda: The homology criteria I (structure) and II (relative position) strongly support homology, but the distribution of the features over the phylogenetic tree contradicts it. The question is, which of the two following hypotheses is more parsimonious: (1) Complete homoplasy: The complex pattern of sclerites, denticles, and apodemes has developed twice independently – in Decapoda, or possibly Eucarida + Peracarida + Pancarida, and in Dicondylia – from a condition where all these structures were absent. (2) Complete homology: This complex pattern was present in the ground-plan of Mandibulata and has been simplified or lost many times independently – also in taxa regarded as "basal" such as Phyllocarida, Diplura, or Archaeognatha.

Both hypotheses are, in different ways, very unparsimonious. Any hypothesis intermediate between (1) and (2), assuming homology for part of the similarities and homoplasy for the remainder, would not be more parsimonious than (1) or (2) (see below). The parsimony problem cannot be decided by a mathematical approach since there are no objective parameters one could insert in a calculation.

7.2. The possibility of complete homoplasy

It could be hypothesised that Decapoda and Dicondylia had, due to a change in nutrition, a similar functional requirement (mastication in foregut), and that the morphological solution was, due to a similar constructional and genetic background, rather similar ("Kanalisierung" sensu SUDHAUS & REHFELD 1992). Such a hypothesis could explain the use of the same material (sclerotised cuticle) and constructional principles (apodemes, denticles) and a similar arrangement and shape of elements which have to fulfil a similar function.

A classical example of a homoplasy of this type are the grasping forelegs of Mantodea (Hexapoda: Dictyoptera) and Mantispidae (Hexapoda: Planipennia). ULRICH (1965), who compares the forelegs of *Mantis religiosa* (Linnaeus) (Mantodea) and *Mantispa styriaca* (Poda) (Mantispidae), finds a similar shape and function of the main parts of the legs and the prothorax, and similar constructional elements are used (spines, articulations as such). Distinct differences are present in the finer structures, e.g. in the details of the articulations or in the distribution of spines. Some points are of importance: (1) The peculiar leg morphology is not so different from an already complex common basic pattern, which is the plesiomorphic Neopteran leg. (2) Some of the elements having the same function are clearly non-homologous (claw-like tarsus of Mantispidae versus tibial claw of Mantodea), i.e. these elements do not fit into the pattern of similarities. (3) All similarities peculiar to these two taxa but absent from the plesiomorphic Neopteran leg are correlated with function. Hence, the pattern of similarities has originated from a common basic pattern, is not so comprehensive, and depends entirely on function. These circumstances render the apomorphic peculiarities easily explainable as homoplasies.

Comparing the proventriculi of *Carcinus* and *Ctenolepisma*, however, the situation is completely different: (1) The similar morphology of the two taxa is, if SIEWING's (1956) hypothesis is followed and homoplasy is assumed, far remote from the presumptive common starting point, which is a foregut without any cuticular elaborations. (2) All elements present in both species fit into the pattern of similarities, i.e. this pattern is very comprehensive. (3) Some elements are similar in details of their structure but not in their shape and certainly also not in their function. This last point is best demonstrated by the denticles **dp2/dp6** of *Ctenolepisma* and **at** of *Carcinus* (Figs. 1–4, 7, 8): **dp2/dp6** and **at** have some structural details in common (compare in chapter 4). In *Ctenolepisma*, when the proventriculus is constricted, the flanks of **dp2/dp6** are in occlusion with the neighboring flanks of **sp1** and **dp3/dp5**. The tubercles on the crest of **dp2/dp6** probably grind upon the lateral area **r** of sclerite **sp1** and upon that flank of denticle **dp3/dp5** facing **dp2/dp6**. Such a grinding action can hardly be expected from denticle **at** of *Carcinus*, whose shape is obviously not adapted to such a function and whose ventral flank is, as seen in a complete proventriculus, not able to reach sclerite **cpv** and to grind upon its lateral area. Also, the setal combs on the folds **m** and **o** would be damaged by such a grinding action. SCHAEFER (1970, p. 324) assumes, for *Cyclograpsus* and other Reptantia, that the "lateral accessory teeth" **at** "assist in preventing food escaping anteriorly". Be-

cause of these functional differences, the structural similarities between **dp2/dp6** and **at** and between some other elements cannot be explained by "Kanalisierung". It seems thus unlikely that the complex pattern of similarities described in chapter 4 has developed twice by pure homoplasy.

One could assume that there was, like in the forelegs of Mantodea/Mantispidae, a simpler basic pattern of cardiac/armarial morphology already present in the ground-plan of Mandibulata which then became, independently in Malacostraca and Dicondylia but in a very similar way, better adapted to the same function. (This would be a hypothesis intermediate between complete homoplasy and complete homology, see above.) This hypothesis, however, is still unlikely since in some elements it is not the shape and the function that are similar but the structural details. Also, the assumption of multiple secondary loss of this basic pattern would be inherent in this hypothesis.

7.3. The possibility of complete homology and multiple secondary reduction or loss

In Malacostraca, frequent secondary reduction of cardiac morphology has to be assumed – also in the frame of SIEWING's (1956) hypothesis on proventricular anagenesis (compare in chapter 5). In the various taxa affected, these reduction trends are often quite similar. Hence, the view that (1) the relatively simple (as compared to e.g. *Carcinus*) morphologies representing the most plesiomorphic condition in Hoplocarida and especially Phyllocarida and Syncarida are already the result of partial reduction and not close to the Malacostracan ground-plan, and that (2) the morphology of Reptantia, which may be the plesiomorphic condition of Eucarida + Peracarida + Pancarida, is close to this ground-plan does not seem completely impossible. Note that Hoplocarida have a peculiarly specialised proventriculus, and that for the Syncarida Anaspidacea reduction was also regarded as possible by SIEWING (1956).

In Odonata, the Corduliidae and Libellulidae, the subgroups whose nymphs resemble Lepismatidae and the Dicondylian ground-plan most closely in armarial morphology (KLASS 1998), are members of a rather subordinate odonatan clade (PFAU 1991). The derivations found in the other Odonata – mainly simplifications but also some positive developments such as the intercalation of subordinate plicae – are, though developed several times independently, often rather similar. Hence, the pattern of the distribution of character states over the taxa in Odonata is quite similar to that speculated above for Malacostraca. A still more extreme situation is also found in Dicondylia as a whole: In nearly all "orders" the ground-plan morphology of the armarium has been strongly modified, simplified, or lost.

In view of the frequent independent reductions and modifications that have certainly occurred, the assumption of complete homology and of multiple independent reduction in Crustacea and Tracheata does not seem too improbable.

7.4. Alternative explanations

There are some concepts that can be "applied" in the explanation of such problematical cases of similarity which are inconsistent with the "knowledge" on the phylogenetic tree. Homology of the similarities is assumed to various extents.

(1) Reactivation of previously lost features ("Reaktivierung aus dem Kryptotypus" according to SUDHAUS & REHFELD 1992): The cardiac/armarial morphology as described above was present in the ground-plan of Mandibulata, was lost, but reappeared in Decapoda and Dicondylia – due to a reactivation of its genetic background, which had been conserved. All similarities except the reactivation itself are homologies. Such a course is hardly probable since the morphology concerned is very complex and since this concept could hardly explain a gradual reappearance as it would be the case within Malacostraca (with a condition like in *Carcinus* representing the final step). Moreover, such an assumption would not be very parsimonious since reappearance would have to be assumed both within Malacostraca and Dicondylia.

(2) Underlying synapomorphy (SAETHER 1979): The preconditions in the genetic background to form the cardiac/armarial morphology were almost completed in the ground-plan of Mandibulata. The last few steps leading to the phenetical appearance of this morphology were performed independently in Decapoda and Dicondylia. The larger portion of each similarity is homologous. Such a procedure can be suspected if closely related taxa are concerned and if the structure completed independently is not very complex. Mainly the latter restriction renders this concept inappropriate for the explanation of the cardiac/armarial similarities.

(3) Parallel anagenesis due to similar selective pressure, starting from a similar basic pattern (a kind of "Kanalisierung"). Only the basic pattern is homologous. This possibility has already been discussed above and regarded as unlikely.

7.5. Conclusion

Complete homology is, in my opinion, the most probable assumption, but it is certainly better to regard the matter as still undecided. Further investigations are necessary.

8. FUTURE PROSPECTS AND APPROACHES TOWARDS A SOLUTION

An important future task to solve this homology problem would be to search in Malacostraca and Tracheata for similar morphologies as present in *Carcinus* and *Ctenolepisma* – focused on the elements and features discussed in chapter 4. In this search, not only taxa regarded as "primitive" but also taxa regarded as derived and also juvenile stages should be included. The situation in Odonata demonstrates this necessity. An additional wide-ranged comparison of the proventricular musculature and innervation, already rather advanced in Malacostraca (e.g. HAFFER 1965; SCHELOSKE 1976) but not in Dicondylia, could also be helpful. In this way we might move from the present incomplete picture to a comprehensive view of the anagenesis of the posterior foregut in Mandibulata. This may contribute to a better understanding of phylogeny, especially in Malacostraca.

Another possible way towards a solution of this homology question is to compare the underlying genetic information and developmental mechanisms. AVEROF & AKAM (1995b) suggest, in a more general discussion, to examine the pattern of gene expression in the various gut sections and to compare them in the various Arthropodan clades – hoping to find conserved molecular markers for specific gut regions. Such a comparison could be focused on the prospective cardiac/armarial area of Dicondylia and Malacostraca and on the un- or less-differentiated posterior foregut of other Crustacea and Tracheata. A comparison of the gene expression patterns could permit conclusions on the (non-)homology of cardia and armarium. Genes responsible for the formation of the peculiar cardiac/armarial pattern could be helpful in this way – but not genes of a more general responsibility such as the in- or evagination of the body surface or the sclerotisation of the cuticle (to form apodemes, denticles, or sclerites).

If this approach should be successful, and if the result should be the homology of the Malacostracan cardia and the Dicondylian armarium, some evidence on the phylogeny of Mandibulata may also come out of such an analysis: The distinction of primary absence and secondary loss is often difficult in the morphological approach. In the genetic approach, under favorable circumstances, such a distinction might be easier. The basic question would be whether the absence or simple state of foregut differentiation in the various respective Crustacea and Tracheata is, as compared to Decapoda and Dicondylia, due either to the same lacks in gene expression or to different lacks. Roughly speaking, the former would suggest primary absence in the respective taxa – with the lack-of-expression set representing the plesiomorphic condition of Mandibulata – whereas the latter would suggest secondary reduction in at least

most of these taxa – with the various lack-of-expression sets being different apomorphic conditions, but with one set possibly representing the plesiomorphic condition of Mandibulata. The presence of a complex cardiac/armarial morphology or of the respective gene expression pattern could then be used as a synapomorphy. This prospect, however, is certainly very optimistic.

The anagenesis of the cardia/armarium is an interesting topic for evolutionary biologists. If the similarities between Decapoda and Lepismatidae are homologies, i.e. if the respective structures belong to the ground-plan of Mandibulata, it would be interesting why so many taxa have independently simplified or lost the complex morphology of the cardia/armarium. If these similarities are not homologies, the cardiac/armarial morphology gives the opportunity for a case study on how extremely similar complex patterns can originate by pure homoplasy in rather closely related taxa such as Malacostraca and Dicondylia.

PATWARDHAN (1935e) demonstrates a correlation between cardiac and mandibular morphology: The better the mandibles are adapted to mastication, the less is the proventriculus, and the less is its structural differentiation. The findings of SCHAEFER (1970) and others indicate a correlation between cardiac morphology and diet: The finer the ingested food particles are, the less are the cardiac adaptations to mastication, the weaker are the cardiac sclerotisations, and the finer are the setae, spines, denticle tips, and other projecting structures. Such anagenetic correlations between armarial morphology, mandibular morphology, and the adaptation to certain food niches, however, are not obvious (or not yet found?) in e.g. Blattaria. Such correlations should certainly be considered in a comprehensive evolutionary reconstruction, but they may be of differing importance in different taxa.

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