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Morphological adaptations of the head and mandibles of some coleopterous larvae burrowing solid substrates

(Coleoptera)

With 4 plates

The locomotion of animals in a solid medium is carried out by either breaking or moving apart substrate particles or by using natural porosity of the substrate. In different animal groups which inhabit soil, wood and other solid substrates, various morphological adaptations to active locomotion are developed.

The insect larvae use their legs, the last abdominal segment, parts of the head capsule etc. for burrowing. Sometimes they have special supporting structures on the abdominal and thoracic segments. In some cases contraction of the body musculature plays the principal role in movement.

A study of animal locomotory mechanisms and of their organs of locomotion is of great interest. The formation of the most effective locomotory apparatus is one of the important factors of progress in animal evolution.

Zenkevich (1944) has pointed out that it is the texture of the environment which appears to be the decisive factor determining the mode of animal locomotion.

Ghilarov (1942, 1949) showed that the mode of locomotion and the structure of locomotory organs of invertebrates depended on the character of the interaction between the organisms and their environment. This author pointed out that not only various environmental conditions but different principles of utilization of the environment by the organisms may cause divergent evolutions (Ghilarov, 1942). It is possible to trace different principles of utilization of the environment at the example of closely related groups of invertebrates inhabiting the same substrates. Instances of great divergence of character in animals living under similar conditions are called "contrast amphigenesis" (Zenkevich, 1944).

The head capsule and mandibles of insects inhabiting solid substrates often have locomotory functions. These organs are used by the larvae of some coleopterous groups to move apart or to break the particles of the substrate.

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The problem of the active locomotion of coleopterous larvae in solid substrates (soil, sand, wood etc.) was repeatedly discussed (CHOLODKOVSKY, 1888; BRASS, 1919; VLADIMIRSKAYA, 1926; SUBKLEW, 1938).

GHILAROV studied the modes of insect locomotion in the soil and their morpho-ecological adaptations to burrowing. In some cases the function of digging and moving apart soil particles is carried out either by the thoracic legs or by mandibles and by the anterior end of the head capsule. These organs are modified according to their function. The modes of burrowing in the soil are studied in some coleopterous larvae (from the families of Tenebrionidae, Alleculidae, Carabidae and Elateridae). The soil-inhabiting elaterid and carabid larvae burrow the substrate by their strongly sclerotized wedge-shaped head. The scarabaeid larvae break the soil by their mandibles mainly. The tenebrionid and alleculid larvae use for this purpose the first pair of legs and, to a lesser degree, their mandibles (GHILAROV, 1949).

GRANDI (1959) described peculiar morphological adaptations of larvae living in wood (Buprestidae) and leaf miners (some Chrysomelidae and Curculionidae). This author compared morphological modifications of the head of the curculionid larvae, both leaf-mining and living openly at the plant surface. The mining larvae are characterized by the strongly sclerotized prognathous head, partly enclosed by the prothorax. The inner part of the head capsule (covered under the prothoracic integument) is reduced and rather less sclerotized. The head capsule is often prolonged by laminar processes which penetrate into the prothorax. The substrate (wood or leaf tissue) is destroyed by strong mandibles which are supported by head capsule and prothorax. The head capsule of the curculionid larvae living at the surface is hypognathous. It has no laminar processes and is not enclosed by the prothorax.

Thus it appears that mandibles and head capsule of the coleopterous larvae inhabiting solid substrates are often used for boring the substrate. The morphological modifications and the movements of these organs vary widely.

The present paper is concerned with the types of morphofunctional adaptations of mandibles and head capsule of the coleopterous larvae breaking solid substrates (soil, timber, mushroom tissues, soft plant tissues etc.). It is possible to distinguish four groups among the coleopterous larvae, differing from each other by the structure of mandibles and head capsule and by the mode of their movement.

1. The first group includes the larvae inhabiting soil or decaying wood. They are representatives of the soil-dwelling families of Tenebrionidae, Alleculidae and some groups of Scarabaeidae. The larvae burrow in the substrate with the external (lateral) edges of the mandibles. They have well-developed large-sized head capsules with strongly sclerotized integuments (Plate I, 1). The head is hypognathous. When digging, the head and the thorax move downwards.

The tenebrionid and alleculid larvae break the substrate by means of their mandibles and their anterior legs provided with strong thorns (Plate I, 2). The mandibles play a subsidiary part in digging through the substrate. The main

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substrate- destroying organs of scarabaeid larvae are the mandibles. GHILAROV (1949) pointed out that the scarabaeid mandibles are plunged into the soil and the pulled to the anal end of the body by means of muscle contraction. The C-shaped body bends more strongly in the process.

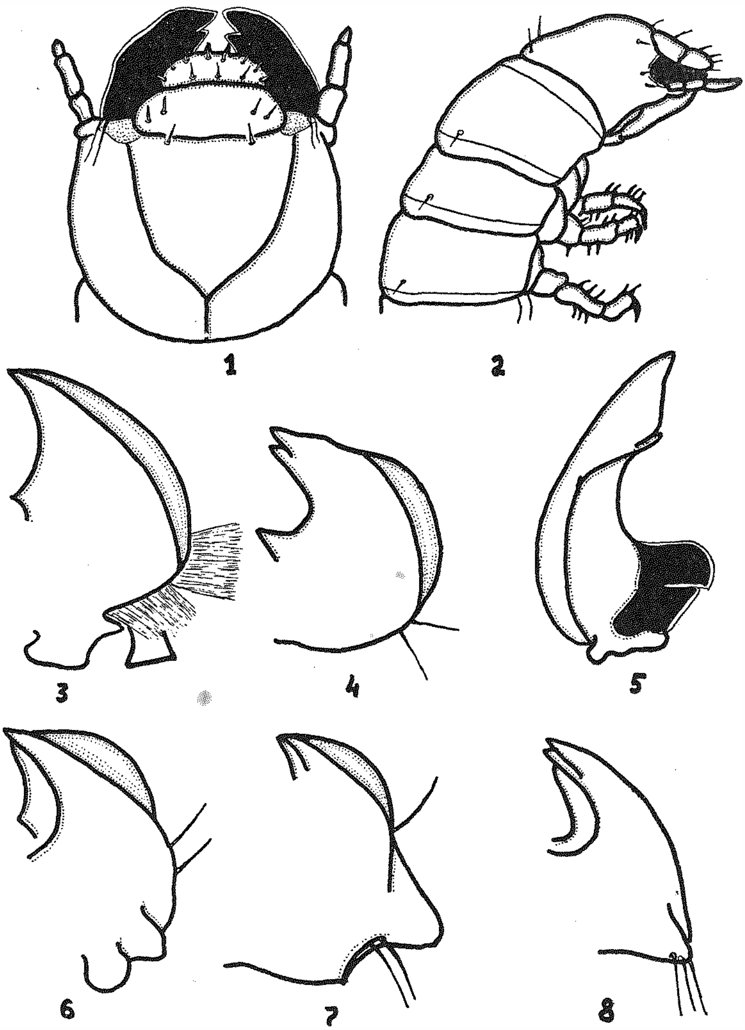

Plate I. Head capsule and mandibles of the larvae from the first group:

1, *Gonodera* sp.: head capsule. — 2, *Cylindronotus brevicollis* KÜST: anterior end of the body. — 3, *Tentyria nomas* PALL.: mandible. — 4, *Omophlus proteus* KIRSCH.: mandible. — 5, *Melolontha melolontha* L.: mandible. — 6, *Blaps lethifera* MARSH.: mandible. — 7, *Gonodera* sp.: mandible. — 8, *Pseudocistela cerambycoides* LINNAEUS: mandible

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The mandibles of all these larvae function as a pickaxe. When the head moves downwards, the mandibles are together. Their lateral parts are ahead, they bear the essential mechanical stress of digging. A comparative morphological study of mandibles in the larvae of this group showed that most tenebrionid and alleculid larvae have sharp sclerotized ridges on the lateral parts of the mandibles (Plate I, 3, 4, 6, 7). The ridges of the mandibles are especially developed in Pimeliini and Omophlini larvae. They are broad or occupy the whole lateral edge of mandible (Plate I, 3, 4, 6). These larvae dwell as a rule in compact heavy soils. Some tenebrionid larvae inhabiting decaying wood have short and narrow ridges (Plate I, 7); the larvae of *Pseudocistela cerambycoides* LINNAEUS (Alleculidae), which inhabit sawdust, have no ridges (Plate I, 8). Thus the size of the mandibular ridges depends on the density of the substrate. The development of these ridges appears to be an adaptation to breaking a solid substrate.

Soil-dwelling larvae of Scarabaeidae (*Melolontha*, *Anisoplia*, *Rhizotrogus*) have no mandibular ridges. Their mandibles are falcate with massive lateral edges (Plate I, 5). However, the movement of the scarabaeids' mandibles in digging are the same as in the other two families mentioned above. MEDVEDEV (1952) has pointed out that the lateral edges of the mandibles of scarabaeid larvae that have moulted long ago are often worn down.

Therefore it is possible to unite the larvae of all three families into one group according to their common feature — the similar character of the movements of mandibles.

2. To the second group belongs a large number of larval forms scraping the substrate with their mandibles. The mechanical destruction of the substrate is carried out by means of modified mandibular apices acting as scrapers. The representatives of this group are the larvae of Ipidae, Oedemeridae, Pyrochroidae, Pythidae, Cucujidae, Anobiidae, Lucanidae, Cetoniini (Scarabaeidae), Chrysomelidae (partly), Cerambycidae, Curculionidae (partly), Buprestidae. Most of these larvae live in decaying wood or under the bark. Some Chrysomelidae and Curculionidae are miners of leaves and of soft plant stems. All such larvae have large, strong, heavily sclerotized mandibles with flattened distal parts. There are 2—5 denticles on the apex, located on the same plane (Plate II, 1, 2, 3, 4, 5). The Cerambycid larvae have chisel-shaped mandibular apices (Plate II, 2—6).

The mandibles of the larvae inhabiting leaf tissue are flattened over the whole length (Plate II, 1). The larvae scraping solid wood have massive bases of mandibles, triangular or subquadrangular in the transversal section. There is a distinct difference between the flattened apices and massive basal parts of the mandibles. This feature is particularly apparent in mandibles with molar lobes (the larvae of Scarabaeidae, Lucanidae, Pythidae etc., Plate II, 4, 5).

Observation of the "scraping" function of the mandibles of *Potosia metallica* larvae has shown that this larva pierces the substrate with its denticled mandibles, cuts it with the flattened apices and pulls out a particle of the substrate. The larvae of Cerambycidae and Lucanidae destroy the substrate (decayed

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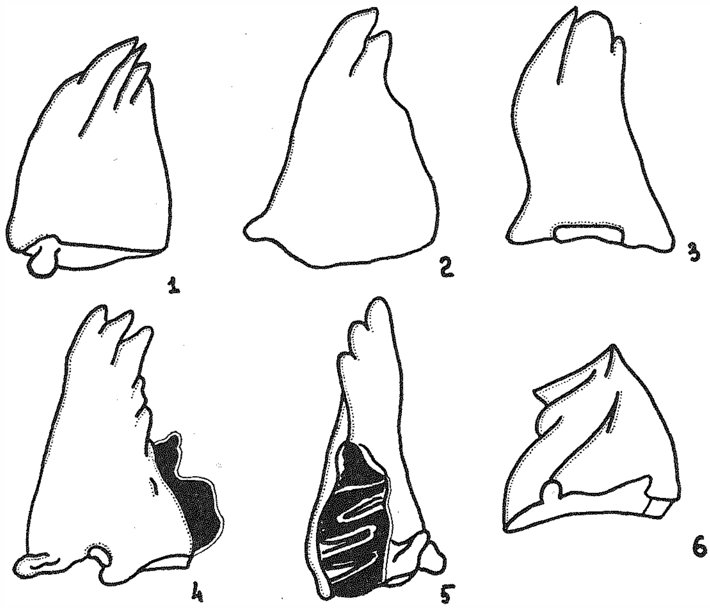

Plate II. Mandibles of the second group of larvae:
1, *Macrotarrhus* sp. — 2, Ipidae sp. — 3, *Zeugophora* sp. — 4, *Dorcus parallelepipedus* LINNAEUS. — 5, *Lucanus cervus* LINNAEUS. — 6, *Prionus coriarius* LINNAEUS

wood) in a similar way. The head capsule of these larvae seems to be the "supporting organ" for the mandibles. When scraping the substrate, the head of these hypognathous larvae jerks vertically downwards. The flattened distal parts of mandibles are almost perpendicular to the direction of the head movement.

The head of many prognathous larvae belonging to this group moves usually sidewards in the horizontal plane. As a rule the apices of their mandibles are in the vertical plane, i.e. perpendicular to the direction of the head movement. Thus the direction of the head movement appears to be correlated with the arrangement of the mandibular flattened apices. This correlation is observed both in hypognathous and prognathous larval forms. Such relation between the orientation and the direction of the movement of the substrate-breaking organs (mandibles) and the supporting organ (the head capsule) seems to be the most effective one for the destruction of solid materials.

The head capsule of many "scraping" larvae of this type shows essential modifications in its structure. The hypognathous forms have as a rule a well developed, rounded head capsule with a uniformly sclerotized integument. The head capsule of the prognathous larvae is far more modified. It is often enclosed by the prothorax. This is clearly manifested in the larvae of Buprestidae and Cerambycidae (Plate III, 2, 4) and less in the larvae of *Pyrochroa* and *Pytho*. The

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free anterior part of the head capsule is much more sclerotized than the inner part (Plate III, 1, 3). It is transverse and short and sometimes the head looks like an obtuse cone at whose apex the mandibles are located (*Sphenoptera*, *Prionus*, Plate III, 2, 4). Many prognathous larvae have an incisor in the middle of the posterior head margin. The incisor in the Cerambycidae larvae is very deep and narrow, dividing the basal part of the head into two lobes (Plate III, 1). The strong prothoracic muscles attached to the top of the incisor fix the head in the prognathous position.

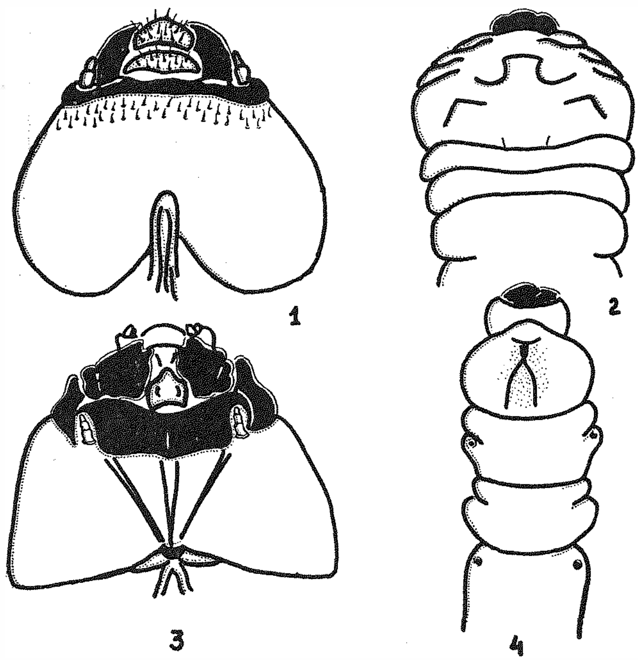

Plate III. Head capsule and anterior end of the body of the second group of larvae:

1, *Prionus coriarius* LINNAEUS: head capsule. — 2, *Dorcadion caucasicum* KÜST: head and thorax. — 3, *Sphenoptera* sp.: head capsule. — 4, *Sphenoptera* sp.: head and thorax

The mining larvae of Chrysomelidae and Curculionidae, as shown by GRANDI (1959), have similar processes in the postero-lateral angles of the head capsule. These processes are located completely in the prothorax, they maintain the prognathous position of the head.

The head of buprestid and cerambycid larvae can move only together with the thoracic segments. The head and the prothorax, functionally connected with each other, strongly support the mandibles and increase their effect.

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Thus all prognathous larvae have a trend to a disintegration of the head, drawing it into the prothorax, and to a functional connection between these parts of the body.

The degree of the development of these features varies in different systematic groups of coleopterous larvae. The most essential modifications of the anterior end of the body are observed in the larval forms characterized by a high activity in breaking solid substrates (Cerambycidae, Buprestidae). The prognathism as such is regarded by the some authors as an adaptation to the dwelling and active locomotion in solid substrate (Ghilarov, 1942; Grandi, 1959; Snodgrass, 1960).

Thus the second group of the larvae considered in this paper is numerous and very diverse. However, all these larvae can be combined on the basis of the similarity of their structure and of the mode of operation of their mandibles.

3. The third group includes larvae of Elateridae (*Selatosomus* type) and Carabidae living in soil and wood and actively digging in these substrates. The digging is carried out by means of the frontal end of the head. This specific way of digging through the substrate was studied and described by Ghilarov (1949).

The head of these larvae is prognathous, strongly sclerotized, and flattened dorso-ventrally. The head is wedge-shaped in profile. The labrum and the clypeus are fused with the frons, the anterior margin of the head capsule terminates in a denticled nasal (Plate IV, 1, 2). The nasal and the mandibles form the apex of the head wedge (Plate IV, 1, 2). The mandibles of *Zabrus* and of some species of *Harpalus* (Carabidae) are flattened with wide ridges on the lateral edges, as they are characteristic of the tenebrionid and alleculid larvae belonging to the first group.

When the mandibles of the carabid and elaterid larvae under consideration are together, their lateral ridges are in the anterior position. When breaking the substrate, the larvae strike forward with the head, which works as a pickaxe. The larvae crush the particles of soil or wood and disjoin them with the head.

Thus the breaking of the substrate is effected in the third group mainly with the head capsule and the mandibles. The main stress is borne by the lateral edges of the mandibles. The common morphological feature of all the larvae of this group is the wedge-shaped flattened prognathous head.

4. The fourth group includes the representatives of Eucnemidae and Phylloceridae. The mechanism of digging the substrate and the morphological adaptations to this function are the same as in the preceding group. The digging of soil and wood, where these larvae dwell, is carried out by means of the wedge-shaped anterior part of the body. The principal digging organ is the prothorax. Many larvae of Eucnemidae and Phylloceridae have a reduced head capsule. Their mouth-parts are drawn into the prothorax. The prothorax is wedge-shaped, strongly sclerotized, flattened dorso-ventrally, with firm denticles on the front margin and in the antero-lateral angles (Plate IV, 3). The larvae dig through the substrate by striking the wedge-shaped prothorax forward and sidewards.

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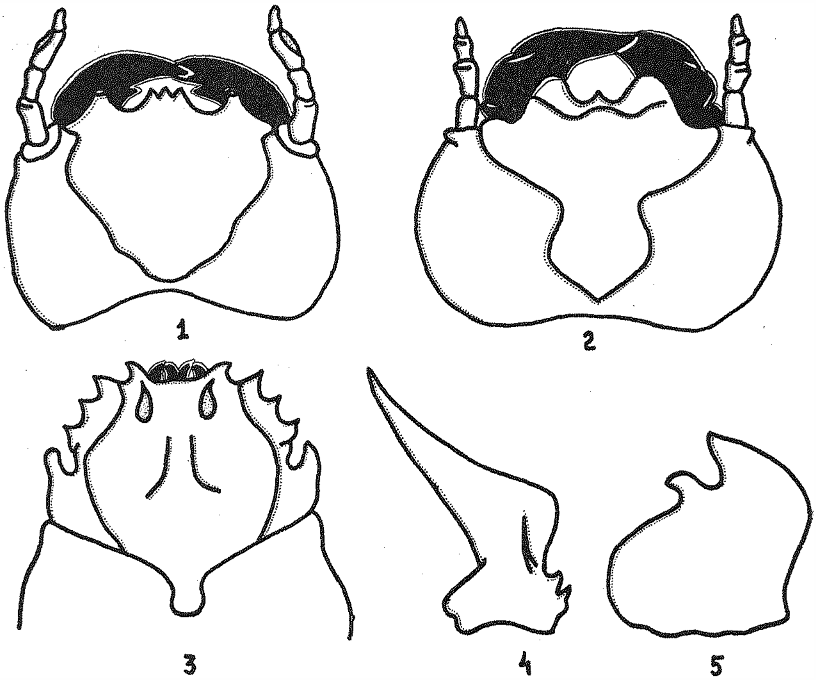

Plate IV. Head capsule and mandibles of the third and fourth groups of larvae: 1, *Harpalus* sp.: head capsule. — 2, *Selatosomus* sp.: head capsule. — 3, *Dirrhagus lepidus* ROSENH.: prothorax. — 4, *Phyllocerus* sp.: mandible. — 5, *Dirrhagus lepidus* ROSENH.: mandible

The mandibles of these larvae are small, flattened, with sharp denticles on the apices. Their apices protrude in front of the prothorax and take part in the digging (Plate IV, 4, 5).

The morphological adaptations in this group have developed accordingly in the form of a reduction of the mandibles and the head capsule. The function of digging is transferred to the prothorax.

The shape of the digging organs and the mechanism of digging the substrate are similar in the third and fourth groups, but the function of digging is carried out by different parts of the body. (This is a case of compensation of functions).

A comparative study of the head capsules of carabid larvae shows that the head of soil-dwelling forms is broader and shorter than in the larvae using ready tunnels in the soil (SHAROVA, 1958, 1960). This correlation is also peculiar to the elaterid larvae.

The adaptation to a high resistance of the medium in which the larvae move causes a shortening and broadening of the head capsule — the principal digging organ of the third group. Such a tendency is characteristic of the prognathous larvae of the second group which live in solid wood. Thus the shortening and

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reduction of the head capsule are peculiar to many larvae dwelling in solid substrates.

This leads to the assumption that the reduction of the head capsule of the larvae of the fourth group is an example of the far reaching specialization in this direction.

The reduction of the head capsule and its enclosure by the prothorax leads to a greater compactness of the anterior end of the body. Consequently the movements of the latter become stronger. The density of the substrate and its texture seem to be one of the cardinal modifying factors in the process of the evolution of digging organs.

Each of the four groups of larvae under consideration is characterized by a specific morpho-dynamic type of digging, combining a peculiar mode of operation and the appropriate complex of morphological features in the structure of the head.

Within the given morpho-dynamic type there seems to be a clearly expressed correlation between the form of digging organs, their local orientation and the mode of their operation.

Similar morpho-dynamic types of substrate-boring are convergently developed in the larvae belonging to different systematic groups of beetles living and actively moving in the solid substrates. The groups of a similar morpho-dynamic type of digging often include larvae belonging to families very remote in the phylogenetic insect system. The development of the morphodynamic type of substrate-breaking in the evolution of insect larvae seems to be the concrete expression of the "principles of utilization of the medium by organisms" mentioned by GHILAROV (1942).

The coleopterous larvae as well as many invertebrates play an essential role in the processes of destroying solid substrates such as soil and wood (GHILAROV, 1949; MAMAJEV & SOKOLOV, 1960; KURCHEVA, 1960). The great activity of these small animals bears witness to the great efficiency of the work of their substrate-breaking organs and to the high level of their morphofunctional specialization.

Summary

The author describes 4 types of morpho-functional adaptations of head capsule and mandibles of the coleopterous larvae actively breaking soil, wood and other natural solid substrates. In some larval forms the head capsule and mandibles are used for digging the substrate. These organs are often modified according to this function.

1st type — hypognathous larvae burrowing in the substrate by the external edges of the mandibles. In some cases sclerotized flattened ridges on the lateral edges of the mandibles are developed. — 2nd type — larvae with modified mandibles resembling a scraper: the distal part of the mandibles is flattened, denticled or chiselshaped. There is a tendency to reduce the head capsule and to have it enclosed by the prothorax. — 3rd type — larvae with a prognathous flattened wedge-shaped head. They dig the substrate with the anterior margin of the head capsule and the lateral edges of the mandibles. — 4th type — larvae with reduced head completely drawn into the prothorax. The digging of the substrate is carried out by means of the flattened wedge-shaped prothorax and denticled apices of the mandibles.

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Each morpho-dynamic type is characterized by a specific mode of burrowing the substrate and an appropriate complex of morphological features in the head structure. Within each morpho-dynamic type there is a clearly expressed correlation between the shape of the digging organs, their local orientation and the mode of their operation. The development of similar morpho-dynamic types in different systematic groups of coleopterous larvae is a consequence of this convergence.

Zusammenfassung

Es werden vier Typen von morpho-funktionalen Anpassungen der Kopfkapsel und Mandibeln der Käferlarven beschrieben, die sich im Boden, im Holz und in anderen harten Substraten aktiv bewegen. Die Kopfkapsel und die Mandibeln dienen oft als Organe zur Auflockerung des Substrats. Bei einigen Larvenformen sind diese Organe entsprechend ihren Funktionen modifiziert.

Type 1: die hypognatischen Larven, die das Substrat mit Hilfe von lateralen Kanten der Mandibeln zerstören. Einige Vertreter dieser Gruppe haben stark sklerotisierte keilförmige Platten an den lateralen Kanten (Rändern) der Mandibeln. — Type 2: die Larven mit schaberförmigen Mandibeln. Der distale Teil der Mandibeln ist gezähnt oder meißelförmig. Man kann eine bestimmte Tendenz zur Reduktion der Kopfkapsel und zu ihrer Einziehung in den Prothorax beobachten. — Type 3: die Larven mit dem prognathischen platten, keilförmigen Kopf. Diese Larven zerstören das Substrat mit dem Vorderrand der Kopfkapsel und mit den lateralen Kanten der Mandibeln. — Type 4: die Larven mit reduziertem Kopf, der in den Prothorax eingezogen wird. Die Zerstörung des Substrates erfolgt mit dem keilförmigen platten Prothorax und mit den gezähnten Mandibeln.

Jeder der beschriebenen morpho-dynamischen Typen wird durch die Art und Weise der Zerstörung des Substrats und durch den entsprechenden Komplex von morphologischen Anpassungen im Bau des Kopfes charakterisiert. Innerhalb jedes morpho-dynamischen Typs ist eine klar ausgeprägte Korrelation zwischen der Form der Zerstörungsorgane, ihrer räumlichen Orientierung und der Arbeitsweise ersichtlich. Die Bildung von ähnlichen morpho-dynamischen Typen in verschiedenen systematischen Gruppen der Käferlarven ist als Folge der konvergenten Evolutionsentwicklung zu erklären.

Резюме

Описаны 4 типа морфо-функциональных адаптаций головной капсулы и мандибул личинок жесткокрылых, активно передвигающихся в почве, древесине и других плотных субстратах. Головная капсула и мандибулы часто служат органами рыхления субстрата. У некоторых личиночных форм эти органы модифицированы в соответствии с их функциями.

тип I — гипогнатные личинки, рыхлящие субстрат латеральными краями мандибул. В некоторых случаях на латеральных краях мандибул развиты плоские гребни. тип 2 — личинки с модифицированными мандибулами, похожи на скребок: дистальная часть мандибул плоская, зубчатая или долотообразная. Наблюдается тенденция к редукции головной капсулы и втягиванию её в переднегрудь. тип 3 — личинки с прогнатной головой. Они рыхлят субстрат передним краем головной капсулы и латеральными краями мандибул. тип 4 — личинки с редуцированной головой, втянутой в переднегрудь. Рыхление субстрата производится плоской клиновидной переднегрудью и зубчатыми вершинами мандибул.

Каждый из описанных морфо-динамических типов характеризуется специфическим способом рыхления и соответствующим комплексом морфологических адаптаций в строении головы. В пределах каждого морфо-динамического типа ясно выражена корреляция между формой органов рыхления, их пространственной ориентацией и характером их работы. Формирование сходных морфо-динамических типов в разных систематических группах личинок жесткокрылых является следствием конвергенции.

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