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The evolution of the mouthparts of insects

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***Abstract*---**We contrasted the expression patterns of several developmentally important genes in insects with mandibulate or stylate-haustellate mouthparts in order to better comprehend both the development and evolution of insect mouthparts. We found no major breaks in the evolution of mouthparts, but six in epochs with numerous innovations and few extinctions, namely the Late Carboniferous, Middle and Late Triassic, 'Callovian-Oxfordian,' 'Early' Cretaceous, and 'Albian-Cenomanian'. The three Permian-Triassic, Triassic-Jurassic, and Cretaceous-Cenozoic crises had no discernible effect on mouthpart types.

***Keywords*---**mouthparts insects, insects, labrum, mandibles, maxillae, hypopharynx, labium.

Introduction

The cockroach has a 'primitive' arrangement of mouthparts, which are used for biting. For the initial collection and processing of food, 5 different structures are used:

1. Labrum - a cover which may be loosely referred to as the upper lip.
2. Mandibles - hard, powerful cutting jaws.
3. Maxillae - 'pincers' which are less powerful than the mandibles. They are used to steady and manipulate the food. They have a five segmented palp which is sensory and often concerned with taste.
4. Labium - the lower cover, often referred to as the lower lip. It actually represents the fused pair of ancestral second maxillae. They have a three segmented palp which is also sensory.
5. Hypopharynx - a tongue-like structure in the floor of the mouth. The salivary glands discharge saliva through it.

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This system is similar in all insects that chew their food, both larvae and adults. When specialised food sources are used, the mouthparts are modified, sometimes significantly, so that the food can be obtained satisfactorily. Insect mouth parts exhibit many examples of perpendicular evolution, with the same goal being achieved independently along similar but not identical lines. Many insects consume food that is liquid. The development of a sucking' arrangement from the mouthparts aids in this. [2-3]A different approach to palaeoecologically studying the past evolution of insects focuses on morphological disparity rather than taxonomic diversity. The first studies of this type on insects focused on mouthparts, examining the evolution of 'feeding guilds' in relation to the diversification of angiosperms. These guilds were formed using mouthpart classes recorded as clusters using distance and agglomeration from a matrix of mouthpart presence/absence. [4]WAPUM, or 'Wagner Parsimony Analysis Applied to Palaeosynecology Using Morphology,' is a recently developed method for establishing a hierarchy ('tree') of geological epochs based on the appearances/extinctions of different types of insect mouthparts over time. Wagner parsimony searches for hierarchies (nested sets of objects) that are most compatible with the distribution of character states among the objects to classify. This method, unlike the cladistic method, is independent of all phylogenetic sequence ideas and is currently used in synecology to classify landscape parts. In palaeosynecology, it is also used to classify geological periods or palaeontological localities [5]. In this section, we categorise the currently accepted geological epochs. Each corresponds to a time period defined by more or less significant extinction events caused by or as a result of changes in ecosystems. We also define two 'artificial' ones, grouping the Callovian with the Oxfordian (for a Middle-Late Jurassic) and the Albian with the Cenomanian because the main outcrops with insects for these periods overlap (Supporting Information). The characters in WAPUM are based on morphology, and the method has already been successfully tested for specific insect clades (Odonatoptera, Thripida, Dermaptera). We define the characters as "the presence or absence of taxa bearing a specific mouthpart type." The mouthpart types are defined in the Supplementary Material [6].

Result and Discussion

We identified fifty-seven different types of mouthparts and tracked their distribution over time (Figure 1, Supplementary Information). Some are found in orders, groups of families, and others in single subfamilies. The chosen types are distinguished by their high specialisation in feeding and biology, as well as significant structural modifications. [7]

Figure 1: The fifty-seven mouthpart types are listed below. A few sentences and a histogram of fossil occurrences are provided. The presence of a fossil with the morphological mouthpart type or belonging to the crown group with it in black. A fossil inside a stem grouping with no mouthparts is shown in blue. The subdivisions 'Callovian-Oxfordian' and 'Albian-Cenomanian' are denoted by the shortest vertical lines within the Jurassic and Cretaceous.

Mandibulate mouthparts are often used as a model to explain the evolution of mouthparts in insects due to their ancestral origin. The most used chewing model is the one observed on orthopterans (such as locusts or grasshoppers).

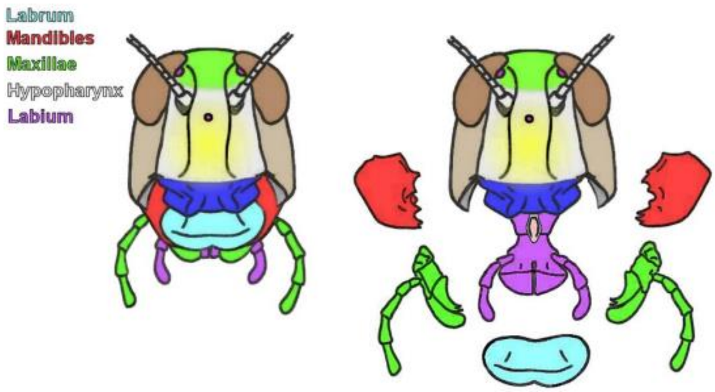

Figure 2: Mandibulate or chewing model of an orthopteran.
Source: John R. Meyer, North Carolina State University.

According to this model, an insect's mouthparts consist of five major structures: the labrum, mandibles, maxillae, hypopharynx, and labium. Mandibles, maxillae, and labium are true or appendicular appendages because they develop from metameres (also known as somites; segments in which their body is divided) during embryonic growth; thus, these three structures are morphologically equivalent to locomotor appendages. Labrum and hypopharynx, on the other hand, are not true appendages due to their non-metameric origin, but they are also considered buccal appendages due to their important role in feeding. [8]

Knowing the original functions of these structures on the mandibulate model allows us to comprehend the changes that have occurred in the various adaptive forms that have emerged throughout the evolution of insect feeding: [9]

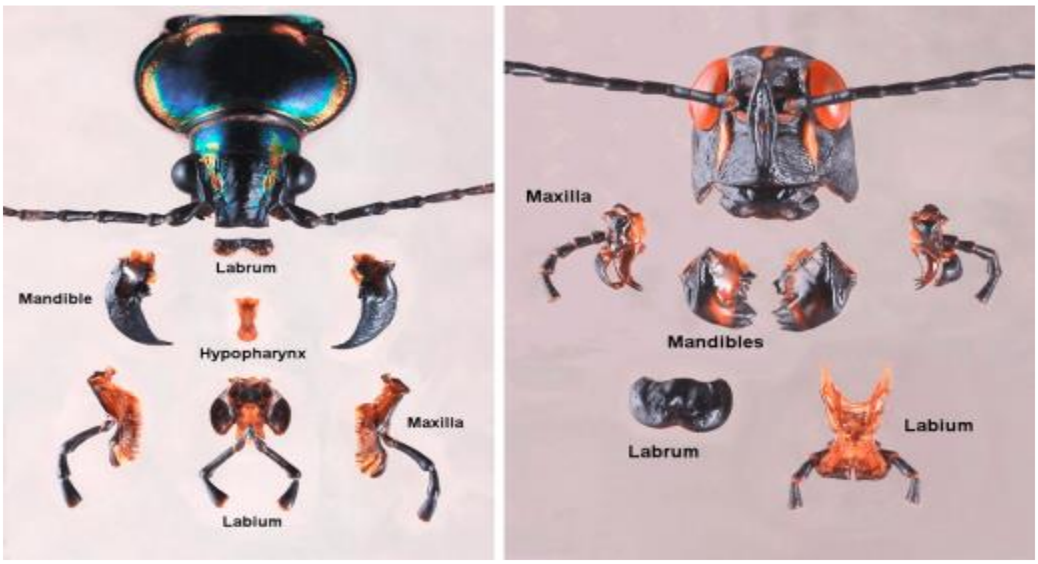

Figure 3: Examples of mandibulate or chewing mouthparts: beetle (left) and locust (right).
Source: John R. Meyer, North Carolina State University.

- Labrum. A plate-like sclerite that protects the rest of the feeding structures. Its size varies between species and aids in the containment of food. The posterior surface is referred to as the epipharynx.
- Mandibles. A pair of jaws for crushing or grinding the food. They operate from side to side.
- Maxillae. A pair of appendages divided into three sections: the cardo, which articulates with the head; the stipes, which encourages a sensory palp; and the galea and lacinia, which act as fork and spoon to manipulate food.
- Hypopharynx. A little process located behind mandibles and between maxillae that helps mix food and saliva.
- Labium. Unlike mandibles and maxillae, the labium's a pair original appendage has fused together along the middle. The labium is also divided into two sections: postmentum, which articulates with the head, and prementum, which supports a pair of sensory palps and divides apically to form four lobes: glossae and paraglossae.

All mouthpart models are thought to have evolved from an ancestral mandibulate form. However, it's more than likely that this process occurred in different groups at the same time, as insects' ranges expanded, food became more accessible, and new sources of food appeared. This is an excellent example of adaptive radiation (when two or more populations diverge from a common ancestor due to different selective pressures).

We know that the appearance of all mouthpart models occurred at least five times between 420 and 110 million years ago, thanks to fossil records (insects preserved in amber, coprolites, and evidence of plant attacks). Some groups eventually switched from a solid-based diet to a liquid-based diet, consuming exposed liquids (such as nectar), tissue liquids (such as sap or blood), or even suspended particles. These changes provided a significant adaptive advantage to those who adopted a liquid-based diet during the Cretaceous period expansion of angiosperms (flowered plants). [10]

The adoption of a liquid-based diet by some insects, such as butterflies, provided these organisms with a significant adaptive advantage during the expansion and diversification of flowering plants. Furthermore, this allowed for the beginning of a coevolved process between insects and plants. Irene Lobato is the author.

Mouthpart types

We revisited previous studies on mouthpart types. Our research was designed to focus on homologous morphological structures in particular. As a result, some differences between Labandeira's and our results can be explained by the way groups were formed in both studies. Labandeira's 'Labellate' type, for example, included some Diptera and the Mecoptera: Nannochoristidae. However, the mouthparts of nannochoristids and tipuloids are very different (Supporting Information). Similarly Labandeira grouped within the guild 'Glossate' the Neuroptera: Nemopteridae and the Hymenoptera: Apoidea and Vespoidea. These two types of licking structures are not related. Also the nemopterid type is 'Early' Cretaceous while the vespoid-apoid type is 'Albian-Cenomanian'. Non-homologous structures are found in other examples (Tubulomandibulata, Segmented Beak, Hexastyle, and so on). The evolutionary message carried by new innovations (which, according to Labandeira, are redundant because they would have appeared in previous taxa with the'same' type of mouthparts) is important because it contains information on morphological types that appeared or disappeared with taxa bearing them, and thus information on the selection pressures that affected these taxa. Analyses of the evolution of feeding guilds (particularly in insects) in relation to angiosperm diversification revealed that by the Middle Jurassic, 65 to 88% of all modern insect mouthpart classes existed. Our updated data show that new mouthpart types have emerged since the 'Callovian-Oxfordian' stages (the Lagerstätten Karatau was previously thought to be Late Jurassic), and that important mouthpart types, particularly those associated with nectarivory, emerged during the Cretaceous. [10-12]

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