

IDENTITY OF THE DISTAL SEGMENTS OF THE MAXILLA 2
AND MAXILLIPED IN COPEPODS:
NEW TEETH FOR CARL CLAUS' OLD SAW

BY

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ABSTRACT

Interpretations by Claus and Giesbrecht of the identity of the distal segments of the maxilla 2 and maxilliped in copepods are reviewed. The developmental pattern of setal additions to these appendages suggests that the distal segments of maxilla 2 are exopodal, while those of the maxilliped are endopodal; these data are consistent with the interpretation of Claus.

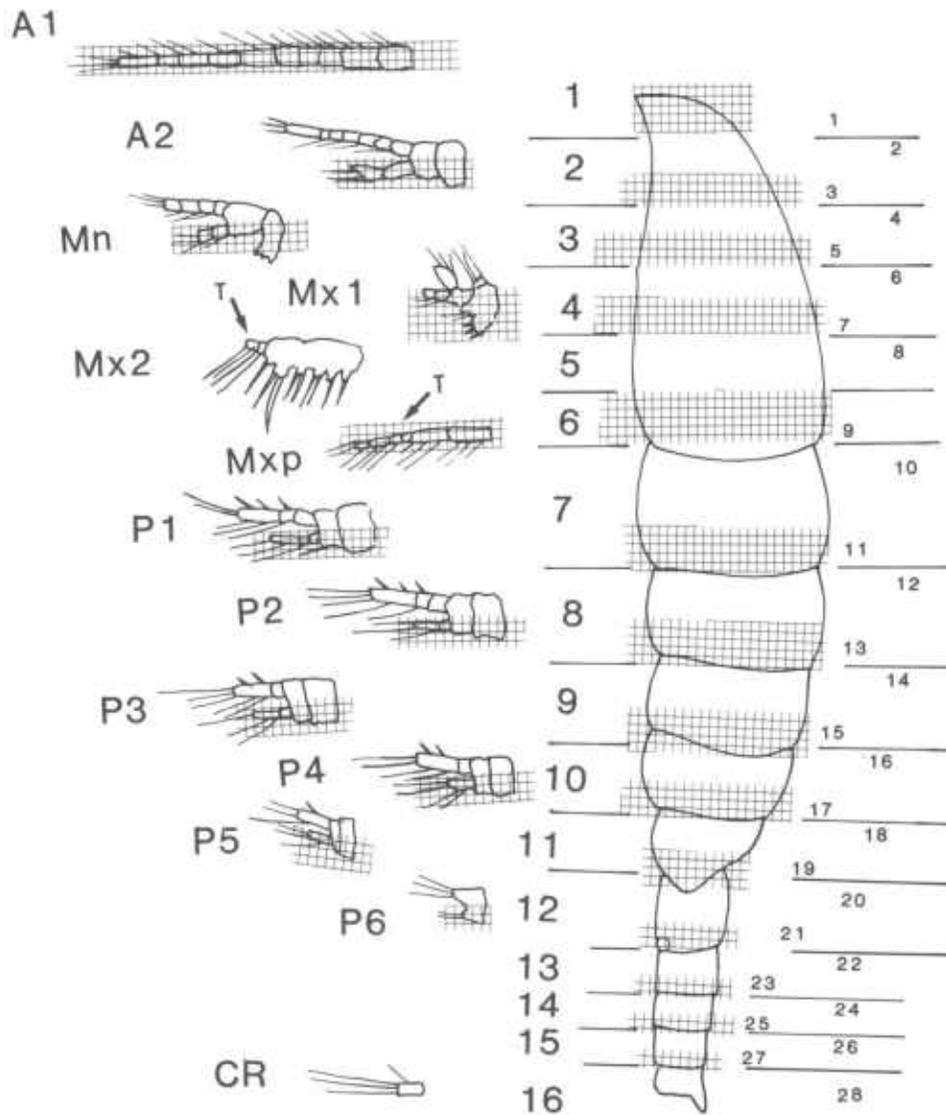
Information about the genetic regulation of development of a fruitfly, and a reinterpretation of a fossil arthropod also support Claus. A general hypothesis identifies a compartment with a contralateral pair of uniramous limbs as the basic division of the body of an ancestral arthropod. Somites, crustacean biramous appendages, and insect uniramous appendages are derived. The general hypothesis is used to explain the structure of a copepod including maxilla 2 and maxilliped.

RÉSUMÉ

Les interprétations par Claus et Giesbrecht de l'identité des segments distaux de la 2ème maxille et du maxillipède chez les Copépodes sont revues. Le mode de développement des additions de soies sur ces appendices suggère que les segments distaux sont exopodial sur la 2ème maxille et endopodial sur le maxillipède. Les données sur la régulation génétique du développement d'une drosophile et une réinterprétation d'un arthropode fossile appuient aussi l'interprétation de Claus. Une hypothèse générale identifie un compartiment avec une paire d'appendices uniramés comme la division basale du corps d'un arthropode ancestral. Somites, appendices biramés des crustacés, et appendices uniramés des insectes sont dérivés. L'hypothèse générale est utilisée pour expliquer la structure d'un copépode incluant la 2ème maxille et le maxillipède.

DISCUSSION

The maxilla 2 and maxilliped of copepods, which are posterior on the cephalosome (fig. 1), are not apparently biramous appendages. Each consists of a linear series of up to seven segments of varying size and armament. Over a century ago the identity of these segments, as defined by their homologs on a biramous appendage, was contended by Carl Claus and Wilhelm Giesbrecht. Claus (1863) believed that the copepod maxilla 2 and maxilliped (which both he and Giesbrecht designated maxilliped 1 and 2) are not appendages homologous to other biramous appendages of copepods. Instead Claus suggested that these appendages are two rami of a single, biramous appendage whose basal segments have fused into the head of the copepod, leaving the exopod and endopod free and separate. Claus had proposed this hypothesis in earlier papers (Claus, 1858; 1862) which included a similar, but incorrect, explanation



Figs. 1. Schematic representation of somites and appendages of unknown copepod. Somite boundaries indicated by horizontal lines, somite numbers to the immediate left, and compartment numbers to the right. Appendages on the far left. Areas on somite and appendage which correspond to odd number compartments crosshatched. A1, antenna 1; A2, antenna 2; Mn, mandible; Mx1, maxilla 1; Mx2, maxilla 2; Mxp, maxilliped; P1-P6, legs 1-6; CR, caudal ramus; T, terminal segments of maxilla 2 and maxilliped; distoventral circle on somite 12 is genital opening.

of the uniramous condition of the mandible and maxilla 1 of some parasitic copepods. Claus' support for his hypothesis about the maxilla 2 and maxilliped, in addition to their condition, was the observation that in several parasitic copepods the maxilliped is located not posteriorly but medially to the maxilla 2, as are the two rami of a biramous appendage. Claus' hypothesis subsequently was cited in general textbooks (Hertwig, 1916; A. Lang, 1891).

Giesbrecht (1893) rejected this interpretation and proposed that both the maxilla 2 and the maxilliped are true biramous appendages whose distal segments are endopodal. Giesbrecht's evidence against Claus's hypothesis can be summarized as follows: the maxilliped is located directly posterior to maxilla 2 in nauplii of *Rhincalanus*, and this naupliar condition is primitive; the largest number of segments on any copepod maxilliped is seven, two more than is known for any endopod, so the proximal two segments of these appendages are basipods which have not fused into the head; given that the basipodal segments are present, no mechanism was known which could split a complete, biramous appendage. In support of his hypothesis Giesbrecht noted that: the largest number of segments on a copepod maxilla 2 or maxilliped is seven, a number identical to two basal plus five endopodal segments of the two maxillae and 1st thoracic segments of some malacostracans; the inner margin of the distal segments of the copepod maxilla 2 and maxilliped are lobe-like as are many crustacean endopodal segments.

Giesbrecht's interpretation of the distal segments of the copepod maxilla 2 and maxilliped subsequently has been accepted by many researchers (Hansen, 1925; K. Lang, 1948; Huys & Boxshall, 1991). However, Hecgard (1947) interpreted the maxilla 2 and maxilliped as two maxillipeds whose distal segments are exopodal. Recent research on morphological transformations during development of calanoid copepods, on the reinterpretation of a fossil arthropod, and on genetic regulation of the development of a fruitfly suggest that Giesbrecht's conclusion is incorrect and Claus' may not be. The following discussion of these interpretations will focus on calanoid copepods, the oldest order for which a large amount of morphological and developmental data are available.

Observations about morphology, and development of the armament of the maxilla 2 and maxilliped present difficulties for Giesbrecht's interpretation. The internal margin of the distal segments of the calanoid maxilliped often is lobe-like where the setae articulate; Giesbrecht suggested this morphology was endopodal. However, distal segments of the maxilla 2 in calanoids are not lobe-like, and distal segments of the exopod of antenna 2 and mandible of some calanoids often are drawn out distally into a lobe where each seta articulates (Ferrari & Steinberg, 1993). A lobe-like, segmental morphology does not provide a definitive means of distinguishing exopodal from endopodal segments.

Developmental patterns of setal additions to appendages of calanoids differ in the maxilla 2 and the maxilliped (table I). After copepodid III (CIII) no setae

TABLE I

Copepodid stages at which setae are added to exopod (Re) or endopod (Ri) of A2, Mn, Mx1, or to A1, Mx2, Mxpd in the following copepods; D, *Drepanopus forcipatus* (from Hulsemann, 1991); P, *Pleuromamma xiphias* (from Ferrari, 1985, and unpublished copepodid I); R, *Ridgewayia* sp. (from unpublished copepodids I-IV); S, *Scopalatum vorax* (from Ferrari & Steinberg, 1993, copepodids II-IV only)

	A1	A2		Mn		Mx1		Mx2	Mxpd
		Re	Ri	Re	Ri	Re	Ri		
CI	-	-	-	-	-	-	-	-	-
CII	D, P, R		D, P, R		D, P, R	R	D, P, R	D	D, P, R
CIII	D, P, R, S		D, P, R, S		D, S	D, P, R	D, R, S	P, R	D, P, R, S
CIV	D, P, R, S		D, P, R		D, P, R, S	D	D, P, R, S		D, P, R, S
CV	D, P, R, S		D, R		D, P, R	D, P, R	D, P, R, S		D, P, R, S
CVI	D, P, R		D, P, R, S		D, P, R, S	D, P, R	D, P, R		D, P, R, S

are added to the distal segments of maxilla 2. Setal addition to the maxilliped continues through the molt to CVI. Comparisons of these patterns to setal additions of calanoid anterior appendages show that endopods of antenna 2, mandible and maxilla 1 continue to add setae through CVI. Addition of setae to exopods of these biramal appendages ends by CII except for maxilla 1 which may or may not add setae later in copepodid development, depending on the species. For post-maxillipedal appendages, setal addition to rami ends for both exopod and endopod during the molt to CV (Ferrari & Ambler, 1992). These data suggest that the distal segments of maxilla 2 differ from those of the maxilliped, that those of maxilla 2 are exopodal, and that those of the maxilliped are more likely endopodal. Data from younger copepod orders are equivocal. Setal additions to maxilla 2 and maxilliped have not been reported during copepodid development of harpacticoids, and setal additions are complete by CIII for other anterior appendages (Itô, 1970; Itô & Takashiro, 1981; Onbé, 1984; Fiers, 1991a, 1991b; Dahms, 1993). Setae may be added to maxilla 2 of cyclopoids in later copepodid stages (Ferrari & Ambler, 1992).

Giesbrecht's data on the number of segments support his point that both maxilla 2 and maxilliped possess basipodal segments. However, his question about a known mechanism which might be responsible for splitting a biramal appendage is relevant only if a biramal appendage is the primitive condition of all copepod appendages. Emerson & Schram (1990) recently have suggested that the crustacean biramal appendage is derived by fusion of the basal segments of two primitive uniramal appendages which are homologous to an insect appendage. These primitive appendages are apparent in the fossil arthropod *Tesnusocaris goldichi* as paired ventrolateral and mid-ventral uniramal

appendages on the same trunk somite. Furthermore, morphology of the separate appendages suggests that they do not result from the fusion of basal segments of a biramal appendage to the ventral area of the body.

Two discoveries from studies of the development of the fruitfly provide support for the hypothesis of Emerson & Schram (1990). Cells of *Drosophila melanogaster* that are allocated to thoracic segments of an embryonic fruitfly are differentiated subsequently into a posterior set of cells which expresses the gene "engrailed" and an anterior set of cells which does not express this gene. The differential expression of "engrailed" effectively divides embryonic segments into an anterior and posterior compartment, although there is no gene equivalent to "engrailed" which is expressed in all of the cells of the anterior set (see Lawrence, 1992, for a more complete discussion of adult segments, larval parasegments and compartments). Later, cells that are allocated to one thoracic limb primordium of an imaginal disc are recruited from both an anterior and adjacent posterior compartment of the same segment. This action is mediated by a protein secreted by the "wingless" gene from a subset of cells of the anterior compartment only. Anterior cells are recruited into the limb primordium directly, by the action of cells of the anterior compartment, while posterior cells of the limb primordium require a protein from the "wingless" gene which is active only in anterior cells (see Cohen, 1994, for a review of the development of imaginal discs in *Drosophila*).

These data can be interpreted in a way which would require a modification of the Arthropod Pattern Theory of Schram & Emerson (1991). As modified, the ancestral arthropod possessed body segments which are homologous to the compartments (monomers of Schram & Emerson) of an insect. Each ancestral compartment/segment possessed a contra-lateral pair of compartmental, uniramal limbs. During the evolution of some arthropods, compartment/segments fused in pairs to form a somite (a diplomere of Schram & Emerson), or in greater numbers in the cephalic region, but often retained the ancestral, uniramal limb associated with each compartment. These compartmental, uniramal limbs appear as the medial and lateral pairs on *T. goldichi*. Later, serial medial and lateral pairs of these limbs fused basally to form the biramal crustacean appendage or completely to form the uniramal appendage of insects. Thus, there may be four kinds of arthropod limbs, three of which are uniramal: (1) a primitive arthropod limb which is a compartmental, uniramal limb; (2) a crustacean biramal appendage which is a serial pair of compartmental, uniramal limbs with their basal segments fused; (3) a uniramal antenna 2 of cyclopoid and poecilostomatoid copepods (Ferrari, 1992) which is a serial pair of compartmental, uniramal limbs whose basal segments fuse while the distal segments of one limb fail to develop in later copepodid stages; (4) a uniramal thoracic limb of an insect which is a serial pair of compartmental, uniramal limbs which are fused throughout their length.

In discussing their Arthropod Pattern Theory, Schram & Emerson (1991) did not anticipate the presence of unfused, uniramous limbs among extant crustaceans. Indeed, most body somites and appendages of extant crustaceans and insects probably are not homologues of an ancestral arthropod compartment/segment or its uniramous limb, but are fused compartment/segments and fused compartmental, uniramous limbs. In addition, during arthropod evolution fusion of compartments may not have been a precondition to fusion of their uniramous limbs, so that homologies of uniramous appendages of all extant arthropods may have to be re-examined and re-interpreted. The developmental morphology of calanoid copepods suggests that the maxilla 2 and maxilliped of copepods deserve such re-consideration. For example, calanoid copepods could be examined for expression of the homologue of the "engrailed" gene in the area of maxilla 2 and maxilliped during embryonic and naupliar development. If "engrailed" is expressed twice the two somites, each comprised of two compartments, probably are present, and maxilla 2 and the maxilliped probably are derived biramous limbs. If one "engrailed" stripe is expressed then only one somite probably is present, and maxilla 2 and maxilliped may be compartmental, uniramous limbs. Similar studies of uniramous copepod appendages which are derived from an ancestral, biramous appendage, e.g., antenna 2 of poecilostomatoids and cyclopoids (Ferrari, 1992), leg 4 of caligids (Boxshall, 1974; Kabata, 1972) and leg 5 of pontellids (Hulsemann & Fleminger, 1975) should provide a useful check of the results.

From the general hypothesis in the preceding paragraph, the structure of a copepod can be described in the following manner (fig. 1). The cephalic complex is composed of nine fused compartment/segments. The uniramous limb of the first compartment is antenna 1. Compartmental, uniramous limbs two through seven have fused pair-wise, but partially, to form the antenna, mandible and maxilla 1 which are biramous appendages. Limbs of compartments eight and nine have not fused; their distal segments are the exopod and endopod of a presumptive maxilla 2; they are designated as maxilla 2 and maxilliped respectively. Twelve compartment/segments (#10-#21) have fused pair-wise to form six thoracic somites each with pairs of partially fused compartmental, uniramous limbs forming biramous thoracic appendages. Six compartment/segments (#22-#27), whose limb development is suppressed, have fused pair-wise to form three, limbless abdominal somites. The terminal abdominal somite is a compartment (#28) whose uniramous limb is the caudal ramus.

One interpretation of this hypothetical copepod is of a crustacean with five cephalic, six thoracic and four abdominal somites, which corresponds perhaps more closely than the previous five-seven-four to a maxillopodan tagmosis (Newman, 1992). However, with advances in developmental genetics, arthropod tagmosis will have to be reinterpreted at the level of compartments, not body segments or somites. Retention by copepods of compartmental, uniramous

limbs, e.g., maxilla and maxilliped, would support the suggestion of Newman (1992) that maxillopodans are an old lineage of crustaceans.

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NOTE ADDED IN PROOF

A recent publication on development of a fruitfly thoracic appendage by Diaz-Benjumea & Cohen (1994, Development, **120**: 1661-1670) and observations of engrailed expression in appendages of embryonic mysids by Patel (pers. comm.) suggest that biramal limbs are a product of dorsal-ventral patterning, rather than anterior-posterior patterning as suggested here.