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Morphological and physiological adaptations
of wood-boring beetle larvae in timber

Abstract - Beetles which develop boring tunnels inside and feed on seasoned wood present morphological and physiological adaptations related to the specific activities of their larvae in such a peculiar substrate. As far as protection of antiquarian goods made of wood is concerned, we are dealing mainly with three Coleoptera families, namely Lyctidae, Anobiidae, and Cerambycidae, which include species with wood-boring larvae. The adaptation to wood-boring and wood-feeding activities in beetle larvae was reached independently by phyletic lines not closely related, as a convergent evolution due to feeding behaviour.
Among these adaptations, the following are examined with reference to the three families mentioned above. The conformation and activity of the larval mandibles and their possible correlations with the characteristics of the wood attacked are considered together with the presence of body structures for anchoring the larvae to the wood substrate inside the tunnel during the gnawing action. Intracellular endosymbiosis (endocytobiosis) with yeasts or bacteria, capable of supplementing larval diets lacking in some essential nutrients, and its main features are summarized. Last, structural and functional characteristics are discussed as regards tracheal spiracles, provided with filter devices important for preventing intrusion of wood powder into tracheae from larval tunnels as well as useful for avoiding dehydration.

Key words: Coleoptera, Lyctidae, Anobiidae, Cerambycidae, convergent evolution, wood-feeding, mouthparts, anchoring devices, endocytobiosis, spiracles.

A unique environment and food

Wood-boring beetles, which develop by digging tunnels in timber, live in a rather unusual environment and substrate, passing their larval life sealed inside the wood mass, without communication with the external environment. Only in the case of heavy or protracted infestations, when there is a higher possibility that new and old tunnels intersect, may they be in communication with the outside, through the exit holes of the previous generations.

The larvae, which penetrate the timbered tissue directly, after having completed embryonic development and hatching, feed exclusively on wood (unless the timber is invaded by fungal mycelia), extracting from this substrate all the main nutrients

and water they need for their metabolism and development. Being confined within the wood mass, they display adaptations to this kind of life and, at the same time, to the food available, i.e. to living within wood and to living off wood (Cymorek, 1968). Of course, these two aspects are closely interconnected.

We first consider the type of environment determined by the xylophagous regime and the endophytic lifestyle. Wood, and timber even more so, is a hard and resistant substrate, which generally is attacked from the inside, so as to have an attachment point. In fact, since larvae remove the wood particles with their mandibles, being able to fracture its surface without having an anchorage would be extremely difficult. As the endophytic larvae explicate their feeding activity, they gradually penetrate the wood mass, thus finding themselves trapped in the tunnel they are digging. Actually, the tunnel is closed in front by sound wood and behind it is smaller than the larvae, because of their minor development during the period when it was dug. Its diameter is usually approximately the same as that of the larva, the empty space around it being very reduced, in order to improve larval digging efficiency.

Therefore, the larvae spend their entire lives in a closed and dark environment, which provides food and protection. Their movement is limited to the digging action, functional to feeding, and consequently to the progression of the tunnel, gradually lengthened forward. Usually only at completion of preimaginal development, mature larvae slightly widen the tunnel in view of pupation.

Their tunnelling activity also causes the production of frass, which occupies the back of the gallery and differs in consistency and granulometry, depending on the wood-boring species.

These are the conditions of preimaginal life shared by most wood-boring beetles which damage cultural artifacts and that determine their functional adaptations. Other conditions, however, may vary; for example the type of wood, which may have a different composition and hardness, depending on the essence and the part of the trunk or branch from which the attacked timber derives (Battisti, 2001). It is known that the duramen contains mainly cellulose, together with hemicellulose and lignin, and very little starch, while the sapwood still maintains a high percentage of starch. Different food preferences, related to a different set of available digestive enzymes, orient the various wood-borers towards one or the other type of substrate.

Feeding and boring in wood, a convergent evolution

Although wood is a food poor in some essential nutrients, among Hexapoda, xylophagy is a rather widespread feeding habit, common to orders, families and genera not closely related to each other. A number of exopterygote insects, such as some Blattaria and all the Isoptera, are xylophagous. For these, wood represents food not only during postembryonic development but also during adult life (Chopard, 1949; Grassé, 1949). A large number of endopterygote insects such as, for example, species of Lepidoptera Cossidae and Sesiidae, Hymenoptera Siricidae and Coleoptera Scarabaeoidea, Buprestidae, Lyctidae, Bostrichidae, Anobiidae, Lymexylonidae, Oedemeridae, Cerambycidae, Curculionoidea (Scolytidae, etc.), are xylophagous as well, but, in this

case, wood-feeding (mostly wood-boring) is generally limited to the larval instars, with a variety of trophic specializations and different needs of ecto- or endosymbiotic associations (Jeannel & Paulian, 1949; Grandi, 1951; Ebeling, 1978; Borror *et al.*, 1989). Therefore, it is obvious that xylophagy represents a trophic specialization independently achieved many times in phylogenetically distant insect orders.

Quality and other characteristics of the wood attacked, as well as the mode of attack and nutrient mobilization, may vary not only from one systematic group to another, but also inside the same group of closely related taxa. Certain species have a more ample range with regard to the conditions of the wood substrate, others a more restricted one; there are species which prefer healthy wood, others which feed on wood already damaged by biotic or abiotic factors, others which disseminate it with microscopic fungi in order to make it more suitable as food, others which need dead but still sound wood, others which, in contrast, require rotten wood (saproxylophagy), etc. (Grandi, 1951; Masutti, 2003).

As far as spatial relationship is concerned, feeding and development can take place inside the wood mass (most frequently) or from the outside (e.g. in buried timber) or also through intermediate modalities. Nevertheless, as the majority of xylophagous beetles do not attack dry, seasoned wood but develop in living wood (even if sometimes suffering or decaying), only a few families of wood-boring beetles, principally Cerambycidae (long-horned beetles), Lyctidae (powderpost beetles), and Anobiidae, are of interest with regard to the protection of timber in various phases of its use, particularly wood structures of antiquarian, historical and artistic value (Chiappini *et al.*, 2001).

Apart from some more recent rearrangements by the subsequent authors, the main traits of the phylogeny of the Coleoptera, according to current opinion (Laurence & Newton, 1982; Grimaldi & Engel, 2006), do not differ substantially from the arrangement outlined by Crowson (1960) around the middle of the last century.

Crowson (1955; 1960), basing his conclusions also on the contributions of some previous authors, recognized four suborders in the Coleoptera order. Of these, two (Archostemata, Mixophaga) are very small and two (Adephaga, Polyphaga) very large. Their adaptive radiation was partly due to the different feeding specializations and resulted in the very scarce and primitive Archostemata (primarily endophytic xylophagous and mainly neotropical), the zoophagous Adephaga, the initially mycetophagous and subcorticicole Polyphaga. This is the most recent and largest Coleoptera suborder, characterized by the greatest evolutionary success as well as by secondary differentiations in an extremely various diversity of trophic niches. The xylophagous beetles of applied interest belong to Polyphaga; in this suborder wood-boring and wood-feeding habits were independently reached many times by single systematic groups pertaining to various lines. Among them are found the series Bostrichiformia, comprising the superfamily Bostrichoidea (with Lyctidae, Bostrichidae, Anobiidae) as well as Cucujiformia comprising, among others, the superfamilies Lymexylonoidea (with Lymexylonidae), Chrysomeloidea (with Cerambycidae), and Curculionoidea (with Curculionidae) (Fig. 1).

In the same way as happened at insect order level, also among Coleoptera, an

extremely large order, xylophagy appears to be the result of a convergence of many phyletic lines more or less distant from each other.
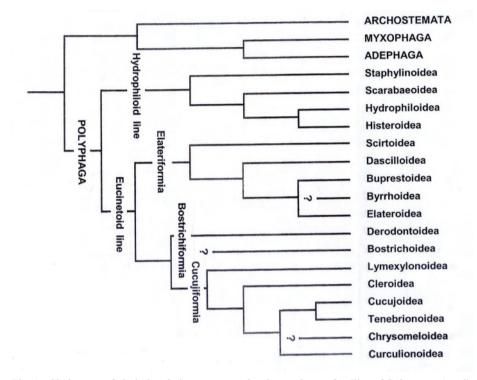

Fig. 1 - Cladogram of phyletic relations among suborders and superfamilies of Coleoptera (modified after Tremblay, 2000).

Adaptations to feeding on seasoned wood

As mentioned above, the nutrients present in the wood are basically starch, hemicellulose and cellulose; the latter, however, is not easy to digest. The larvae of some species of wood-boring beetles may be restricted to using starch alone, but others are able to digest cellulose. Depending on whether the larva is able to use it or not, the feeding mode can vary, starting from the conformation and function of the mouth appendages, to producing and ingesting more or less fine wood particles.

The attack on a substrate as hard as wood may also require that the larva has on its body surface some structures that enhance its grip on the wooden substrate while the action of the jaws is performed (Cymorek, 1968).

In addition, considering the wood as the food substrate, besides requiring that the larva have a set of enzymes for cellulose digestion, which not all wood-boring species

do, wood is also deficient in essential nutrients, such as vitamins, amino acids and lipids, that have to be found elsewhere, generally by means of symbiosis with microorganisms (Nardon & Grenier, 1989).

The following notes refer to such features in the three main families of wood-boring beetles in which we find the most common and important pests of seasoned wood and timber.

Biting off and type of wood attacked

Watanabe & Tokuda (2010) state the importance of the digestive system morphology in order to understand cellulose digestion. The first step of digestion takes place at mouth level. In wood-boring Coleoptera, both adults and larvae have chewing mouthparts. In the larvae of different taxa of wood-boring Coleoptera, the general organization is the same: the labrum is subrectangular and bordered with setae on the distal margin; laterally and posteriorly to it mandibles are present and, behind these, the maxillae with galea, lacinia and palps; back and medially, the labium, with postmentum, prementum and palps (Fig. 2).

Mandibles are the appendages used to break down wood. They are usually short and heavily sclerotized, especially along the medial margin, where the strength of the jaws seems to be due to the presence of zinc and manganese that have been found in larval mandibles of anobiids and long-horned beetles (Hillerton *et al.*, 1984, Morgan *et al.*, 2003).

The overall shape of the mandibles of wood-boring larvae is very much the same; even if morphological differences are present between different taxonomic entities. In most Anobiidae, the larvae exhibit toothed mandibles with a medial margin characterized by triangular teeth (Fig. 2, A). This shape makes it possible to detach little wooden pieces from the timber mass, which are subsequently brushed into the cibarium by means of labrum, laciniae, and labium setae.

Lyctid larvae, such as those of *Lyctus linearis* (Goeze) (Fig. 2, B), have "chisel-shaped" mandibles, with the medial margin, perpendicular to its major axis, without teeth but linear and sharp.

The same type of mandible is present in cerambycid larvae (Haack & Slansky, 1987) like, for example, those of *Hylotrupes bajulus* (Linnaeus) (Schmidt & Parameswaran, 1977) and those of *Trichoferus holosericeus* (Rossi) (Fig. 2, C). Mandibles shaped much like these are also found in *Ptilinus pectinicornis* (Linnaeus) (Anobiidae), where the remains of a small tooth are present in the lower corner of the medial margin (Fig. 2, D).

Being present in Coleoptera families phylogenetically far from each other (Anobiidae, Cerambicidae, Lyctidae) (Fig. 1), contrary to what was stated by Schmidt (1966), the peculiar shape of these jaws does not appear to be linked to the systematic group but could represent an evolutionary convergence due to the type and mode of feeding and digestion.

Watanabe & Tokuda (2010) assumed that the reduction in size of the mandibles in wood-eating insects would confer an advantage by allowing finer wood powder to be produced, that would correspond to an increased "exposure of cellulose fibers buried
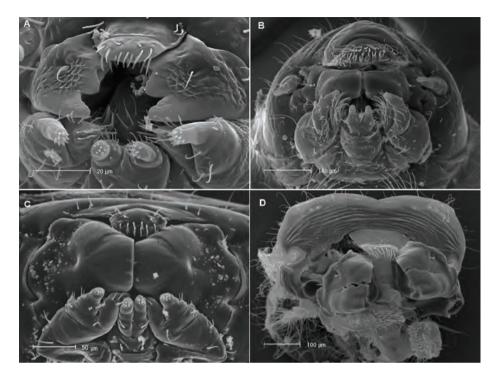
Fig. 2 - Larval biting mouthparts of four species of wood-boring beetles: A. *Stegobium paniceum* (Linnaeus) with mandibles characterized by triangular teeth on their medial margin. B. *Lyctus linearis* (Goeze) with "chisel shaped" mandibles, with linear and sharp medial margin. C. *Trichoferus holosericeus* (Rossi) with chisel-shaped mandibles. D. *Ptilinus pectinicornis* (Linnaeus), with mandibles very similar to chisel-shaped ones but with remains of a small tooth in the lower corner of the medial margin.

in hemicellulose and lignin", thus enhancing "the access of cellulolytic enzymes to cellulose". Nevertheless, they specifically state that "it has not been elucidated so far whether a reasonable correlation exists between designs and sizes of mandibles and the efficiency of wood crushing in coleopterans".

The study of the frass produced by these different types of larvae, considering the size of the individuals producing it, can help to elucidate larval habits (Solomon, 1977). The species having toothed mandibles produce gritty frass consisting of fusiform faecal particles, thus indicating that all the dug wood passes through the alimentary canal. On the contrary, all the species considered that possess chisel-shaped mandibles produce a very fine frass, mixed with faeces, thus signifying that they dig more wood than they ingest. In addition, we observed that toothed mandibles are able to detach little pieces of wood from the mass, while chisel-shaped mandibles make it possible to pulverize the wood to very fine fragments.

In agreement with Watanabe & Tokuda (2010), this could be functional to better digestion of cellulose but we hypothesize that the rupture of cell walls would expose the starch granules which should thus be available for digestion. Therefore, these mandibles would be suited to larvae that feed mainly on starch and which, being unable or not very efficient in cellulose digestion, need to gain access to starch without necessitating the digestion of the cell walls.

This interpretation is consistent with the kind of wood attacked by these different larvae. Most anobiid species, which possess toothed mandibles, also attack the duramen or very seasoned wood, both very low in starch, because they feed also on cellulose and hemicellulose (Eaton & Hale, 1993). Of the larvae that show chisel-shaped mandibles, lyctid larvae feed exclusively on starch and attack sapwood of "susceptible hardwood species which have sufficient starch (ca. >3%)" and they are called powderpost beetles because they "reduce the wood to flour-like powder" (Eaton & Hale, 1993). *Hylotrupes* and *Trichoferus* larvae generally attack sapwood, even if they can also tunnel in heartwood (Eaton & Hale, 1993) and their frass also is composed of extremely fine wood fragments mixed with faeces (Chiappini *et al.*, 2010). *P. pectinicornis* larva attacks sapwood and produces a fine, silky frass, densely packed (Eaton & Hale, 1993). It seem obvious that wood-boring Coleoptera that cannot digest cellulose or that digest it at a low rate take advantage of the disruption of wood walls operated by chisel-shaped mandibles and, in search of starch, dig more than what they ingest, producing a fine frass, mixed with faeces. These type of mandibles could therefore represent an evolutionary convergence towards better starch utilization.

Body adaptations for anchorage

The peculiar lifestyle of the larvae of wood-boring beetles, which have a minimal need of movement but necessitate a tight hold on the wood, essential for their gnawing, involves morphological adaptations which can differ according to the systematic groups and regarding the taking off the food and the correlative locomotion. A more or less evident reduction of the legs in the larvae, sometimes even their total absence, corresponds to the limited requirement of moving in a narrow space. In the oligopod larvae of the Lyctidae (e.g. *Lyctus* spp.) and of some Anobiid species (e.g. in gen. *Anobium*, *Stegobium*, etc.) the legs, developed even if relatively short and tiny, seem to perform different functions besides moving (Cymorek, 1968). On the other hand, cerambycid larvae are either apod or only keep vestigial rudiments of legs (e.g. gen. *Hylotrupes*, *Trichoferus*) (Gardiner, 1960; Peterson, 1960).

The need to gnaw a compact, and often very hard substrate, such as wood is, in addition to the structure and constitution of the mandibles mentioned above, is therefore met by other devices such as rough areas on the thoracic and abdominal surfaces of the body, as well as rows of spicules, which can be useful also for movement, but which principally permit the anchorage necessary to the larva during its prolonged feeding activity. In cerambycid larvae, for example, besides the nearly prognathous head, immersed into the prothorax, and bearing short and extremely strong mandibles, the surface of thorax and abdomen often show ambulatorial areas consisting of dorsal and/or ventral integumental corrugated and thickened plates (Grandi, 1951). Without

any doubt, the larva is helped in taking off the food also by the limited diameter of the tunnel and by filling it behind with compact frass and excrement.

The anobiid larvae are generally scarabaeiform (C-shaped), with a hypognathous head (but sometimes nearly prognathous); therefore it is likely that their activity of excavation, alimentation and progression differs in comparison with that of cerambycids. In the majority of their larval forms, anobiids (e.g. *Anobium* spp.) bear transversal rows of hooks on the anterior dorsal folds of most of the toracic and abdominal segments and on the sides of the ninth abdominal segment (Parkin, 1933; Böving, 1954). Towards the end of the abdomen, these hooks can be larger, clearly curved. These larvae bend and push their distal end towards the tunnel wall; they subsequently straighten, stretching forwards.

Also in lyctids the larva is C-shaped, but the body surface (e.g. in the genus *Lyctus*) is completely free of anchoring hooks, possibly because larval activity occurs in a relatively tender wood, that can be tunnelled more easily.

Endosymbiosis and nutrition

The ability of many insects to use unpromising foodstuffs, as also wood is, is due to cryptic microbial assistance (Dadd, 1985). Besides ectosymbiosis with fungi in ambrosia beetles (Scolytidae), and in other wood-boring beetles (e.g. *Anobium punctatum* (DeGeer) and *Xestobium rufovillosum* (DeGeer)) that develop preferably in rotten wood (Bletchly, 1953), it is well known that two other types of symbiosis with microorganisms occur in wood-boring beetles, namely extracellular endosymbiosis, limited to intestinal lumen, and intracellular endosymbiosis (endocytobiosis) (Nardon & Grenier, 1989). Both types are mutualistic symbioses, not excluding each other and with possible intermediate forms.

In wood-boring beetles, the presence and the role of gut extracellular endosymbiosis is still very little known (Vasanthakumar *et al.*, 2007). The role of this type of endosymbiosis could be that of entirely or partly supplying enzymes, necessary for cellulose utilization (Chapman, 1972). In fact, even if the formerly hypothesized acquisition of cellulases has been challenged by the discovery of endogenous enzymes in anobiids and cerambycids (Parkin, 1940; Martin, 1983), the microorganisms could play a role in freeing cellulose and hemicellulose from lignin (Genta *et al.*, 2005). The detoxification activity, that has been demonstrated for the anobiid *Lasioderma serricorne* (Fabricius) (Shen & Dowd, 1991), could also be proved for wood-boring species.

Endocytobiosis is the third type and best known symbiosis in wood-boring beetles infesting timber. It is a complex type of endosymbiosis which seems to have the main function of supplementing insect diets lacking in some essential nutrients, i.e. vitamins (especially of the B-group), lipids, sterols, amino acids and, maybe, other growth factors, increasing the fitness of the insect to the environment and substrate (Nardon & Grenier, 1989). In their turn, intracellular symbionts (endocytobiotes) take advantage of being protected from a dry environment and having availabile a substrate rich in carbon sources. There are, however, more complex metabolic interactions between host and endocytobiotes that behave as cellular organelles regulated by the host itself. In fact, they can modulate enzymatic activities, metabolism of certain amino acids, etc..

Endocytobiotes are yeasts or bacteria included in specialized cells, mycetocytes and bacteriocytes respectively, lodged singly between the epithelial cells of the midgut, or grouped to form organs (symbiosomes), variously located as to the gut, named mycetomes and bacteriomes, respectively.

According to the host species, symbiosomes are present only in the larvae, or both in larvae and adults. Endocytobiotes are always maternally inherited, following two main routes, as mentioned later on.

In powderpost beetles, for example in *L. linearis*, symbiotes are bacteria or bacterium-like organisms in bacteriomes located in the posterior third of the larva, close to the fat body; the matrifilial transmission is transovarial. In the adult female, symbiotes migrate into ovaries and infect ovocytes so that the intracellular condition of the symbiotes in the host is therefore almost permanent. Also in Bostrichidae (a family which also includes some species that damage seasoned wood), for example in the genus *Sinoxylon*, endocytobiotes are bacteria or bacterium-like organisms which are transmitted with transovarial modality (Nardon & Grenier, 1989).

In anobiids, endocytobiosis is widespread and relatively well-known; symbiotes are yeasts or yeast-like organisms, located more or less close to the midgut of the larva and present also in adults, in the same location. The matrifilial transmission is performed by the ovipositor, which is provided with intersegmental tubules and vaginal pouches from which the symbiotes, which secondarily transmigrated here, are expelled during the oviposition and fixed with secretions on the corion (egg smearing). The emerging larva is re-infected when it devours part of the eggshell. In *Stegobium paniceum* (Linnaeus), mycetocytes are located in ceca of the midgut, close to its junction with the foregut; in *Anobium* spp. they are gathered similarly in blind sacs, not connected with the gut; in *P. pectinicornis*, instead, mycetomes are connected with the midgut by a narrow canal.

Numerous species of Cerambycidae have been observed to be symbiotic. In cerambycid endocytobiosis, similarly to anobiid ones, symbiotes are yeasts or yeast-like microorganisms, mycetocytes are kept in evaginations located at the beginning of the larval midgut (described for example in *Tetropium*), the matrifilial transmission occurs through deposition of yeasts on the egg surface. Nevertheless, endocytobiosis is less widespread in Cerambycidae than in Anobiidae as in many long-horned beetles (*H. bajulus* among them) it has not been found. In larvae of Cerambycidae having endocytobiotes, a constant elimination of mycetocytes in the lumen of the gut can be observed, and constant replacement by re-infection of gut cells by yeasts exists. Therefore, as in this case symbiotes present an intracellular and an extracellular phase, they could represent an example of an intermediate condition between endocytobiosis and extracellular intestinal symbiosis (Nardon & Grenier, 1989).

Considering that the significance of endocytobiosis should be that of providing lacking nutrients to the larva and not enzymes for cellulose digestion, it is difficult to explain why it is absent in *H. bajulus*, which lives on seasoned wood. In fact, in Lyctidae, which feed exclusively on starch, these symbioses are present all the same. Not for this reason alone, it must be admitted that the biological significance of endocytobiosis in wood-boring beetles is still relatively unknown.

Peculiar features in tracheal spiracles

Undoubtedly, the presence of more or less fine frass inside the gallery and the fact that such an environment is often rather or very dry also affects the respiratory system. Structural and functional adaptations, some evidence of which is found in the surface respiratory devices, the tracheal spiracles, are needed. In wood-boring larvae, the most obvious risk is that tiny wood fragments enter the tracheal lumen, compromising gas exchanges. Indeed, when the trachea is in communication with the outside, and air penetrates as an effect of the depression, small wood particles could be sucked into the inner space of the tube and occlude it. At the same time, there is the need to minimize water vapour losses through spiracles, due to transpiration, as a consequence of the gradient existing between the lumen of tracheal ramifications and the dry air in the tunnel.

Spiracles with highly developed filter mechanisms in order to exclude extraneous particles and/or to reduce loss of humidity, are suited to preventing both risks (Mill, 1985; 1998). Nevertheless it is noteworthy that many other kinds of insects (beetles of other families, flies, etc.) living in heterogeneous habitat conditions, have, as Berlese (1909) already noted, analogous exigencies and are provided with spiracular 'filters' morphologically varying but with a common structural feature that is the presence of
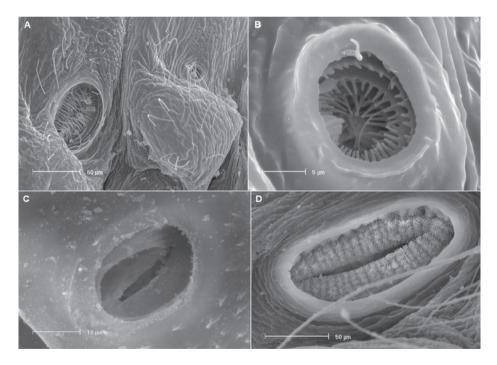

Fig. 3 - Spiracles of wood-boring beetles observed under SEM. *Lyctus linearis* (Goeze): A. Abdomen extremity of the larva with the last two spiracles; B. Penultimate abdominal spiracle; C. adult abdominal spiracle; D. *Trichoferus holosericeus* (Rossi), larval thoracic spiracle.

ramified and intersected hairs, in order to create a barrier at the level of spiracular entrance.

The observation of spiracles of some of the wood-boring beetle larvae considered above shows clear morphological adaptations responding to the double requirement (Fig. 3). The operating mode of the respiratory system in insects could also explain the function of the filtering spiracles. When air is sucked into the tracheal lumen by means of the depression existing between the outside and the inside, wood particles are stopped by the hairs, but when the air is actively pushed out, it cleans the spiracle sieve.

The idea that this kind of spiracle represents an adaptation to the peculiar conditions in which wood-boring Coleoptera larvae live could be validated by the observation that adult spiracles in the same species do not present such structures.

In conclusion, all the abovementioned structural and functional adaptations of wood-boring beetles, with particular reference to those damaging timber, demonstrate "the strong moulding force which wood passively exerted on its insect inhabitants", and reflect one of the most marked specializations of beetles to a very challenging environment (Cymorek, 1968).

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