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Rejection of the “Uniramia” Hypothesis and Implications of the Mandibulata Concept

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With 6 Figures

Abstract

The Uniramia hypothesis, widely used as a basis for discussions of the phylogeny of arthropods, is rejected on the basis of previously published morphological and physiological data. A number of important synapomorphies makes it highly probable that crustaceans and tracheates are sister-groups. Convincing evidence, as required by the strict logical phylogenetic systematics, does not exist for the Uniramia hypothesis. The mandible of the Tracheata is not homologous to the onychophoran jaw, but it is part of a complex mandibulate head. The Mandibulata are a monophyletic group with very specific characters such as the moulting gland, certain neurohormones, the segmental innervation of the pericardial organ, the structure of the ommatidia of the lateral eyes. Recent physiological literature is reviewed to compile data on homologies between crustaceans and tracheates. The Mandibulata concept implies that many crustacean-like fossils can not be classified as crustaceans or tracheates. The Mandibulata concept implies that many crustacean-like fossils can not be classified as crustaceans as long as synapomorphies of extant crustaceans are not discovered in the fossils. Species derived from the stem-lineage of the Mandibulata will in general morphology resemble crustaceans though the tracheates are derived from the same stemlineage.

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1. Introduction

Phylogenetic speculation on the evolution of arthropods exists in large numbers, but only few main ideas have found wide acceptance, some of which are absolutely incompatible. These are the ideas about monophyly versus polyphyly of arthropods, the derivation of tracheates from onychophoran-like ancestors or from a mandibulate ancestor, the derivation of crustaceans from trilobitomorpha¹⁾ or from a mandibulate ancestor. The concept of the parallel evolution of "Uniramia" and Schizoramia is not compatible with the division of arthropods into Protarthropoda and Euarthropoda; the sistergroup-relationship Crustacea/Chelicerata implies a different evolution of arthropods than in the case of the close relationship of Crustacea and Tracheata²⁾. These ideas have consequences for the interpretation of the similarities seen in insects and crustaceans, which could be analogies or homologies, and for the position of many fossils in the system of the Arthropoda, which could be either early representatives of the stem-lineage of the mandibulates, or of the crustaceans. Furthermore the definition of what a crustacean really is depends on the type of concept of arthropod evolution. Because these conflicts have not been resolved, current textbooks display a confusing lack of consensus about arthropod systematics. MEGLITSCH (1972) depicts "phylogenetic grass" with the branches Trilobita/Chelicerata, Crustacea, Tracheata, Onychophora, Tardigrada, but discussing a common ancestry of Crustacea and "Myriapoda", while CLARKE (1973) preferred to group 9 classes in 3 lines ("Uniramia", Trilobita/Merostomata/Arachnida, and Crustacea); FRETTER and GRAHAM (1976) present in their textbook polyphyletic arthropods; ALEXANDER (1979) divides arthropods into several classes without discussing their relationships (Trilobita, Onychophora, Merostomata, Arachnida, Crustacea, Insecta, Chilopoda, Diplopoda); RUSSELL-HUNTER (1979: 303) writes: "the old association of the Crustacea with the insects and myriapodous groups in the subphylum Mandibulata is almost certainly erroneous and should be discarded."; WEBB et al. (1979) classify the Trilobitomorpha, Chelicerata, Crustacea, and "Uniramia" as separate phyla; PEARSE et al. (1987) divide the phylum Arthropoda into the subphyla Crustacea, Chelicerata, and "Uniramia", while BRUSCA & BRUSCA (1990) additionally discern between the subphyla Cheliceriformes and Trilobitomorpha, excluding the Onychophora from the "Uniramia"; WILLMER (1990) discusses in detail the characters of the Arthropoda, but tends to accept MANTON's hypothesis.

¹⁾ The name "Trilobitomorpha" has a diffuse usage in literature. A strict definition is necessary to avoid confusions; a similar term is "Arachnomorpha" (= Trilobitomorpha + Chelicerata) (STÖRMER 1944); a monophyletic group "Arachnata" was defined by LAUTERBACH (1980: 195ff.), the Trilobitomorpha sensu BERGSTRÖM (1979) seem to comprise the same monophylum.

²⁾ The name "Antennata" will be more convenient than "Tracheata" the day marine stem-lineage Tracheata are identified.

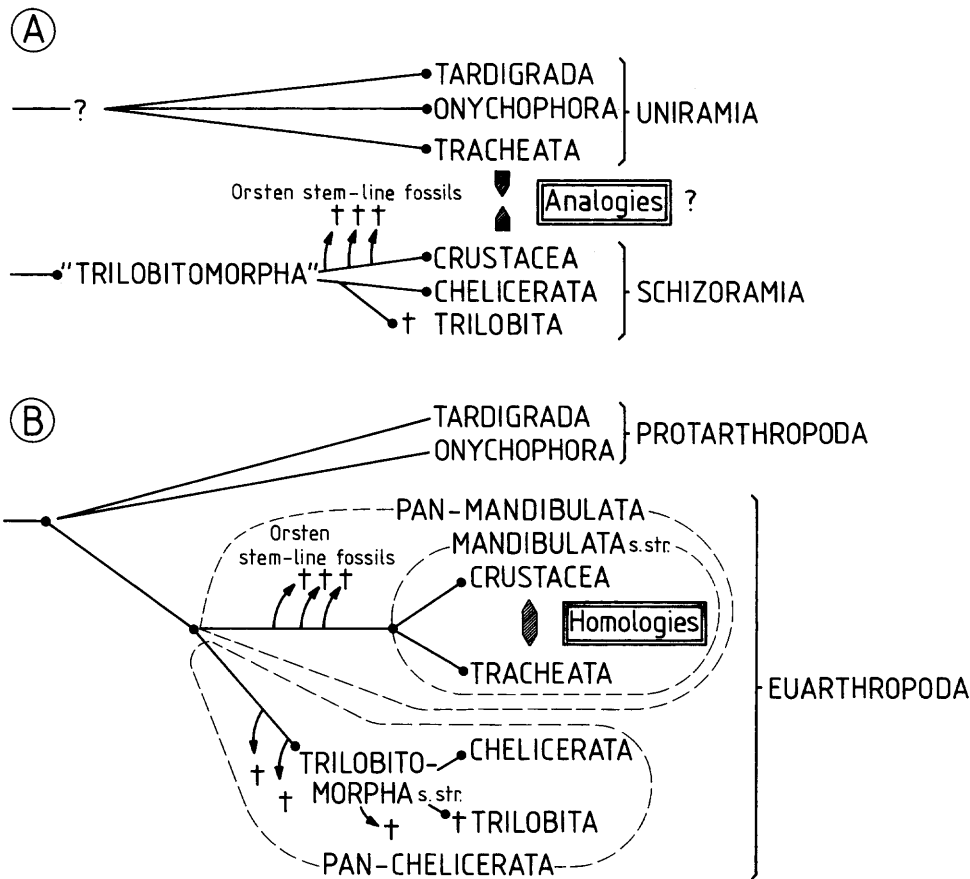


Fig. 1. Arthropod phylogeny according to the Uniramia hypothesis (A) and the Mandibulata hypothesis (B). Similarities between Tracheata and Crustacea are either analogies (A) or homologies (B). The same crustacean-like fossils can be either early crustaceans (A) or early pan-mandibulates (B). The names "Uniramia" and "Schizoramia" are superfluous in (B).

The "Uniramia" concept has been rejected by several authors, and a sistergroup relationship between Mandibulata and Chelicerata/Trilobitomorpha has been retained in several recent publications and textbooks (e.g. SHAROV 1966, KÄSTNER 1967, LAUTERBACH 1972a, 1980a, BOUDREAUX 1979a, b, WEYGOLDT 1979, CLOUDSLEY-THOMPSON 1988).

Arguments pro and contra have been repeated many times in literature (compare e.g. SHAROV 1966 with later publications; description of the historical background in HESSLER & NEWMAN 1975). The aim of the present paper is to review briefly previously published important arguments, and to present some more recent data that support the older Mandibulata concept (SNODGRASS, 1938) and which rarely are cited by taxonomists, data which are partly found in physiological and biochemical literature.

2. The "Uniramia" hypothesis

The concept "Uniramia" gained much of its prominence through the vigorous promotion of MANTON (e.g. 1964, 1973, 1977). This hypothesis in the version described by MANTON (e.g. 1977) implies several ideas: the taxon Uniramia consists of the Onychophora, Myriapoda and Hexapoda, which form a separate phylum within the Arthropoda, of terrestrial habit in extant species. Therefore similarities with crustaceans are only analogies (Fig. 1). According to MANTON diversification of the Uniramia must have taken place on land, from soft-bodied animals with lobopodial, unjointed limbs. A model for primitive ancestral uniramians are the extant Onychophora, which possibly are derived from soft-bodied marine ancestors.

For the "Uniramia" the following bauplan has been proposed (see e.g. WEBB et al. 1979): antenniform appendages on the first segment, whole-limb mandibles biting with the tip (not with coxal endites as in Crustacea), which evolved more than once (see e.g. MANTON 1977: 132), 2 or 3 (Hexapoda) tagmata and 3 pairs of mouthparts that evolved from the onychophoran bauplan, uniramous walking limbs on the thorax. Using this short characterization, which does not reflect MANTON's inclusion of the Onychophora, one could easily place the terrestrial Isopoda (Oniscidea) within the "Uniramia": they have only one pair of large antennae, 3 pairs of cephalic mouthparts, uniramous walking limbs, furthermore trachea-like respiratory organs (on the pleopods) and 3 tagmata (cephalothorax, pereon, and pleon).

First difficulties arise when the Onychophora are included in the taxon "Uniramia" (in the sense of MANTON 1973, 1977). The Onychophora are much more primitive in comparison with the Tracheata, possessing only a pair of jaws and a pair of oral papillae, but no further mouthparts, a thin cuticle, no suboesophageal ganglion, simple eye vesicles, unjointed legs, etc. A more restricted "Uniramia"-concept without the Onychophora (see BRUSCA & BRUSCA 1990) postulates the following synapomorphies for this taxon: second antenna reduced (absent), whole-limb mandibles, ectodermal Malpighian tubules, a tracheal respiratory system, and eventually secondarily acquired uniramous limbs (exopod reduced). This latter version is composed of characters of the Tracheata, the taxon "Uniramia" then simply being a junior synonym of the Tracheata and therefore superfluous.

Further differences between arthropod groups have been discussed in the literature (summary in WILLMER 1990): the supposed impossibility to design functional intermediates, the embryological differences (according to ANDERSON 1979), indications of multiple arthropodization in the fossil record, differences in hemoglobin structure of insects and crustaceans, differing intercellular junctions. Some "differences" are only apparent, due to the lack of data. The fat body for example was supposed to be absent in crustaceans and present in insects (discussed in SHAROV 1966: 57), but there are adipocytes in crustaceans forming a diffuse fat body, which plays an important role in vitellogenesis and for the accumulation of lipids for the ovaries (e.g. Isopoda: review in WÄGELE, 1992).

SCHRAM's defence of the "Uniramia" hypothesis (SCHRAM 1986) is mainly based

on MANTON's work. The variations seen in mouthparts or anterior limbs (Chelicerata) are thought to be "so different that there is little possibility that they are related in any way to each other and are therefore only analogous". This hypothesis of analogous development of the head appendages seems to be based only on the lack of attempts to discuss homologies and to reconstruct ground-patterns.

An especially eccentric hypothesis resulting from the Uniramia concept is Schram & Emerson's "arthropod pattern theory" (1991), which is based on the idea that biramous limbs are formed by basal fusion of uniramous appendages. Thus their dendrogram (Schram & Emerson 1991: fig. 12) shows a line leading to "schizoramian" taxa (Crustacea, Trilobita, Chelicerata), with uniramian taxa as early derivatives (Onychophora, Euthycarcinoides, Myriapoda/Insecta).

In view of the discussion of the polyphyly of arthropods, HESSLER and NEWMAN (1975), though accepting the Uniramia as separate line, presented important arguments to show that it is possible to derive crustaceans from trilobitomorphs. So at least for the marine euarthropods monophyly seemed to be more probable than an independent origin of trilobite-like arthropods and crustaceans. The main idea is acceptable also from the point of view of the friends of the Mandibulata concept, with the only difference that the "urcrustacean" represents elements of a groundpattern of the Mandibulata, a character set from which the crustacean groundpattern can be derived.

Important arguments against the interpretation of characters in the sense of the "Uniramia" hypothesis have been discussed already in several publications. WEYGOLDT (1979, 1980) explains that even within the Crustacea the blastoderm fate maps vary greatly, thus rejecting ANDERSON's arguments (1973, 1979) in favour of the polyphyly of arthropods. Much more specific and uniform are the anlagen of the head appendages that appear during early embryonic development. The fact that crustaceans still show a spiral cleavage and still retain an annelid-like anamorphic development, while the terrestrial arthropods had to reduce their larvae, does not discourage SCHRAM (1986: 21) from stating that the uniramians are more similar in their development to annelids than the Crustacea. Anyhow this sort of argumentation does not help: similarities often are plesiomorphies, as the above-mentioned characters of crustaceans (similarities between crustaceans and annelids), which can not be used as evidence for sistergroup-relationships within arthropods. While numerous homologies and synapomorphies can be shown for the Mandibulata (see below), the arguments in the published defences of the "Uniramia" hypothesis are based only on "differences" and "similarities".

Among others SHAROV (1966), KÄSTNER (1967), LAUTERBACH (1972a), WEYGOLDT (1979), BOUDREAUX (1979b), and SIEWING (1985) do not accept TIEGS and MANTON's (1958) and MANTON's (1964) view that the insect mandible is a whole-limb mandible. It is true that the jaw of tracheates never possesses a palp, not even in embryonic development, and that in some myriapods this appendage is segmented in contrast to the insect mandible. MANTON (1973) therefore believed that the mandible evolved at least twice within the tracheata. But, as BOUDREAUX (1979b) pointed out, the "segments" of the myriapod mandible are not cylindrical

podomeres. The bi- and tripartite mandible of myriapods is a unique feature. It could have been acquired in the stem-lineage of the Tracheata, a character still retained in some myriapods (Diplopoda, Symphyla) but reduced again in the Insecta and also within the "Myriapoda" (Pauropoda) (DOHLE 1980). It could also be a special myriapod feature, but it must not necessarily indicate an analogous evolution of mandibles.

The absence of a palp is no evidence for the whole-limb nature of the mandible. It is also reduced in several adult crustaceans (e.g. Oniscidea, Valvifera, Talitridae, some Caprellidae, some Tanaidacea, Branchiopoda, Cephalocarida), and often even does not appear during embryonic development (discussion in LAUTERBACH 1972a). Furthermore in all those crustaceans which only retain the endopod as part of the palp the mandible is a 'uniramous' appendage. The apalpalate mandible of an idoteid isopod is different in detail from an ectognathous insect mandible, but it has the same outline and a similar function, and it is derived from an appendage with a coxal endite. There is no reason why it should be impossible to derive an apalpalate insect mandible from a gnathobasic jaw. The postulated homology of mouthpart anatomy of crustaceans and tracheates (SNODGRASS 1950, 1951), and the similar construction of the "chewing chamber" (see below, 4.1.) are a strong evidence for a homology of all structural elements involved. It must also be remembered that endites of trunk appendages still may occur in the tracheata (Scutigermorpha; discussed in SHAROV 1966), and protopodal endites are also retained on the maxilla and labium of insects, which are more an euarthropod than an onychophoran character.

The position of the mandible, i.e. of the anteriormost specialized mouthpart in the third head somite of tracheates, which is **homologous to the position in crustaceans**, indicates that the second somite probably once also had an antenna and not a mouthpart; otherwise the appendage equivalent to the second antenna could have evolved into a mandible in tracheates (WEYGOLDT 1979), especially as the second antenna is a mouthpart during ontogeny of crustaceans. Also the fossil record of pan-mandibulate arthropods (see WALOSSEK & MÜLLER, 1990) shows that the second antenna had in early pan-mandibulates an endite rather similar to that of the appendage that later evolved to the mandible. These antennal endites are reduced in **adult** extant crustaceans, where the antenna has reached a preoral position (while during the ontogeny of insects and crustaceans the A2-anlagen first appear in the plesiomorphic poststomodaeal position: e.g. BRUCKMOSER 1965, SHAROV 1966, BITSCH 1973) (Fig. 6). Of course we know nothing about the function of the second antenna in the (unknown) marine crustacean-like representatives of the stem-lineage of the tracheata. But the reduction of the second antenna suggests that the mandibles were the more important mouthparts. Furthermore the "chewing chamber" between labrum and hypopharynx encloses the mandibles and has — as in adult crustaceans — no room for an additional antennal mouthpart. Therefore there is a reason allowing to speculate that the stem-lineage of the Tracheata might include animals with weak or no endites on the adult second antenna and with stronger mandibular endites.

BUTT (1960) is of the opinion that the insect mandible can not be derived from

the onychophoran jaw, because the latter arises from the segment which is homologous with the intercalary segment (premandibular segment of insects, segment of the crustacean second antenna, tritocerebral segment), while the insect mandible is an appendage of a more posterior segment. MANTON (1960) does not accept BUTT's interpretation of the head segmentation, but there remains the fact that the onychophoran jaw is the second head appendage, while the second head appendage of tracheates (the appendage of the tritocerebral segment) is reduced during ontogeny (e.g. BITSCH 1973; see also below, 4.1).

Another argument in favour of the "Uniramia" hypothesis is the presence of differences in the structure of the ommatidia of the compound eyes (SCHRAM 1986). This problem is discussed below (paragraph 4.3). Again only differences are seen, the homologies not. Of course major differences exist between crustaceans and insects. But only to seek for differences does not help in a phylogenetic analysis. The crucial question is whether there are homologies, and if some of these could be synapomorphies.

The absence of an exopod in the "Uniramia" is not a unique character. It is an adaptation of predominantly walking arthropods useful for terrestrial life, where an exopod can not be used to produce water currents for swimming, feeding or respiration. Among the Pan-chelicerata and also among crustaceans (Brachyura, Amphipoda, Isopoda) those groups that have amphibic or terrestrial representatives have also uniramous legs (which are a preadaptation acquired by their marine ancestors). Also it must be remembered that some tracheates have possibly vestiges of exopods, the "coxal" styli.

To distinguish the uniramian terrestrial line from the marine arthropod line with the supposed sistergroup relationship Biantennata (= Crustacea/Arachnomorpha), BERGSTRÖM (1976, 1979, 1980) introduced the term *Schizoramia* for the marine line (Fig. 1 A). Indeed most trilobitomorphs, Crustacea and crustacean-like fossil arthropods have limbs with exopods and endopods, while the terrestrial line has uniramous legs. But, if we reject the "Uniramia" hypothesis, the Tracheata can be included within the Mandibulata (see below) and therefore the *Schizoramia* are identical with the Euarthropoda.

3. The Mandibulata concept

The basis sine qua non for the Mandibulata concept is the assumption of the monophyly of the euarthropods. Usually the arguments presented to prove the monophyly of arthropods are in reality characters of the Euarthropoda.

The monophyly of euarthropods is widely accepted, there are too many characters that characterize the group and that are homologies and often good autapomorphies. Several of these features are correlated with each other (e.g. articular membranes/musculature). These are discussed in most textbooks and in other publications (e.g. MEGLITSCH 1972, LAUTERBACH 1972a, b, RUSSELL-HUNTER 1979, BOUDREAUX 1979a, b, WEYGOLDT 1979, HOFFMANN & PORCHET 1984, WILLMER 1990). Though several of these characters need a closer examination or precise definition, the following list gives an idea of the wealth of data used to

characterize euarthropods in published literature: the presence of lateral compound eyes, of frontal eyes, the protocerebral innervation of these eyes; the presence of a 'labrum' (originally only a hypostome), possibly derived from a preantennular segment (?); a cephalic shield; a first antenna, always in the same somite, always innervated by the deutocerebrum; a head composed of acron and at least 4 appendage-bearing segments (probably not correct: see paragraph 4.1); the arthropodium; originally a midventral food transport (not seen in extant tracheates); a cuticle composed mainly of protein and chitin, sclerotized through tanning of protein; articular membranes between metameric segments; intersegmental tendon-systems; metameric dorsal and ventral muscles; tendon cells with tonofilaments penetrating the cuticle; a modification of the annelid-like body wall muscles, suppression of the circular muscles; moulting of the cuticle and ecdysteroids as moulting hormones; mechano- and chemosensory ciliate sensilla within cuticular 'hairs'; a chitinous stomodaeum (with a stomach) and proctodaeum; a circulatory system with an ostiate heart in a pericardium, and hemocoel lacunae; modified nephridia with an endsac; a supraesophageal brain with an ocular protocerebrum, an antennular deutocerebrum and a tritocerebrum connected with the ventral nerve chain; a stomatogastric nervous system with a frontal ganglion (stomodaeal bridge in chelicerates) and a nervus recurrens; glutamate as one of the neurotransmitters; no motile cilia on the epidermis (sensory cilia are present); larvae without ciliary locomotion. It might be possible that lateral tergal folds also belong to this set of characters. According to WEYGOLDT (1979) the embryological data do not contradict the view that the Euarthropoda are monophyletic, despite all the differences in the details of individual ontogeny.

If the Euarthropoda have so many apomorphic characters in common, which do not occur anywhere else in the animal kingdom, monophyly is highly probable. Therefore it is possible to search for further monophyla **within** the Euarthropoda. In order to verify the Mandibulata concept in the sense of SNODGRASS (1938, 1950, 1951), we must prove that the Crustacea and Tracheata share important synapomorphies, which are absent in other arthropod groups (see below). Important synapomorphies are characters of very specific quality, which with high probability did not evolve more than once. A combination of many such synapomorphies that occur together increases considerably the probability of monophyly. This seems to be the case for the Mandibulata.

Remarks on the term "panmonophylum": LAUTERBACH (1989) introduced the term "panmonophylum", complementing the Henningian terminology. The term "monophylum" has been used in literature for different portions of a phylogenetic system: the Crustacea or the Tracheata are those arthropods that can be derived from a groundpattern which embodies the characters of the hypothetical urcrustacean (or the urtracheate), i.e. the last common ancestor of the crown group, which already has all constitutive characters of the Crustacea (or of the Tracheata). But a monophylum can also be the complete line that emerges from the point where it is separated from the sister-group (see Fig. 1B). In this sense all stem-lineage crustaceans would also belong to the monophylum, even if they do not have all the characters of the groundpattern. LAUTERBACH prefers to distinguish between the

panmonophylum, which includes the stem-lineage, and the monophylum s.str., which is the crown group with its last common ancestor. This distinction proves to be very useful for the following discussions (see also WALOSSEK & MÜLLER, 1990). The stem-lineage Mandibulata do not have all the characters of the crown group, for example a specialization of the mandible as the anteriormost mouthpart of the adult; nevertheless this line is the sister-group of the trilobite/chelicerate line (Arachnata³) = Arachnomorpha = Pan-chelicerata) (see below, paragraph 5.) and a monophyletic group, which can be named "Pan-mandibulata" (= stem-line and Mandibulata s.str.). LAUTERBACH proposes to introduce these names as **technical terms**, not as taxonomic names, as in several cases the taxonomic names might already exist.

4. Some homologies within the Mandibulata

Plesiomorphic homologies within the Mandibulata, which probably are inherited from the euarthropod groundpattern, indicate that the Tracheata can not be derived from an onychophoran groundpattern. Synapomorphic homologies are evidence in favour of the monophyly of the Mandibulata. Both type of characters are mentioned in the following paragraphs.

Typical mandibulate characters used as synapomorphies of Crustacea and Tracheata in textbooks (e.g. BRUSCA & BRUSCA 1990) are the structure of the ommatidia in the lateral compound eyes, the tripartite brain (which might be a plesiomorphy: see 4.4), the presence, position and function of mandibles and maxillae. These characters have been questioned by the friends of the "Uniramia" hypothesis (e.g. SCHRAM 1986), but there are many more homologous characters than these 'classical' ones (Fig. 5). Of these the morphological characters can be studied in well-preserved fossils, but the physiological, biochemical, and most of the anatomical characters are homologies and synapomorphies seen only in extant mandibulates. Some of these must have evolved already in the stem-lineage of the Mandibulata, but we can not state whether such characters are autapomorphies of the Pan-mandibulata or only of the crown group.

4.1. Head capsule, mouthparts and antennae

The Mandibulata concept was first based on the similar arrangement of head appendages (see e.g. SHAROV 1966, MEGLITSCH 1972): these arthropods all have a preoral antennule (antenna 1), a second antenna without endites in par- or preoral position in the **adult** (not necessarily in crustacean larvae) which can be reduced during ontogeny; a mandible specialized as the first mouthpart on the third

³) LAUTERBACH (1980) introduced the name "Arachnata" to avoid the names "Trilobitomorpha" and "Arachnomorpha" because the latter have been used for polyphyletic groupings, including some Burgess-Shale arthropods of unknown affinities. If one excludes all fossils that do not show the derived characters of the Trilobitomorpha sensu BERGSTRÖM (1976, 1979) all these names may become synonyms. "Pan-chelicerata" is a more neutral term.

metameric head somite, embedded between labrum and hypopharynx, 2 further head appendages, of which the first one is differentiated into a maxilla (maxillule).

The head capsule, of at least 4 appendage-bearing somites (WALOSSEK & MÜLLER, 1990), does not occur outside the Euarthropoda and has been considered to be an autapomorphy of the Euarthropoda (LAUTERBACH 1972b, 1980a). As some fossil euarthropods have (according to the reconstructions!) a head with probably only an antennular segment and no further appendages (*Sidneyia*: BRUTON 1981), this concept of the euarthropod head is questionable. Nevertheless there is a typical mandibulate head construction, which, together with the differentiation of the head appendages, is an autapomorphy of the Mandibulata s.str. (see below).

The Chelicerata have several thoracic segments fused to the original euarthropod head, the plesiomorphic condition can not be seen in extant forms. But the Trilobita had a more primitive tagmatization, originally with maximally 5 somites plus acron (compare LAUTERBACH 1972b, 1980a, CISNE 1975, 1981, WHITTINGTON 1975, WEYGOLDT 1979: preantennal (?), antennal segment, 3 pairs of postantennal appendages). The prosoma evolved in the stem-lineage of the Chelicerata. In comparison with trilobites the head capsule was not enlarged in the stem-lineage of the Mandibulata, with the exception of an addition of the segment corresponding to the second maxilla, which possibly happened more than once (WALOSSEK & MÜLLER 1990). This head construction with 5 pairs of appendages (2 pairs of antennal appendages and 3 pairs of mouthparts) is present in both, crustaceans and tracheates.

As already mentioned the second antenna is retained in crustaceans, but reduced in tracheates. Vestiges of the anlagen of the second antenna are seen during the embryonic development of some insects (e.g. SHAROV 1953, BRUCKMOSER 1965) (Fig. 6). The ontogeny of the second antenna in larval stages of crustaceans clearly reflects the history of the evolution of this appendage in the stem-lineage of the Mandibulata (LAUTERBACH 1988): it moves forward and reduces the functional endites.

The homology of the mandible in tracheates and crustaceans is based on the same position, basic structure and function. This pair of mouthparts is embedded between the upper lip (labrum) and the hypopharynx (see e.g. SNODGRASS 1951), thus forming a "chewing chamber" laterally closed by the mandibular body, caudally by the hypopharynx, which usually has a medial cleft to allow food to be pushed through it by the maxillules. Such a "chewing chamber" does not exist in trilobites (e.g. CISNE 1975, 1981) or in *Limulus* (e.g. MANTON 1977). The mandible movements are coordinated with those of the 2 pairs of maxillae.

Details in the morphology of mandibles vary (e.g. SNODGRASS 1951), but in any case the mandible is the anteriormost of the mouthparts of the adult, always situated on the third appendage-bearing head somite, with a strong protopodal endite used for food manipulation (WEYGOLDT 1979). To derive the tracheates from the onychophorans SCHRAM (1986: 26) assumes that in onychophorans the jaw is homologous to the tracheate mandible. But even MANTON did not accept such a homology (1949: 557; 1973: 125, 1977: 493), which is not supported by her own embryological studies: the jaws of the Onychophora develop in MANTON's opinion

from the second segment, the jaws of the Tracheata (her Dignatha + Trignatha) from the fourth segment (see also e.g. SHAROV 1966: 171). This opinion is also shared by ANDERSON (1973: p. 120ff., 460).

The first maxilla is usually a specialized mouthpart in mandibulates, though in some crustaceans not much different in its basic structure from more posterior appendages, as in Mystacocarida (similarity with maxilla 2), which in this respect resemble the Cambrian Skaracarida, or in Cephalocarida, where it is small but biramous, with a 4-jointed endopod. The variations in the structure of this appendage seen within the Crustacea and also when comparing crustaceans and insects are a product of the separate differentiation of an originally gnathobasic, schizoramous cephalic appendage, as present in the stem-lineage mandibulates.

The second maxillae originally resemble closely the thoracic appendages (as in extant Cephalocarida) and evolve several times to specialized mouthparts. Nevertheless they always belong to the mandibulate head. The corresponding segment is part of the head capsule and the ganglion is part of the suboesophageal ganglionic chain, which in insects is more fused than in crustaceans. The reduction of these appendages in some Myriapoda (Diplopoda + Pauropoda: TIEGS 1947) is a secondary phenomenon (DOHLE 1980), the corresponding segment is visible at least in early embryonic stages. Maxillae can also be reduced in crustaceans (as in parasitic isopods).

Based on a comparison of plesiomorphies found within extant Mandibulata LAUTERBACH (1980a) reconstructed a **groundpattern** of this taxon. The head of this hypothetical animals bears the first antenna, a biramous second antenna without endites in the adult, in paroral position, the mandibles, and 2 pairs of maxillae, which do not differ essentially from thoracic appendages. Some years earlier HESSLER and NEWMAN (1975) came to similar results, reconstructing the urcrustacean after recognition of the primitiveness of the Cephalocarida. LAUTERBACH's hypothetical **representative of the mandibulate stem-lineage** is similar, but the second antenna is a mouthpart in paroral position and still possesses an endite, which is comparable in form and function with that of the following appendage (later the mandible). WALOSSEK & MÜLLER (1990) were able to reconstruct in great detail the changes that lead from a trilobite-like spinose protopod to the crustacean-like endites of the second and third postantennular limbs. The discovery of the Orsten stem-lineage mandibulates (WALOSSEK & MÜLLER 1990, named therein stem-lineage crustaceans) fully confirms LAUTERBACH's hypothesis, with the exception that the "epipods", which are present in extant (originally microphagous) cephalocarids, branchiopods, malacostracans and in LAUTERBACH's mandibulate groundpattern, are absent in the Cambrian stem-lineage mandibulates and in most extant crustaceans.

So despite all differences in the position of mandibular joints and biting planes, in the type of movements and the position of the mandibular muscles, which occur in different variations (biting, stinging, sucking mouthparts . . .) even within the Crustacea or within the Tracheata, there remains a complex synapomorphy for the Mandibulata s.str., which is not present in any other arthropod: the first pair of postantennular appendages (antenna 2), at first during ontogeny in par- or

poststomodaeal position (also in insects!), is displaced anteriorly by the second pair, which in the adult is the anteriormost mouthpart (mandible), characterized by a very strong biting endite, innervated by the first ganglion of the suboesophageal mass, and forming the lateral parts of the "chewing chamber".

4.2. Frontal eyes

All euarthropods must have had primarily lateral compound eyes and small frontal eyes, if we do not accept polyphyly of these sense organs. From the various arrangements of frontal eyes found in chelicerates, crustaceans, and tracheates, a common groundplan can be reconstructed (see PAULUS 1979, LAUTERBACH 1983), which consists of 8 ommatidia arranged in a dorsal, a medial, and a ventral group. This number is still present for example in leptostracans. A symplesiomorphic character of the Mandibulata (see PAULUS 1979, WEYGOLDT 1979, LAUTERBACH 1983) is that the median complex is composed of maximally 4 ommatidia (of which in many crustaceans and in insects usually only 3 remain), which in crustaceans form a compact naupliar eye. An analogous evolution of frontal eyes within mandibulates, suspected due to some variation in the ultrastructure (ELOFSSON, pers. comm.), seems to be very improbable, since the median eyes are not an isolated system but always correlated in euarthropods with the protocerebral innervation, the occurrence of lateral compound eyes, of protocerebral neurohemal organs, etc. (see following paragraphs). The frontal eyes therefore must be part of the euarthropod groundpattern and a plesiomorphy within the Mandibulata.

4.3. Lateral eyes

Of course the "Uniramia" hypothesis (polyphyly of mandibulates) requires parallel evolution of the compound eye, a sense organ of very specific structure that occurs in this specific form nowhere else (!) outside the Arthropoda. The Mandibulata concept does not require parallel evolution of this structure. On the contrary, the fine structure of the lateral eyes supplies further synapomorphies as evidences for the monophyly of the Mandibulata. The arguments have been dicussed already by PAULUS (1979) and must not be repeated in great detail here. All euarthropods primarily possess compound eyes with a faceted cuticle, that externally shows the number of ommatidia. Basic elements of the euarthropod eye are transparent cuticular lenses, hypodermal cells (corneagenous cells) secreting the lense and situated beneath the lense, each lense belonging to a single ommatidium; the sensory cells are arranged in groups of 4 to 20, each group forming a central rhabdom. In *Limulus* (FAHRENBACH 1968) and in trilobites the dioptric apparatus consists of basally elongated cuticular cones. The trilobite eye is composed of ommatidia with an external thin, usually hexagonal corneal layer of radially orientated calcite and beneath it lenses of a single calcite crystal, probably secreted by hypodermal cells underlying the visual surface (HARRINGTON 1959, CLARKSSON 1975). In *Limulus* the number of retinular cells and of corneagenous cells (about 100: FAHRENBACH 1968) is high, probably a primitive character. Synapomorphies of

the Mandibulata are the reduced number of reticular cells (usually 8) and of corneagenous cells (2), the acquisition of a crystalline cone formed by 4 cone cells (2 may be reduced). In some mandibulates conditions that resemble somewhat the *Limulus*-eye evolved secondarily: some beetles and also some myriapods have an enlarged cornea that replaces the crystalline cone (PAULUS 1979); a progressive reduction of the crystalline cone to a condition where only the cornea remains is well documented for collembolans (PAULUS 1979: 328); a larger number of reticular cells is known from *Scutigera* (NILSSON 1989). These examples clearly are single cases of specializations, not elements of the groundpattern of the tracheate eye.

There is always an outer lamina ganglionaris and an external medulla. In mandibulates further neuropiles evolve, even within the Crustacea (ELOFSSON & DAHL 1970).

Naturally the ommatidial groundpattern evolved into a large number of varieties. In a small group such as the undoubtedly monophyletic Isopoda, for example, the ommatidia can have 6 to 8 reticular cells, the rhabdom can be fused continuous or fused layered or open, the lens can be biconvex, externally flat, or absent, there can be 2 to 4 main cone cells, a variety of cone morphologies, the number and arrangement of pigment cell varies, reflecting pigment cells can be present or absent, the retinula cell nuclei can be located above or below the thick basement membrane of the eye (most data from publications of H. L. NILSSON, summarized in WÄGELE, 1992). These differences can never indicate a parallel evolution of the faceted eye starting from an annelid visual system; they are variations of the eye of the Mandibulata. Though apposition and superposition eyes have a completely different function, it is not impossible to understand how the superposition type evolved from the original apposition eye (NILSSON 1989).

4.4. Central nervous system

To find homologies within the Mandibulata a comparison with the chelicerates is necessary. A characteristic feature of the Arachnida is the absence of a head capsule and instead the presence of the prosoma with fused ganglia from the anterior somites. Also abdominal nerves arise from the suboesophageal mass (BABU 1965), an indication of the high degree of fusion between ventral ganglia. In scorpions the syncerebrum contains 5 large neuropile areas, the first one corresponding to the brain. The suboesophageal ganglion of scorpions consists of only 9 neuromeres, the first 5 corresponding to prosomatic metameres (HABIBULLA 1970). Scorpions still have 7 well developed abdominal ganglia. The poor development of optic masses of arachnids (BABU 1965), correlated with the absence of lateral compound eyes, is another specialization in comparison with insects, crustaceans and *Limulus*. Nevertheless it seems to be established that the brain consists originally of the 3 parts also known in the Mandibulata, of which the deutocerebrum, the part corresponding to the lost antenna, is reduced. The cheliceral ganglia form the tritocerebrum (the appendages of the corresponding segment are without doubt homologous with the crustacean second antenna; e.g.

CHAUDONNERET 1987). The first segmental nerves in the suboesophageal mass innervate the pedipalps and are homologous to the mandibular nerve.

Thus the anteriormost part of the central nervous system of extant euarthropods has the same groundpattern in all groups, with at least 2 appendage-innervating ganglia (deuto-, tritocerebrum) united with the protocerebrum to form a brain, the tritocerebrum being connected with the ventral nerve chain. According to CHAUDONNERET (1987) the presence of 2 neuropiles in the area of the tritocerebrum indicates the existence of a fourth brain neuromere (the "tetrocerebrum"), a character seen in crustaceans and tracheates and possibly present in the euarthropod groundpattern (CHAUDONNERET 1987). Another common character is the presence of a *nervus recurrens*, which innervates the stomatogastric ganglion.

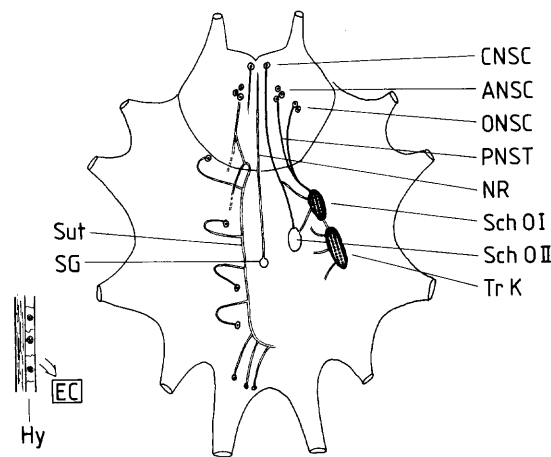
Though the second antenna is reduced during the ontogeny of the Tracheata and the tritocerebrum of the adults is therefore rather small, this part of the brain together with the tritocerebral commissures is nevertheless present in myriapods and insects (e.g. CHAUDONNERET 1987, JOLY & DESCAMPS 1987). This basic structure of the brain is a plesiomorphic homology of the mandibulate taxa. To find autapomorphies for the mandibulates is difficult due to the derived (fused) condition of the central nervous system of the chelicerates, where the plesiomorphic state of a specific character must be discovered. However, if details of brain architecture are compared many similarities between insects and crustaceans and profound differences between mandibulates and arachnids can be discovered (see BREIDBACH 1982).

The suboesophageal ganglionic mass retains in some Crustacea and in Chilopoda separated mouthpart ganglia, while in higher evolved taxa these ganglia are often fused. It seems that the suboesophageal ganglion complex is a higher motor centre in insects (ALTMAN & KIEN 1987), but a comparison of details of the integration of functions in different arthropod taxa does not exist.

Also the ventral nerve chain has peculiar characters that occur both in Crustacea and Tracheata, such as the presence of the segmental innervation of the lateral heart nerves (pericardial organs of crustaceans) and the segmental arrangement of the crustacean cardioactive peptide (CCAP) — producing pericarya (identified with immunotechniques) with their ipsilaterally projecting axons (DIRCKSEN & KELLER 1988, DIRCKSEN et al., 1991). The latter seems to be an autapomorphy of the Mandibulata.

4.5. Protocerebral neuroendocrine system

Early descriptions of the cerebral glands produced a confusing variety of terms, which often had been used for completely different organs. An example are the "frontal organs", which are partly frontal eyes, neurosecretory cells, or Bellonci's organ (see discussion in DAHL 1965). This difficulty was and still is a major obstacle for the discovery of homologies. But new techniques, especially the immunocytochemistry and the use of very specific monoclonal antibodies allow the identification homologous organs and even single homologous cells within the nervous system. These new results support the widespread assumption, that the X-organ-sinus gland system in Crustacea and the *pars intercerebralis-corpora cardiaca-*



CHELICERATA

Fig. 2. Simplified scheme of the anterior central nervous system of the terrestrial Chelicerata with important neurohemal organs (modified and combined after BABU 1973, JUBERTHIE 1983). ANSC – aboral (protocerebral) neurosecretory cells; CNSC – cheliceral neurosecretory cells; EC – ecdysteroids; Hy – hypodermis; NR – nervus recurrens; ONSC – oral neurosecretory cells; PNST – protocerebral neurosecretory tract; Sch O I, II – Schneider's Organ I, II; SG – suprapharyngeal ganglion; Sut – subesophageal neurosecretory tract; TrK – Tropfenkomplex.

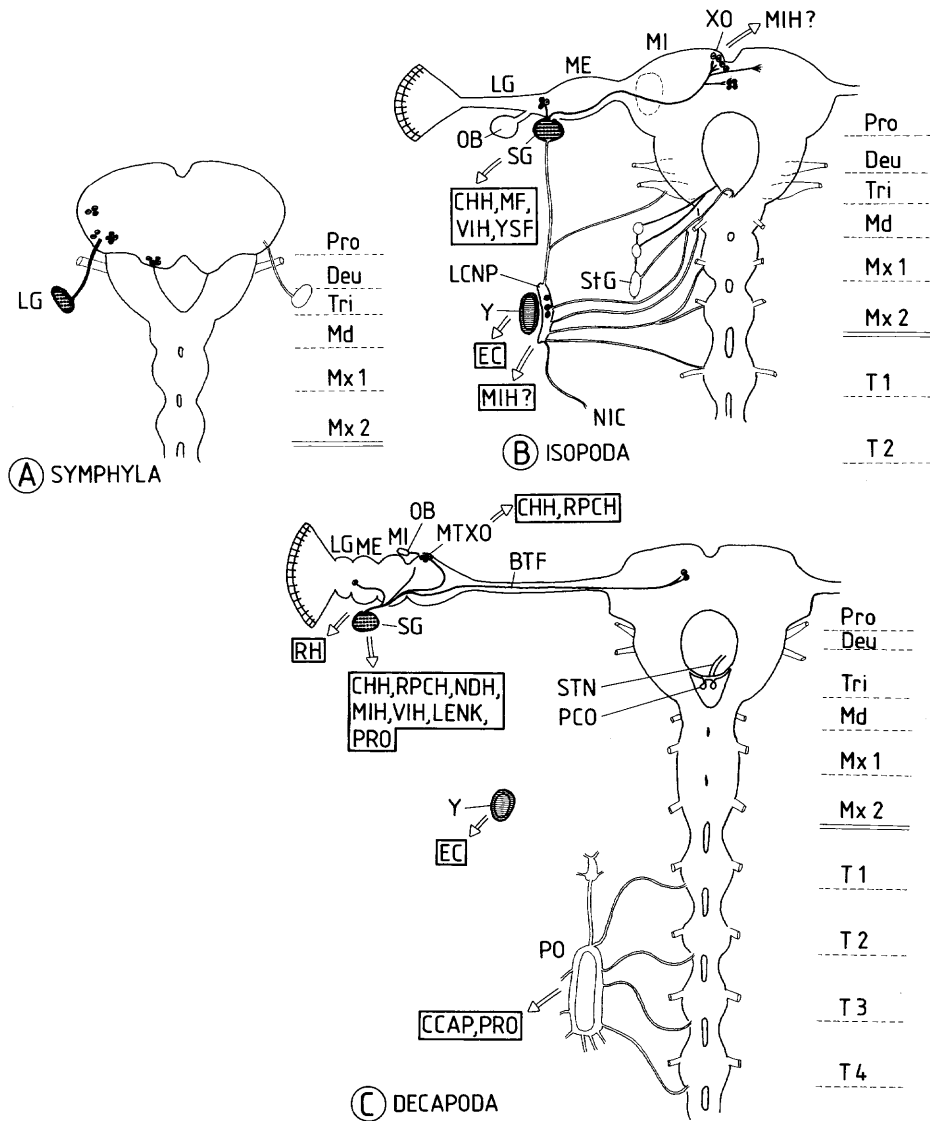
corpora allata system in Insecta are derived from the same homologous ground-pattern.

The presence of a neuroendocrine system consisting of neurosecretory cells (NSC) in the dorsomedial and mediolateral area of the protocerebrum, which are connected by axon bundles with a pair of neurohemal organs situated caudal to the protocerebrum, often near the optic nerve, is a character common to all extant Euarthropoda (CHAIGNEAU 1983, GUPTA 1983). This system evolved in various ways but shows some special features common only to the Mandibulata.

In chelicerates (Fig. 2) this system consists essentially of protocerebral and tritocerebral neuroendocrine cells, which are connected with the paired neurohemal Schneider's Organ I and II respectively. The protocerebral neurosecretory cells of Scorpiones and Opiliones are arranged in three groups (dorsomedial, lateral and near the optic lobes) as in insects (HABIBULLA 1970). Some confusing aspects have their roots in the variations and reductions that occur and in the presence of further neurohemal areas (such as the paraganglionic plates, and glands as the tick 'retrocerebral organ' which is associated with the periganglionic sheath (BINNINGTON 1983)). The system homologue with the sinus gland or the corpora cardiaca/corpora allata (CC/CA)-complex can only be the protocerebral Schneider's Organ I with its neurohemal area, that is sometimes distinct ("Tropfenkomplex": e.g. BABU 1973; BANARIC et al. 1980, JUBERTHIE 1983) from a glandular region. The protocerebral paraganglionic plates of some arachnid taxa are homologous with Schneider's Organ I (Opilionida, Solifugae, Ricinuclei, Pseudoscorpionida), but in

other groups these plates are a different neurohemal system (review in JUBERTHIE 1983). The protocerebral NSCs of *Limulus polyphemus* are also located in the association area of the lateral and frontal eyes. In their position and number they resemble similar cells of other chelicerates (FAHRENBACH 1973). Interestingly the brain of *Limulus* produces as in crustaceans a chromatotropic factor and a hyperglycemic factor (DORES & HERMAN 1980), but the chemical nature of these is not known.

In all myriapods (Fig. 3A, 4A) the cephalic or cerebral glands (retrocerebral glands, Gabe's organ) are innervated by neurosecretory cells of the protocerebral frontal lobes. These glands exhibit a cyclic secretory activity correlated with the moulting cycle, inhibit moulting and stimulate oogenesis (JOLY 1970, SEIFERT &



EL-HIFNARI 1971, SEIFERT & ROSENBERG 1974). Also in myriapods there is a large variety of names and of patterns in the construction of the protocerebral neurohemal system (SAHLI 1977, JUBERTHIE-JUPEAU 1983). The central neurohemal organ is the cephalic gland of the Symphyla and Chilopoda, named Gabe's Organ (sometimes also simply "cerebral gland": SEIFERT 1971) in the Diplopoda, innervated by a protocerebral (Gabe's) nerve. It can be purely neurohemal, but the glands in some species (Chilopoda) also contain intrinsic secretory cells (as in the chelicerate Schneider's Organ I) (e.g. SEIFERT & EL-HIFNARI 1971, 1972), otherwise the pericarya belong to glial cells, as in the Symphyla (JUBERTHIE-JUPEAU & JUBERTHIE 1973). In some Diplopoda there is a differentiation of additional organs, such as the parabasal bodies, which are also connected to Gabe's nerve. The more primitive types are comparable with the CC-like neurohemal organs of some apterygote insects (JUBERTHIE-JUPEAU 1983). SEIFERT (1971) reports that in the cephalic gland of *Craspedosoma rawlinsii* also tritocerebral secretions have been found (see Schneider's Organ II of chelicerates).

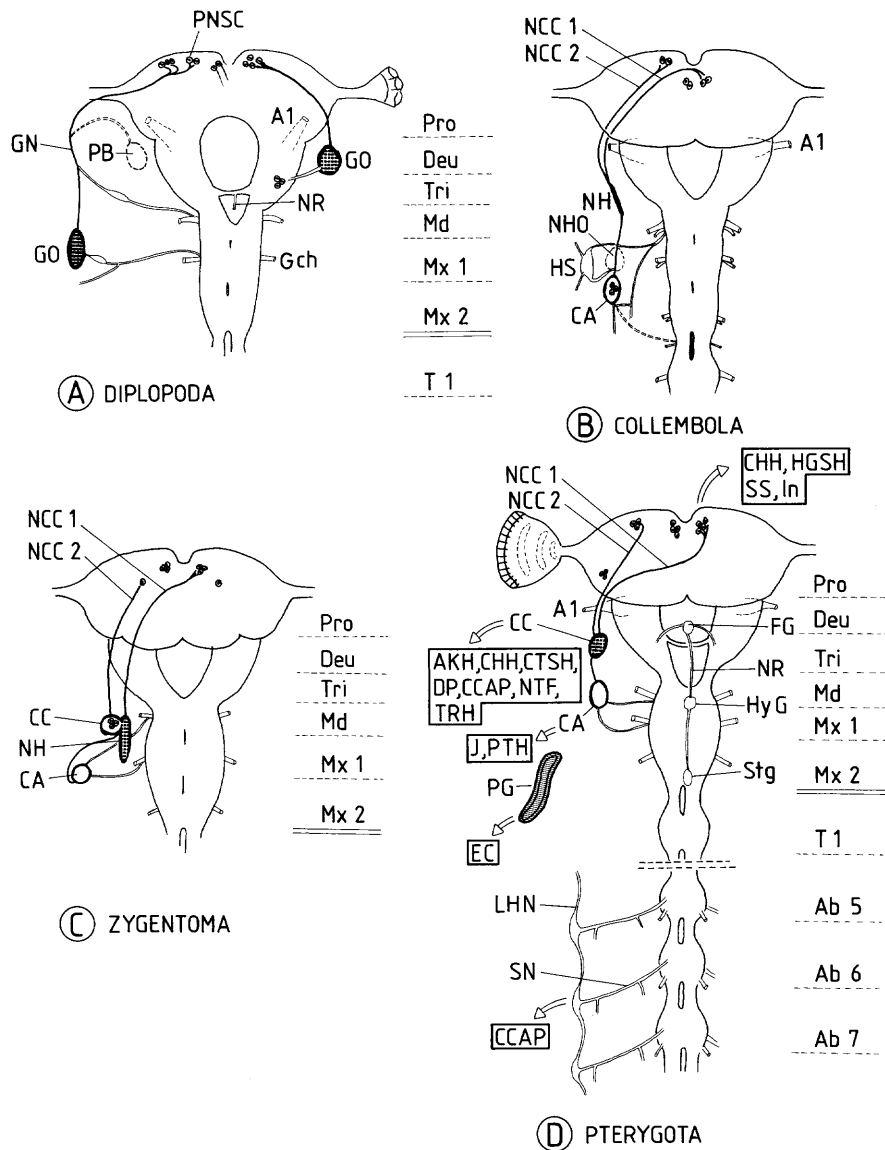
Some aspects of the evolution of the well known insect corpora cardiaca/corpora allata (CC/CA) system can be reconstructed. The myriapod Gabe's organ is split into 2 portions of different functions (Figs. 4B–D). The corpora allata (CA) obviously are a new acquisition of the Insecta (BÜCKMANN 1989). They are still absent in myriapods. The neurohemal corpora cardiaca are reduced and rudimentary in some entognathous insects. The neurohemal area is united with the CA in many Collembola, separated in Diplura and Protura (CASSAGNAU & JUBERTHIE 1983). In 'Thysanura' and Pterygota the CC is well developed and associated with the aorta. Pterygotes also possess within the CC intrinsic neurosecretory cells (review in GUPTA 1983). The CC/CA system originally consists of a pair of separate CC/CA units, which in the course of pterygote evolution fuse medially.

Among crustaceans most studies have been carried out in decapods (Fig. 3C), which have a derived protocerebral structure: part of the protocerebrum is found within the eye-stalks, together with the organ of Bellonci, the main neurosecretory

Fig. 3. Simplified schemes of the anterior nervous system of some Mandibulata with endocrine and neurohemal organs. A – Symphyla (modified after JUBERTHIE-JUPEAU 1983). B – Isopoda (combined after JUHAULT & KOIGAN 1975, CHATAIGNER et al. 1978, DEMASSIEUX 1979, MARTIN et al. 1983, CHIANG & STEEL 1984, 1985b). C – Decapoda (combined after HIGHNAM & HILL 1969, CHAIGNEAU 1981, 1983, ANDREW 1983, DIRCKSEN & KELLER 1988).

BTF – brain tract fibers; CCAP – crustacean cardioactive hormone; CG – cephalic gland; CHH – crustacean hyperglycemic hormone; Deu – deutocerebrum; EC – ecdysteroids; LCNP – lateral cephalic nerve plexus; LENK – leukenkephalin; LG – lamina ganglionaris; ME – medulla externa; MI – medulla interna; MIH – moult inhibiting hormone; MTXO – medulla terminalis X-organ; Mx1, 2 – maxilla 1, 2; NDH – neurodepressing hormone; NIC – nerve from ipsilateral cardiac nerve; OB – organ of Bellonci; PCO – postcommisural organs; PO – pericardial organs; PRO – proctolin; Pro – protocerebrum; RH – retinal pigment hormones; RPCH – red pigment concentrating hormone; SG – sinus gland; StG – stomatogastric ganglion; StN – stomatogastric nerve; T 1–4 – thoracal somites 1–4; Tri – tritocerebrum; VIH – vitellogenesis inhibiting factor; XO – X-organ; Y – Y-organ; YSF – Y-organ stimulating factor.

cells (the medulla terminalis X-organ, **MTXO**, or Hanström's organ) and the neurohemal organ (sinus gland, **SG**) (reviews e.g. in CHAIGNEAU 1983, SKINNER 1985). The protocerebral area bearing the neurosecretory cells is obviously secondarily displaced into the eye-stalks of decapods. The exact position of the MTXO varies, it can also be found near the medulla interna or the medulla externa (review in GUPTA 1983). A situation more similar to that seen in insects is found in the also well-studied Isopoda, where the eye-stalks are completely reduced (summary e.g. in WÄGELE, 1992). Here the cells of Hanström's organ (or homologues of the MTXO) are found near the medulla externa in the protocerebrum and near the midline



of the protocerebrum (e.g. JUCHAULT & KOUIGAN 1975, CHIANG & STEEL 1985 a, b), a position equivalent to that of the myriapod protocerebral NSCs (Fig. 3B). These isopod NSCs produce at least some of the neurohormones known from the decapod MTX-organ, such as the CHH (MARTIN et al. 1984). The SG is usually associated with the medulla externa and has no intrinsic endocrine cells. It has been studied in Malacostraca, Anostraca, Branchiura, but not in other, often minute "lower" crustaceans. In some malacostracans (Natantia, Stomatopoda) another neurohemal organ is known, viz. the postcommissural organs, which might correspond to the perisymphatic organs of the Insecta (CHAIGNEAU 1983). The lateral cephalic nerve plexus (LCNP) is only known from the Isopoda; it has few intrinsic neurosecretory cells, is connected with the sinus gland and has a segmental innervation from the segment of the second antenna to the maxillipedal segment (e.g. BESSE & LEGRAND 1964, CHATAIGNER et al. 1978). From its position in the nervous system it resembles the corpora allata of the Pterygota, an analogy evolved from similar anlagen. The LCNP activity is correlated with growth and moulting (review in WÄGELE, 1992).

GUPTA (1983) argues that those protocerebral neurohemal organs that are devoid of intrinsic neurosecretory cells are the more primitive ones. This implies that with respect to the NSCs, the corpora cardiaca of pterygotes are more advanced than in apterygotes, the Gabe organ of Chilopoda is more specialized than in Symphyla and Diplopoda, the lateral cephalic nerve plexus of the Isopoda is a new acquisition compared to the sinus gland system of decapod crustaceans. GUPTA (1983) also suggests that the more dispersed system of neurohemal organs in tracheates is a consequence of the simplification of the circulatory system, another outcome of life in terrestrial habitats.

Fig. 4. Simplified schemes of the anterior nervous system of Tracheata. A – Diplopoda, with variations of the protocerebral neurosecretory system, right side of the brain with a more primitive arrangement (combined and modified after SEIFERT 1971, SEIFERT & EL-HIFNARI 1972, JUBERTHIE-JUPEAU 1983). B – Collembola (modified after CASSAGNAU & JUBERTHIE 1983). C – Zygentoma (modified after CASSAGNAU & JUBERTHIE 1983). D – Pterygota (combined and modified after HIGHNAM & HILL 1969, GRASSE 1975, GERSCH & RICHTER 1981, WHEELER et al. 1988, DIRCKSEN et al. (1991)).

Al – antennular nerve; Ab 6–7 – abdominal somites 6–7; AKH – adipokinetic hormone; CA – corpus allatum; CC – corpus cardiacum; CCAP – crustacean cardioactive hormone; CHH – crustacean hyperglycemic hormone; CTSH – chloride transport stimulating hormone; Deu – deutocerebrum; DP – diuretic peptides; EC – ecdysteroids; FG – frontal ganglion; In – insulin; J – juvenoids; Gch – gnathochilarium; GN – Gabe's nerve; GO – Gabe's organ; HS – HOFFMANN's swelling; HGSH – hindgut stimulating hormone; HyG – hypocerebral ganglion; LHN – lateral heart nerve; Mx 1, 2 – maxilla 1, 2; NHO – neurohemal organ or neurohemal area; NCC 1, 2 – nervus corpus cardiacum 1, 2; NR – nervus recurrens; NTF – neurotropic factor; PB – paraesophageal body; PG – prothoracic gland; PNSC – protocerebral neurosecreting cells; Pro – protocerebrum; PTH – prothoracotropic hormone; SN – segmental nerve; SS – somatostatin; StG – stomatogastric ganglion; T 1 – thoracal somite 1; TRH – trehalose regulating hormone; Tri – tritocerebrum.

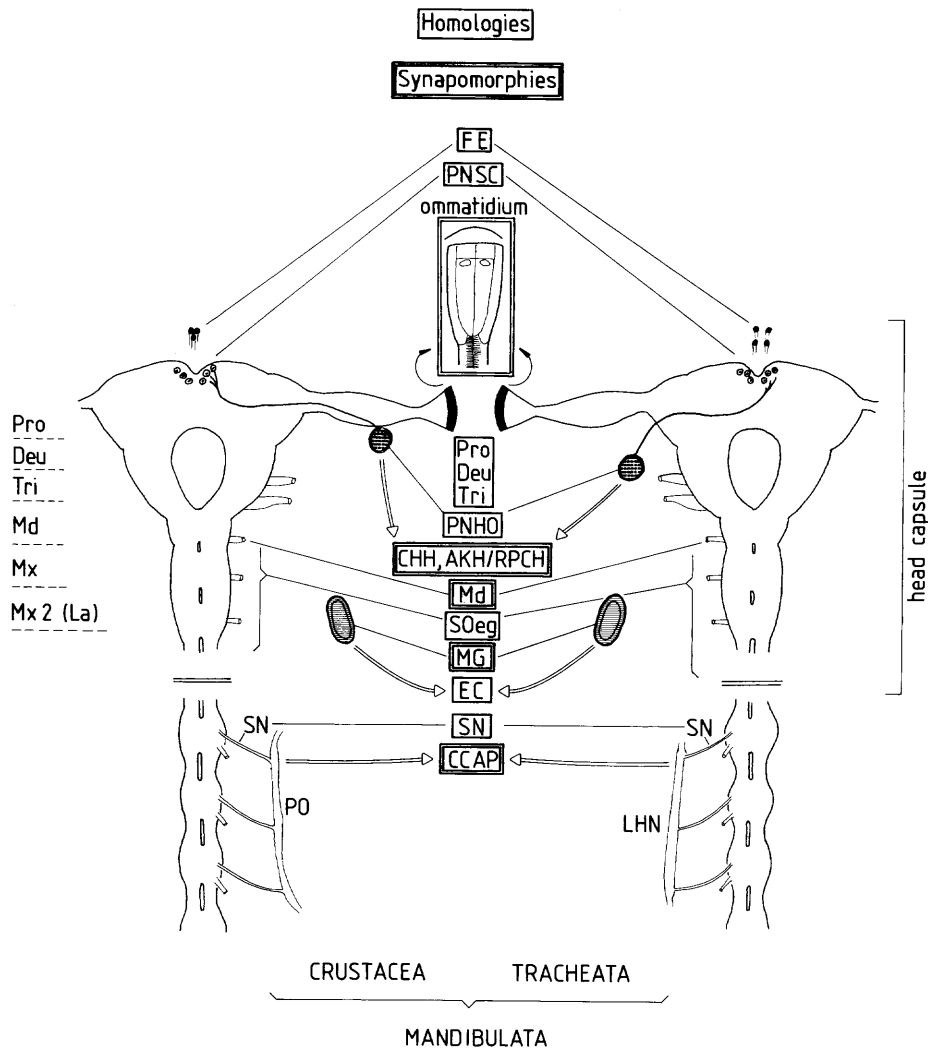


Fig. 5. Scheme visualizing important homologies and synapomorphies of Crustacea and Tracheata (further explanations in the text).

AKH – adipokinetic hormone; CC – crystalline cone; CCAP – crustacean cardioactive peptide; CHH – crustacean hyperglycemic hormone; Deu – deutocerebrum; EC – ecdysteroids; FE – fronal eyes; La – somite of labium; LHN – lateral heart nerve; Md – mandible; MG – molting gland; Mx – somite of maxilla (1); Mx 2 – somite of maxilla 2 or labium; PNHO – protocerebral neurohemal organ; PNSC – protocerebral neurosecretory cells; PO – pericardial organ; Pro – protocerebrum; RPCH – red pigment concentrating hormone; SN – segmental nerves connecting the ventral nerve cord with the lateral heart neurohemal areas; SOeG – suboesophageal ganglion; Tri – tritocerebrum.

Some neurohormones such as enkephalines occur throughout the animal kingdom in vertebrates and invertebrates. Several vertebrate hormones have been detected with immunocytological techniques in insects (REMY & VIEILLEMARIN 1988). The existence of these is of course of no use for any analysis of arthropod phylogeny, but the site of their production (e.g. MTX-organ) is a specific character.

An important biochemical homology (based without doubt on the same genetic information) between the insect and the crustacean protocerebral neurosecretory/neurohemal system is the ability to produce the same, very specific substances. One of these is the **AKH**-family of neuropeptides. These have been isolated from the corpora cardiaca (adipokinetic hormones, **AKH**) and from the decapod eyestalk (red pigment concentrating hormones, **RPCH**), where it also has been localized with immunocytochemical techniques in the **MTXO** (MANGERICH et al. 1986). "It is very interesting that AKHII-S and AKHII-L are different from the crustacean **RPCH** in only one amino acid at position 6, which demonstrates that these molecules are, in evolutionary terms, closely related" (MORDUE & SIEGERT 1988). The **RPCH** had been first isolated and sequenced from eyestalks of *Pandalus borealis* (FERNLUND & JOSEFSSON 1972; review in KELLER 1983):

● **RPCH:**

PCA-Leu-Asn-Phe-Ser-Pro-Gly-Trp-Nh₂

The **RPCH** is concentrated in the SG, but can also be found in other parts of the crustacean nervous system. The **AKH** is very similar:

PCA-Leu-Asn-Phe-Thr-Pro-Asn-Trp-Gly-Thr-Nh₂

These substances do have multiple functions within the same species, a fact that explains the evolution of a different "use" of similar molecules in insects and crustaceans. The **RPCH** for example affects not only the erythrocytes but also the pyloric rhythms (summary in JAROS 1991).

Very similar is the case of the crustacean hyperglycemic hormone (**CHH**), the "diabetogenic factor" of ABRAMOWITZ et al. (1944). **CHH** is synthesized in the crustacean X-organ-sinus-gland complex (JAROS 1979). This peptide is unique and has no resemblance to any other of the hitherto sequenced hormones (KEGEL et al. 1989). Antibodies raised against the **CHH** produced a positive reaction in the pars intercerebralis and corpora cardiaca of the stick insect, *Carausius morosus* (JAROS & GÄDE 1982). Furthermore, according to preliminary studies the **CHH** of *Locusta migratoria* has a roughly similar aminoacid composition as in crustaceans (JAROS et al. 1987), making it very probable that **CHH** exists also in insects, though the peptide must have another function than in crustaceans. This is another evidence for the homology of the crustacean X-organ-sinus-gland complex with the insect pars-intercerebralis-NSC-CC-CA complex.

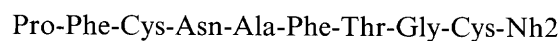
Several other "factors" of the endocrine systems have been discovered (e.g. proctolin, neurotropic factors, heart stimulating factors), some of which might yield further homologies between insects and crustaceans when identified and sequenced (e.g. GERSCH & RICHTER 1981). The protocerebral neuroendocrine system of *Lithobius* and of decapods for example controls spermatogenesis and inhibits moulting. The *Lithobius* system also controls the ovarian cycle as in the isopod *Ligia oceanica* (DESCAMPS 1975); in decapods peptides also control the activity of the ovary (see remarks in KEGEL et al. 1989). A melanophore dispersing hormone is possibly present in the brain of crustaceans, *Limulus* and insects (KELLER 1983). Other hormones that deserve a more detailed study are the enkephalines, which are

present in insects and crustaceans, and the FMRF-amide that was localized immunocytochemically in the eye-stalk of decapods (JAROS 1990).

In summary, the homology of the protocerebral neuroendocrine system of the Mandibulata is proved by the 3 criteria for homologies of REMANE (1961): the NSCs have the same position (dorsomedial area of the protocerebrum) (criterium of similar position within an anatomical system) as long as the protocerebrum is not prolonged into eyestalks, as in decapods; also the neurohemal areas evolve in the same region; this neuroendocrine system produces some very similar or identical peptides (criterium of the special quality of a character); where variations occur, as in the case of the Myriapoda, which evolved additional neurohemal areas and glands, or in insects, where fusions of the paired CC/CA-system occurs, the aberrant forms can be derived from the plesiomorphic condition due to the existence of intermediate stages (criterium of the transitions). To the same category belongs the similar ontogenetic origin of the arachnid Schneider's Organs and of part of the insect CC/CA-system, that induced LEGENDRE (1958) to postulate the homology of these organs. Of these homologies at the present state some seem to be autapomorphies of different taxa: the presence of 2 main axon bundles innervating the neurohemal organ (NCC1/NCC2) in Insecta, the absence of a tritocerebral neurohemal organ (Schneider's organ II) in the Mandibulata, the shortening of the axon bundles and consequently the association of the neurohemal organ with the optic nerve in Crustacea; the presence of specific neuropeptides in the Mandibulata (CHH, CCAP, AKH/RPCH-family) are biochemical synapomorphies. GUPTA (1983) reviewed what was then known on arthropod neurohemal organs and depicted a system for monophyletic arthropods with Crustacea and Chelicerata arising from the Trilobitomorpha, the Insecta being a separate line. In view of the above mentioned synapomorphies of the Mandibulata this opinion can not be maintained any more.

4.6. Crustacean cardioactive peptide (CCAP)

The crustacean cardioactive peptide is produced in various NSCs of the crustacean nervous system. This peptide was also discovered in insects (*Locusta migratoria*). This insect CCAP also was isolated and sequenced, with the result that it is identical with the crustacean CCAP of *Carcinus maenas* (STANGIER et al. 1987, STANGIER et al. 1989). It is a nonapeptide of the sequence



As long as no CCAP is discovered in chelicerates it seems that this peptide is another very specific autapomorphy of the Mandibulata. Furthermore the arrangement of the neurosecretory cells that probably produce CCAP (immuno-reactive pericarya) within the ventral nerve chain (see 4.4.) and of their axons that lead to the lateral heart areas (lateral heart nerves in insects, pericardial organs in crustaceans) are similar in the Mandibulata (DIRCKSEN & KELLER 1988, DIRCKSEN et al., 1991).

4.7. Moulting gland

A moulting gland does not occur in chelicerates. Chelicerates, including pycnogonids and *Limulus*, have ecdysteroids that are involved in the control of moulting, but this hormone seems to be produced in a diffuse way by hypodermal cells (WINGET & HERMAN 1979, BEHRENS & BÜCKMANN 1983, summary e.g. in BÜCKMANN 1989). Mandibulates have a specialized gland that evolved from the hypodermis, i.e. the production of the moulting hormone is restricted to a part of the hypodermis, which during embryonic development evolves as a hypodermal derivative in the segment of the second maxilla. Usually later during ontogeny the gland separates from the integument (in crustaceans a connection with the ventrolateral integument of the maxillary segment can persist). In insects it can penetrate into the prothorax. The position, ontogenetic origin and biochemical characteristics (production of nearly identical ecdysteroids) prove that the Y-organ of the Crustacea and the prothoracic gland of Tracheata are homologous organs. This moulting gland is considered an autapomorphy of the Mandibulata.

4.8. Other arguments

The analysis of the fossil record was not very successful until now in finding the ancestors of the tracheates. There is no clue allowing to derive the Tracheata from a certain point (taxon and/or period) of the mandibulate fossil record. But an important argument is the impossibility to postulate a *major* terrestrial tracheate radiation in a period previous to the Silurian (when the first tracheates and terrestrial plants appear, e.g. LABANDEIRA et al. 1988): the evolution of terrestrial tracheates (and in consequence also of terrestrial chelicerates) requires the presence of vascular plants (e.g. CLOUDSLEY-THOMPSON 1988). This does not necessarily mean that the stem-lineage of the tracheates or crown-group tracheates did not exist during the Cambrian. Ostracod-like fossils, possibly maxillopodans (MÜLLER & WALOSSEK 1988) and with them the crustacean line, are known from the Cambrian; if these really are crustaceans then the sistergroup, i.e. the stem-lineage of the Tracheata, must have existed also. Possibly representatives of this line are among those fossils which are regarded as early crustaceans; as they must have been crustacean-like marine animals it will be difficult to identify them among other taxa of the mandibulate crown group.

(The interpretation of a worm-like fossil with filamentous appendages as Middle Cambrian uniramian (ROBINSON 1990), which was claimed to be the earliest known arthropod comparable in general body form to myriapods, is highly speculative.)

The fossil record shows that early Paleozoic arthropods either had laterally directed trunk appendages, or pendant appendages. Laterally directed appendages occur in the Trilobitomorpha together with autapomorphies of this group (dorsal eyes, broadened and flattened head, lamellae on exopods, used by BERGSTRÖM (1979) as characters of the Trilobitomorpha). The pendant appendages, typical for extant Crustacea and Tracheata, were also present in paleozoic fossil euarthropods

that do not belong to extant taxa (as *Martinssonina*: MÜLLER & WALOSSEK 1986), but that can be derived from the mandibulate stem-lineage. It seems that this type of trunk appendage evolved at the base of the Pan-mandibulata.

Probably a detailed study of the anatomy of crustaceans and insects can yield a wealth of further synapomorphies. Examples are the segmental musculature (BOUDREAUX 1979a) or the segmental innervation of the laterocardiac neurohemal areas (DIRCKSEN et al., 1991). The digestive glands seem to have originally a pattern based on a segmental arrangement of paired tubes arising from different points of the midgut, as seen in the anterior midgut of some trilobites (e.g. fig. 35 in HUPE) and in chelicerates. This might be the primary structure of the euarthropod digestive system, while in mandibulates the insertion of the entodermal digestive glands is restricted to the junction between stomodaeum and midgut. In crustaceans these glands (as far as they are not reduced) begin directly behind the stomach, in tracheates they are often absent, but the gastric caeca of insects are, when present, also situated at the anterior end of the midgut; when present they are the principal sites of food resorption. A homology with the caeca of crustaceans is not very probable.

It would be worth the effort to study the possibility of a homology between the pseudocula (Pauropoda, Collembola) or Tömösváry Organs (Symphyla) of tracheates with the Bellonci Organs of crustaceans, sense organs of unknown function, innervated by the protocerebrum, located near the lateral eyes, with ciliary structures in a subcuticular space.

Details of the circulatory systems might yield further data. PASS (1991) for example studied the antennular circulatory organs in Onychophora and tracheates and described the evolution within the Tracheata. PASS concluded that within the Mandibulata the antennular blood vessels are homologous, originally being lateral arteries of the antennular segment. Within the Hexapoda the ectognathous insects have lateral vessels separated from the dorsal vessel, pulsatile "antennal hearts" evolve in the Neoptera.

Blood pigments still have not been studied in terms of homologies. That blood pigments are different in insects and crustaceans has to be expected, as the respiratory systems of these taxa are completely different as a consequence of terrestrial life of the Tracheata. GHIRETI-MAGOLDI & TAMINO (1977) found a great similarity of hemocyanin of molluscs and arthropods, and MARKL (1986) points out that with immunotechniques it can be shown that the hemocyanin subunits of all arthropods have maintained some common ancient (immunoactive) surface, though it is not clear if there are common apomorphic characters for the Mandibulata. It is also interesting that erythrocrucorins are found in some crustaceans (Branchiopoda) and in larvae of insects (ILAN & DANIEL 1981). In insect larvae the erythrocrucorins are composed of a small polypeptide chain with a single heme, in Branchiopoda there are larger polypeptide chains with several hemes. But the polypeptide weight per heme is equal in both groups. Other arguments may be found in biochemical data. HACKMAN (1984) for example remarks that in tracheates and crustaceans cuticular acid mucopolysaccharides have been found. It is also interesting that crustacean larvae are sensitive to in-

sect juvenile hormone analogues used as biochemical biological control agents (MCKENNEY & MATTHEWS 1990).

Comparisons of r-RNA sequences are another promising technique. The problem with these analyses is that 'distances' are not only a product of the elapsed time of evolutionary isolation of a taxon, but also sometimes of rapid radiation of a small taxon in a comparatively short period. Furthermore similarities are not rated, though it should be possible to find complex synapomorphies.

Many of the physiological and anatomical characters of the Mandibulata mentioned above can not be seen in fossils. Among these characters the synapomorphies prove that extant Tracheata and Crustacea are sister-groups, but we will never be able to discover at which point of the stem-lineage these characters evolved, in contrast to the morphological features, which are clearly visible. It is therefore not possible to state which of these characters belong only to the mandibulate crown group (Mandibulata s.str.). The peptide sequences are convincing synapomorphies, but it is nevertheless still important not to neglect comparative external morphology.

4.9. Important differences between Crustacea and Tracheata

The Mandibulata concept explains the differences between crustaceans and tracheates as reductions or new acquisitions. Several of these have already been discussed in the previous paragraphs. The absence of the second antenna in tracheates clearly is a reduction. The presence of androgenic glands and hormones of Crustacea might be a new character that evolved in the crustacean stem-lineage or even within the crown group. Several hormones have until now been found only within one group: the moult-inhibiting-hormone (MIH, a peptide of the MTXO/SG system possibly belonging to the CHH family: summary in JAROS 1991), the neurodepressing hormone and several pigment hormones in Crustacea (summary in WEBSTER & KELLER 1988), the prothoracotropic hormone (a peptide) and juvenoids (terpenoids) in insects (summary in WHEELER et al. 1988, BÜCKMANN 1989). But we can not be sure whether all of these substances really are absent where they have not yet been found. A moult-inhibiting factor for example has also been found in the 'cephalic glands' of myriapods (JOLY 1961, 1966, JOLY & DESCAMPS 1968, SCHEFFEL 1965, DESCAMPS 1975). Many "factors" have not been sequenced; they may be slightly modified in different taxa and have gained different functions in the course of evolution.

5. Implications of the Mandibulata concept

The acceptance of the Mandibulata concept has two important consequences:

1) The Crustacea can not be discerned with characters that possibly are only mandibulate synapomorphies or symplesiomorphies, such as the presence of 2 pairs of antennae or of a large headshield-fold. This difficulty has been noted by several authors (e.g. WEYGOLDT 1979, LAUTERBACH 1983). The characters used in the stimulating study of HESSLER and NEWMAN (1975), which is also based on the "Uniramia" hypothesis, are plesiomorphies from the point of view of the Mandibulata concept, apomorphies only if one ignores the existence of the Tracheata.

2) Crustacean-like arthropods that do not have the complete set of the mandibulate apomorphic characters can not be classified as primitive crustaceans; these fossils are derived from the mandibulate stem-lineage and belong to the Pan-mandibulata.

A typical set of characters that have been discussed as autapomorphies of the Crustacea is that of BRUSCA & BRUSCA (1990):

- The nauplius larva.
- The gnathobasic mandible.
- Possibly the stalked eyes.
- Possibly the biramous antenna 2.

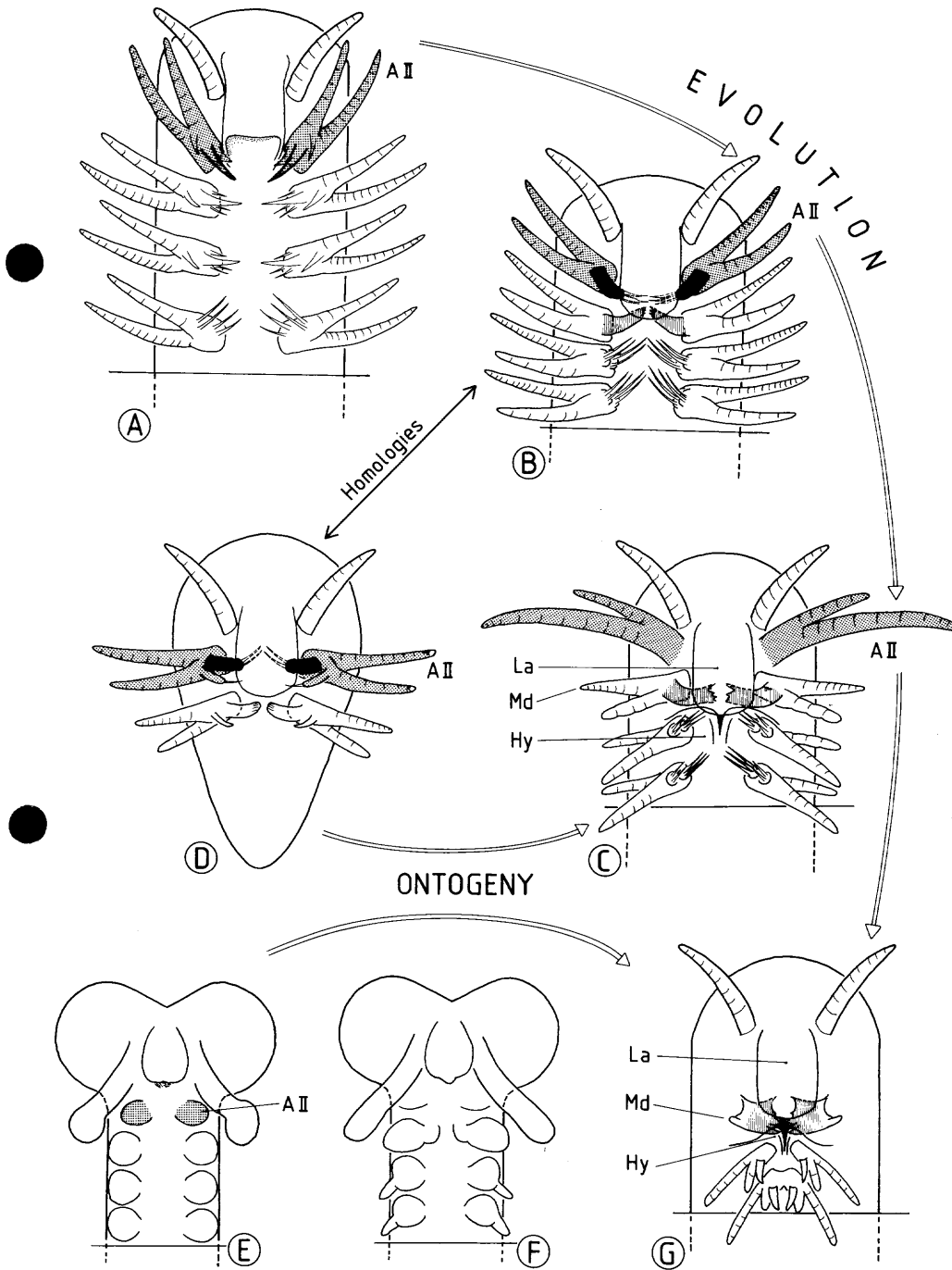
Other characters used in literature are epipodial gills or simply epipods, the carapace, the naupliar eye, schizoramous limbs, the excretory organs (antennal and maxillary glands).

LAUTERBACH (1983, 1988) explained that several of these characters are plesiomorphies and only of diagnostic value for extant crustaceans, but of no use if one wants to place a fossil within the phylogenetic system, because the characters must have been present already in the stem-lineage of the Mandibulata. The larva with very few pairs of appendages is a character of the euarthropod groundpattern, because such larvae and anameric development are also present in trilobites and in aquatic merostomates. In comparison with other oligomeric arthropod larvae the nauplius has distinct characters, bearing only 3 instead of 4 pairs of appendages (WALOSSEK & MÜLLER 1990). Nevertheless this type of larva must not necessarily be a character present only in crustaceans. It is as well possible that it is a feature of the groundpattern of the Mandibulata s.str., which is secondarily lost in all terrestrial groups (Tracheata) as well as in several marine crustaceans (e.g. Peracarida). We have to face the problem that the larval development of the unknown marine stem-lineage Tracheata can not be reconstructed.

The gnathobasic mandible s.str., i.e. the first mouthpart embedded between labrum and hypopharynx, is a character of the crown-group of the Mandibulata, not only of crustaceans. Epipods could (according to LAUTERBACH 1979) be derived from the trilobite exopodal lamellae and would be a character of the mandibulate

Fig. 6. Scheme illustrating aspects of the evolution of mandibulate head appendages (head in ventral view). A – C and G represent evolutionary steps, D – F ontogenetic stages of extant mandibulates (D – scheme of generalized crustacean nauplius; E, F – scheme of embryonic stages of insects). The second antenna (A II) of early pan-mandibulates primarily was one of four pairs of rather similar schizoramous head appendages (A). The antenna (A II) is a mouthpart in the nauplius (D) of Crustacea, a reminiscence of an ancestral morphology probably inherited from the late pan-mandibulate stem-lineage (B). It is suggested that in the crown-group Mandibulata as in extant Crustacea the adult A II is not a mouthpart (C), but a limb used mainly for swimming and mechanoreception, while the mandible became the anteriormost mouthpart. The (extant terrestrial) tracheates (G) reduce the A II during ontogeny (E–G), but retain the mandible as the first mouthpart as in Crustacea. These Mandibulata s.str. possess an anterior “chewing chamber” formed by the labrum (La), the mandibles (Md), and the hypopharynx (Hy) (figures were prepared using data from SANDERS 1963, BRUCKMOSER 1965, MÜLLER & WALOSSEK 1985, 1986b).

crown group. The study of the Orsten arthropods and of other fossils together with the fact that epipods are only present in cephalocarids, branchiopods, and malacostracans, convinced HESSLER (personal communication) that the epipods evolved within the Crustacea, though convincing evidence for the homology of



different types of exites that exist among Crustacea is still wanting. Even then, they do not seem to be an autapomorphy of the Crustacea. Stalked eyes are known from many fossils that are not or seem not to be crustaceans (e.g. *Opabinia*, *Actaeus*, *Odaraia*, *Waptia*, *Yohoia*, *Sidneyia*). The special quality of the stalked eyes of Malacostraca could be an autapomorphy for the Malacostraca (but not of the Crustacea in general) if defined by the internal anatomy of the stalks, but details still have to be studied outside the Decapoda. The fact that the antenna 2 is biramous is a character of the stem-lineage of the Mandibulata: the second antenna is derived from a schizoramous leg of the Euarthropoda. The carapace is a character that needs more precise definition. It might be that certain types of carapace-folds are typical for taxa like the Malacostraca, but there exist no indisputable concepts for the description of this character. For the discussion of further crustacean characters see LAUTERBACH (1983).

If one accepts the Mandibulata concept, it is really difficult to discern crustaceans. LAUTERBACH (1983) recognizes 2 autapomorphies of the Crustacea: the nauplius eye, composed of 4 (Nr. 1–4) or (if 1 ommatidium is reduced) of 3 ommatidia that are grouped close together, while in the Tracheata the ommatidia 1–4 are separated (e.g. Collembola; LAUTERBACH 1983: Fig. 1). The second character is the reduction of the segmental excretory organs to only 2 pairs, while tracheates originally possess an additional pair in the maxill(ul)ar segment. WALOSSEK & MÜLLER (1990) argue that other segmental organs are also present in Crustacea, but these are only embryonic mesodermal cells (the case of the Anostraca described by BENESCH 1969), or with high probability (according to published micrographs) only special integumental glands (the case of the Remipedia, described by SCHRAM & LEWIS 1989), which occur in many crustaceans (e.g. segmental lobed glands in oniscid isopods: WÄGELE, 1992). The presence of antennal and maxillar nephridia has recently been confirmed for the Cephalocarida (HESSLER & ELOFSSON 1991). Nephrocytes, which can occur in thoracic segments (in Isopoda: WÄGELE & WALTER 1990) should not be homologized with functional nephridia. From what we know until today it could also be that the sinus gland, i.e. a protocerebral neurohemal organ associated with the optic nerve, and not separated from it in retrocerebral position, is an autapomorphy of the Crustacea. If no other valuable apomorphic characters are discovered, i.e. characters which should not be potentially present in the hypothetical marine ancestor of the Tracheata, a critical paleontologist can only identify a fossil as a crustacean when it shares the special features of one of the extant taxa (as *Nahecaris* with its biramous antennule, a derived character found only in crustaceans) or when it clearly shows naupliar eyes.

A phylogenetic system of the Euarthropoda that includes the monophyly of the Mandibulata leaves us with a large number of taxa that do not belong to the Pan-mandibulata. Most of these remaining animals are either extant chelicerates or trilobite-like fossils. This group is according to LAUTERBACH (1980b: Arachnata) and BERGSTRÖM (1979, 1980: Arachnomorpha = Trilobitomorpha + Chelicerata) possibly a monophylum with distinct characters: the anterior part of the body is broadened, with a large, flattened head shield, dorsal (never terminal) compound, often seleniform eyes, laterally directed appendages (not pendant appendages as in

the Pan-mandibulata) with lamellar setae forming combs on the exopod (not epipods on the sympod, as in some Crustacea). The stem-lineage of the Mandibulata must have its roots in a group of euarthropods with pendant appendages, frontal eyes, and no exopod combs, the second large group of Cambrian arthropods besides the trilobite-like taxa. It is not very probable that a reversed arthropod cladogram with a stem-lineage composed of polyphyletic Crustacea and leading step by step to trilobitiforms, as proposed by BRIGGS and FORTEY (1989), really represents aspects of arthropod evolution.

6. Zusammenfassung

1. Die „Uniramia“-Hypothese wird diskutiert und auf der Grundlage von Literaturdaten abgelehnt. Diese Hypothese hat im angelsächsischen Sprachraum eine weite Verbreitung, was zu vielen Widersprüchen in Lehrbüchern und zu Kontroversen zwischen Wissenschaftlern geführt hat.

2. Die „Uniramia“-Hypothese basiert auf Unterschieden der Morphologie von Crustaceen und Tracheaten. Bisher gab es keine auf der Logik der konsequent phylogenetischen Systematik basierenden Argumente, die belegen, daß diese Unterschiede auch bereits in den Grundmustern dieser Taxa vorhanden sind und daß Übereinstimmungen Analogien sind.

3. Die Mandibel der Tracheata ist nicht homolog mit den Mundhaken der Onychophora und ist auch keine „Ganzbeinmandibel“. Proximale Enditen gibt es nicht nur bei Cheliceraten und Crustaceen, sondern auch bei Tracheaten. Mandibeln ohne Palpen, wie für Tracheaten typisch, kommen analog auch bei mehreren Crustaceen vor. Die Mandibel der Tracheata ist von einem Mundwerkzeug mit proximalen Enditen abzuleiten, das in der grundlegenden Funktion, Position, Ontogenese und Innervierung homolog mit der Mandibel der Crustaceen ist.

4. Einästige Laufbeine sind kein singuläres Merkmal der Tracheata und Onychophora, sondern eine Anpassung oder eine Präadaptation an die terrestrische Lebensweise aller terrestrischer Arthropoden, zu finden bei Protarthropoden, Cheliceraten, Crustaceen und Tracheaten.

5. Eine große Zahl apomorpher Merkmale rezenter Cheliceraten, Tracheaten und Crustaceen belegen die Monophylie der Euarthropoden. Damit ist es unmöglich, die Tracheaten direkt von den Onychophora-ähnlichen Vorfahren abzuleiten.

6. Die rezenten Tracheaten und Crustaceen sind überlebende Linien der Kronengruppe der Mandibulata und weisen zahlreiche plesiomorphe und synapomorphe Homologien auf. Die Mandibulata sind eine monophyletische Gruppe.

7. Einige der den Crustaceen und den Tracheaten gemeinen Plesiomorphien, welche z. T. vom Grundmuster der Euarthropoden (= Symplesiomorphien der Pan-Mandibulata) oder von der Stammlinie der Pan-Mandibulaten abzuleiten sind, sind die Mindestzahl der Anlagen von Kopffextremitäten (4), das Vorhandensein einer 1. Antenne, der Frontalozellen und der Komplexaugen, das die Augen und ersten beiden Gliedmaßenpaare innervierende dreigeteilte Gehirn, die die folgenden 3 Kopffextremitätenpaare innervierenden suboesophageale Ganglien, die Existenz von protocerebralen neuroendokrinen Zellen mit Axonen zu einem Paar retrocerebraler Neurohämalkanalen, die Produktion von Ecdysteroiden (Häutungshormonen), das Vorhandensein von Enditen an den Protopoditen.

8. Das ursprünglich erste Mundwerkzeugpaar der Pan-Mandibulata hat sich im Verlauf der Evolution in die zweite Antenne der Kronengruppe umgebildet, beim adulten Tier fehlten wahrscheinlich die Enditen. Die 2. Antenne ist bei den Tracheata sekundär reduziert.

9. Die Struktur der Facettenaugen, die Anordnung der Kopffextremitäten, die zweite Antenne, die Integration der Mandibel in einer „Kaukammer“ zwischen Labrum und Hypopharynx sowie spezielle Merkmale des endokrinen Systems sind Autapomorphien, die

zur Kopfkapsel der Mandibulata gehören, welche daher eine sehr spezialisierte und komplexe, im Tierreich einmalige Struktur ist.

10. Die Facettenaugen weisen folgende Autapomorphien der Mandibulata auf: Eine verringerte Zahl von Retinulazellen (ca. 8) und von korneagenen Zellen (2), die Präsenz eines Kristallkegels. Variationen lassen sich vom Grundmuster des Mandibulatenommatidiums ableiten. Dieser Ommatidientyp kommt außerhalb der Mandibulata nicht vor.

11. Die Neuropeptide der AKH-Familie, wahrscheinlich auch das hyperglykämische Hormon (CHH) und weitere Hormone des proto-retrocerebralen Neurohämalsystems sind biochemische Homologien und z. T. wahrscheinlich Synapomorphien (AKH/RPCH; CHH) von Tracheaten und Crustaceen.

12. Die CCAP-Neurone der Bauchganglienkette, die das kardioaktive Peptid (CCAP) produzieren, und die dazugehörigen Axone, die die lateralen Herznerven innervieren, sind nach dem derzeitigen Kenntnisstand Synapomorphien der Crustacea und Tracheata. Diese sehr speziellen Merkmale sind nirgendwo sonst im Tierreich bekannt.

13. Die Häutungsdrüse (Y-Organ, Prothoraxdrüse) ist eine Autapomorphie der Mandibulata und hat bei Crustaceen und Tracheaten denselben ontogenetischen Ursprung und dieselbe Funktion (Produktion von Ecdysteroiden in Korrelation mit den Häutungszyklen). Diese Drüse kommt bei anderen Taxa nicht vor.

14. Weitere anatomische und physiologische Merkmale weisen auf eine nahe Verwandtschaft von Crustaceen und Tracheaten hin, es sind jedoch künftige physiologische und biochemische Analysen (z. B. Sequenzierungen) notwendig, um die spezifische Qualität der Merkmale beschreiben zu können.

15. Das Konzept der Monophylie der Mandibulata impliziert die Unmöglichkeit, den Crustaceen ähnelnde Fossilien in jedem Fall von der Stammlinie der Crustaceen ableiten zu dürfen, da es auch die Möglichkeit gibt, daß es sich um Abkömmlinge der Stammlinie der Mandibulaten handelt.

16. Daraus ergibt sich, daß Merkmale, die als diagnostisch für die rezenten Crustaceen eingestuft werden, in vielen Fällen auch Merkmale der Kronengruppe der Mandibulata sein können und damit Plesiomorphien der Crustacea sind. Die Schwierigkeit, Crustaceen zu erkennen oder zu definieren und frühe marine Stammlinienvertreter der Tracheata zu identifizieren, wird diskutiert.

7. Acknowledgements

The author is grateful to Prof. Dr. E. DAHL and Prof. Dr. J. STRÖMBERG for the invitation to the workshop in Kristineberg, Sweden. The discussion with Dr. P. JAROS (Oldenburg) on the neuroendocrine systems of arthropods was very stimulating; I must thank Dr. P. JAROS, Prof. Dr. A. WILLIG and Dr. H. DIRCKSEN for the literature they put at my disposal. Dr. D. WALOSSEK spent many hours discussing with me the phylogeny of crustaceans and helped to improve the manuscript. Prof. Dr. O. KRAUS, Prof. Dr. J. BERGSTRÖM and Prof. Dr. R. R. HESSLER kindly commented the manuscript and provided constructive criticism.

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Received: March 24, 1992

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