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ZOOLOGY

General Brain Structure of Newly Hatched Larva and Neuroblasts in Larval Mushroom Bodies in *Pterostichus niger* Deg. (Coleoptera: Carabidae)

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Abstract—It is revealed that the larval brain of *Pterostichus niger*, an active predator with well-developed long-distance sense organs (the set of antennal sensilla and lateral ocelli, or stemmata) at hatching already contains optic lobes, which include two groups of optic neuropils and complex antennal lobes of glomerular neuropil. It is shown that the central complex of the protocerebrum is represented by a bipartite protocerebral bridge and the upper part of the central body and the mushroom bodies include numerous Kenyon cells, a well-developed calyx, a peduncular apparatus, and numerous neuroblasts.

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INTRODUCTION

A recent study of mushroom bodies in ground beetles (Carabidae) confirmed their tripartite general structure and revealed considerable differences in the degrees of their development between representatives of different taxa within this family. It was found that mushroom bodies are especially strongly developed in representatives of the supertribes Pterostichitae and Harpalitae (Panov, 2013). Their mushroom bodies contain large calyces with an extended glomerular neuropil zone and numerous Kenyon cells, which occupy the entire volume of the dorsocaudal protrusions of the brain, the so-called frontal tubers.

It has long been known that Kenyon cells are formed by proliferation of single or grouped neuroblasts (Bauer, 1904; Schrader, 1938; Panov, 1957). Carabids with poorly developed mushroom bodies have only three single neuroblasts in each brain hemisphere; these neuroblasts produce three subgroups of Kenyon cells and are preserved even in some adults (Panov, 2013). At the same time, numerous neuroblasts, both single and grouped, were found in the mushroom bodies of juvenile adults in those carabid species that have many Kenyon cells. For instance, in juvenile specimens of *Pterostichus niger*, up to 11 such proliferation centers were found in each mushroom body, each of these centers containing one to five neuroblasts. A total of 19 to 28 neuroblasts were found in each mushroom body in different specimens.

This raised the following questions: When and how do proliferating cells multiply during ontogeny? Is there only a set of three single neuroblasts, which corresponds to the number of subdivisions of the mushroom body and has been found in species with poorly developed mushroom bodies, during early postembryonic development, or does a newly hatched larva already have a complicated set of neuroblasts? In looking for answers to these questions, I found that there are no published data on the general structure of the brain in carabid larvae. Therefore, in this study a general description of the brain of a newly hatched *P. niger* larva is provided and then the neuroblasts of larval mushroom bodies are described.

MATERIALS AND METHODS

P. niger is a species with the late-summer–autumn breeding type; mature females are found near Moscow mainly during August. Males and females of *P. niger* were collected in a mixed forest in the environs of Moscow using pitfall traps; the beetles were kept in the laboratory in pairs, in 10 × 8 × 3.5 cm plastic containers half-filled with earth from a vegetable garden. Each container was provided with a small tube with water and stopped up with a cotton wool wad and one or two dry tree leaves as shelter. The beetles were fed with larvae of *Lucilia* sp. and fragments of *Tenebrio molitor* larvae, replaced daily. The eggs were removed from the earth after 3 or 4 days, so as not to disturb the females too much. The duration of embryogenesis in the laboratory was about 10 days.

The larvae were fixed in Bouin's fluid, embedded in paraplast, and 6-μm sections were stained with iron hematoxylin by Heidenhain's method (Romeis, 1953). Digital images were taken with a JVCKYF55B camera (Japan) using a Leica DMR microscope (Germany). The images of the head and eyes were taken using a Keyence VHX-1000 microscope (Japan). All

images were processed using the program Adobe Photoshop CS2.

RESULTS

The head of a newly hatched larva is relatively large and has well-developed sense organs. When the first instar larva molts, the head becomes larger, but the other characteristics of the head remain unchanged (Fig. 1a). The antennae are large and directed anteriad, as in other predaceous hemicryptobiont larvae (Sharova, 1981). Six stemmata are situated on each side of the head in two rows behind the antennae. The three stemmata of the anterior row are larger and have protruding corneas. The three stemmata of the posterior row are smaller and not so convex (Fig. 1b).

The brain is situated directly under the hypodermis of the frontal triangle. It is clearly subdivided into two hemispheres by a deep dorsal furrow, with groups of neurosecretory cells of the pars intercerebralis and groups of Kenyon cells on both sides of this furrow. The rather small mammiform optic lobe is situated anterolaterally on each half of the brain; the long optic nerve runs from this lobe to the stemmata. The long antennal nerves connect deutocerebral regions of the brain to the antennae.

The brain of a newly hatched larva of *P. niger* is strongly differentiated. The optic lobes include two well-structured neuropils (Fig. 1c). The distal neuropil, into which fibers of the optic nerve enter, is formed by six elongate cylindrical bodies, which are less strongly stained along the axis and have a denser periphery. In some sections, which run across the distal neuropil, rings of pale structures were visible in the most external layer of the cylindrical bodies; these structures are tentatively interpreted as thick fibers that have been cut (Fig. 1d).

The distal neuropil is connected by a short layer of noncrossing fibers to the larger proximal neuropil lying between the distal neuropil and the brain, to which it is connected by a slender bundle of fibers. This second neuropil, principally similar to the first neuropil, consists of elongated cylindrical bodies, which are thicker than the cylinders of the first neuropil and lack the pale peripheral areola (Fig. 1c).

The optic lobes in newly hatched larva of *P. niger*, as in larvae of other insects (Schrader, 1938; Panov, 1960; Meinertzhagen, 1973), contain two proliferative centers represented by neuroblast clusters near the distal neuropil and between the proximal neuropil and the neuropil of the protocerebrum per se. These so-called Bildungsherde, according to the terminology of German authors (Bauer, 1904), are very poorly developed in newly hatched larvae, but at the end of larval development they become clearly visible formations consisting of numerous neuroblasts (Fig. 1e).

The antennal lobe has a complex structure. Two main neuropil masses can be recognized within this lobe. The first, larger one, most strongly resembles the typical antennal lobe of the adult. It consists of numerous glomerules, which form a morula-shaped structure; fibers of the antennal nerve run into the central part of this structure, and fibers of the antennoglobular tract run out of it. The second neuropilar mass is shaped like a horseshoe placed anteriorly onto the antennal globular tract near its entrance into the main neuropil mass of the antennal lobe. Therefore, the second neuropil mass is visible in sections that run along this tract as divided by the tract into two halves (Fig. 1f).

The central complex of a newly hatched larva is represented by two structures: the protocerebral bridge and the upper part of the central body. After staining with iron haematoxylin, regular compartmentalization of the neuropil was revealed in neither of the centers. The protocerebral bridge consists of two elongated bands of the homogeneous neuropil separated by a gap in the area of the medial plane of the brain (Fig. 2a). The lateral ends of the protocerebral bridge are, as usual, curved backwards, and therefore, in sections more caudal than the one shown in Fig. 2a, the protocerebral bridge appears as two rounded sections of the neuropil situated above the medial part of the protocerebral lobes. The upper part of the central body appears as a narrow band of dense neuropil, rounded in cross section and crossed by numerous slender fibers (Fig. 2b).

All parts of the mushroom bodies are well differentiated. The Kenyon cells are numerous; their bodies occupy almost all frontal tubers of the protocerebrum and clearly differ from bodies of other neurons in the smaller size and extremely narrow layer of the cytoplasm around the nuclei. If the preparation is well fixed, the bodies of the Kenyon cells are in tight contact with each other, and the entire group appears as one (Fig. 2c). If the preparation is unsatisfactorily fixed, the cells become somewhat shrunken, and then the Kenyon cell group in each mushroom body is seen as divided into three subgroups (Fig. 2d).

The peduncular apparatus includes the pedunculus and both lobes. A characteristic feature of the structure of all parts of the peduncular apparatus is the presence of a pale axial zone, which begins already in the calyx, runs through the entire pedunculus, and ends near the very apices of the lobes (Fig. 2c). This pale zone is especially wide in newly hatched larvae, but it gradually narrows and becomes looser in the course of larval development.

The calyx includes a well-developed glomerular neuropil zone; fibers of the antenno globular tract pass through this zone. The dorsocaudal part of the calyx consists of a homogeneous neuropil perforated by three bundles of loosely located fibers, which run at the base of the calyx into the pale core of the pedunculus (Fig. 2c).

In most cases, 18–22 neuroblasts were found in each mushroom body of a newly hatched larva. They were either distributed singly among Kenyon cells or formed groups of 2–8 neuroblasts (Fig. 2c). It was possible to determine to which of the three Kenyon

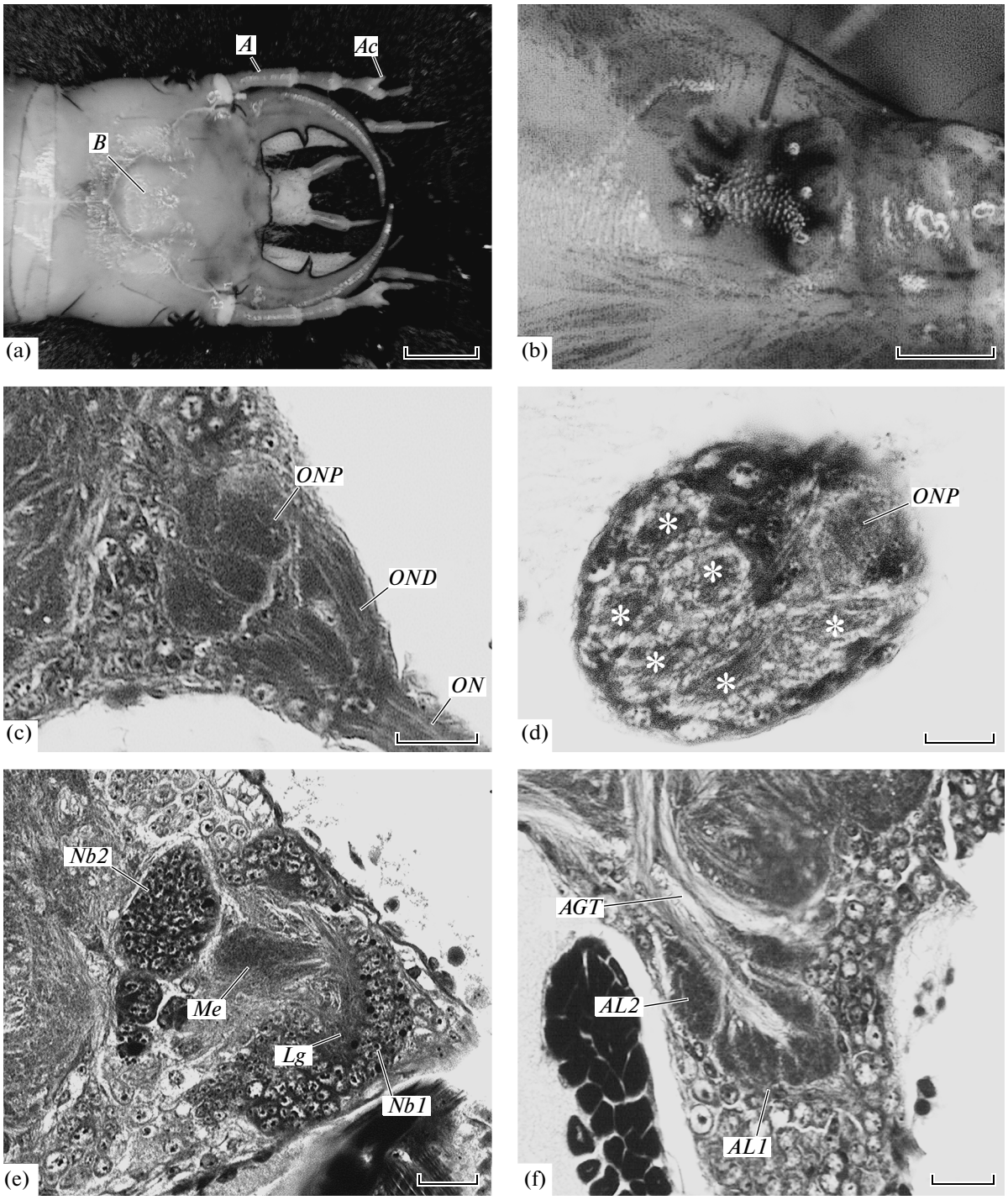

Fig. 1. Sense organs and brain in larva of *Pterostichus niger*: (a) habitus of head; (b) stemmata; (c) optic lobe; (d) zone of distal neuropils of the optic lobe (asterisks mark sections of six distal neuropils); (e) optic lobe with clusters of neuroblasts; (f) deutocerebral region ((a) newly molted 2nd instar larva; (b–d, f) newly hatched larva; (e) early 3rd instar larva; (c, e, f) frontal sections; (d) oblique cross section); notation: (*A*) antenna; (*Ac*) antennal sensitive cone; (*AGT*) antennoglobular tract, (*AL1, AL2*) 1st and 2nd glomerular masses of antennal lobe; (*B*) area of frons overlying brain; (*Lg*) lamina; (*Me*) medulla; (*Nb1, Nb2*) 1st and 2nd clusters of neuroblasts in optic lobes; (*ON*) optic nerve; (*OND*) distal optic neuropils; (*ONP*) proximal optic neuropils. Scale bars: (a) 0.5 mm; (b) 0.1 mm; (c, e, f) 20 μm; (d) 10 μm.

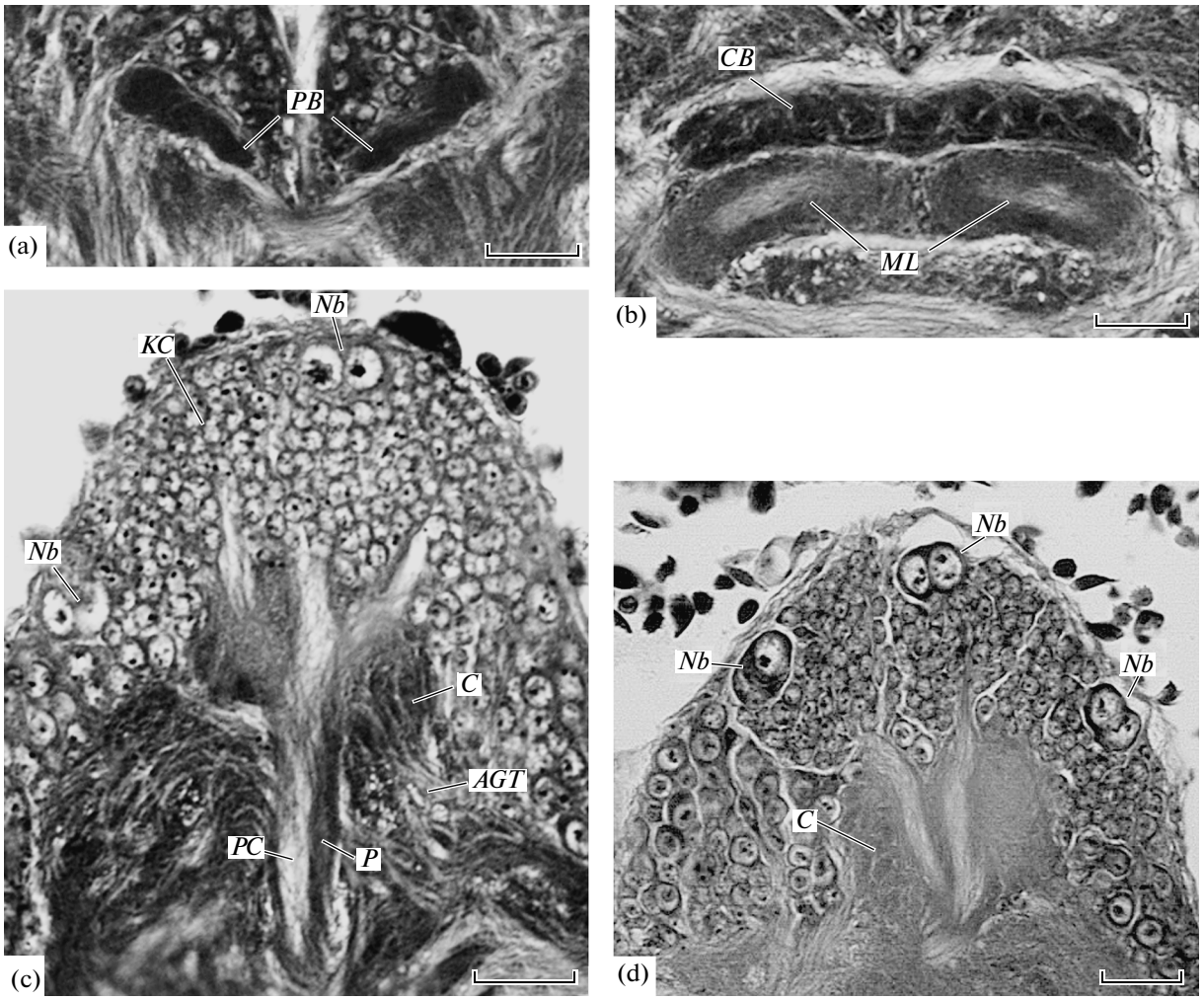

Fig. 2. Frontal sections of the central protocerebrum of newly hatched larva of *Pterostichus niger*: (a) protocerebral bridge; (b) upper part of central body and apices of medial lobes of mushroom bodies; (c) group of Kenyon cells and mushroom body calyx; (d) three subgroups of Kenyon cells and their corresponding neuroblasts; notation: (*C*) calyx; (*CB*) upper part of the central body; (*ML*) medial lobes of mushroom bodies; (*Nb*) neuroblasts; (*P*) pedunculus; (*PB*) protocerebral bridge; (*PC*) loose core of pedunculus; other notation as in Fig. 1. Scale bars, 20 μm.

cell subgroups the neuroblasts belong only in some preparations with slightly unsatisfactory fixation, which resulted in shrinkage of cells that revealed the boundaries between cell subgroups (Fig. 2c).

Divisions of both single and grouped neuroblasts could be seen in the preparations. These divisions were mostly mitoses at metaphase, from which it is impossible to draw conclusions about the type of division. At late anaphase or early telophase, only uneven divisions of neuroblasts into the daughter neuroblast and ganglion mother cell were visible. Even divisions of ganglion mother cells occurred frequently.

As shown by the rather few preliminary calculations, the number of neuroblasts in mushroom bodies remains approximately unchanged in newly molted 2nd instar larvae. However, in the early 3rd instar larva their number approaches 30, and in one such larva a total of 35 neuroblasts were found in one mushroom body. Moreover, in 3rd instar larvae the proportion of single neuroblasts increases and the number of neuroblasts in groups decreases compared to newly hatched larvae.

DISCUSSION

Larvae of the genus *Pterostichus* are nonspecialized predators, which according to their morphoecological characteristics belong to litter–soil hemicryptobionts (Sharova, 1981). As shown by this study, the general organization level of their brain already in the newly hatched larva is one of the highest among insects studied so far. Their brain contains almost all principal sensory and associative centers, which are highly differentiated.

Visual system. Larval ocelli (stemmata) are extremely variable morphologically among beetles

(Gilbert, 1994). The initial state for larvae of the suborder Adephaga is the presence of six or seven stemmata on each side of the head. The composition and degree of development of stemmata in the larva of *P. niger* are apparently close to this initial state. However, in larvae of many other species of Carabidae, the visual apparatus becomes reduced (Sharova, 1981), and in some members of other families of the suborder Adephaga, considerable differentiation of stemmata has been noted. Thus, in tiger beetle larvae, which are burrowing ambush predators, two stemmata on each side of the head are considerably enlarged and play a crucial part in catching prey (Friederichs, 1931). A similar increase in the size of some stemmata is found in the larva of the diving beetle *Thermonectus marmoratus* (Mandapaka et al., 2006), and the larva of the whirligig beetle *Dineutus sublineatus*, an ambush predator waiting for prey bedded in the substrate, stemmata are divided into two groups: three for the upper field of vision and three for the lower field of vision (Lin and Strausfeld, 2013).

The larval optic centers have been studied only in a limited number of beetle species. It was suggested earlier based on preliminary observations that the visual system of campodeous beetle larvae includes a complete set of three sequentially located ganglia; in fact the structure interpreted as the third visual ganglion (the lobule) was probably a rather small lateral process of the protocerebral neuropil (Panov, 1960). Modern studies have shown that even if the organs of sight are well developed, beetle larvae of the suborder Adephaga—*Cicindela chinensis* (Toh and Mizutani, 1994), *D. sublineatus* (Lin and Strausfeld, 2013), *P. niger* (this study)—probably have only two optic ganglia. Furthermore, in *T. marmoratus*, although it has well-developed stemmata, only one "floor" of optic neuropils was found (Sbita et al., 2007).

The optic neuropils closest to the stemmata are traditionally viewed as corresponding to the first optic ganglion (the lamina) of the compound eyes of adults, as confirmed by a study on the ontogeny of the visual system in some insects (Panov, 1960). The more proximal row of neuropils is usually considered as corresponding to the medulla of the compound eye (Toh and Mizutani, 1994).

However, it was proposed recently that the second row of neuropils (or the second single neuropil) in adephagan larvae might correspond to the prematurely differentiated lobular plate (Lin and Strausfeld, 2013). This interpretation was based on the absence of crossing of fibers running between the first and second rows of neuropils (such a crossing is typical of connections between the lamina and medulla in visual centers of adults) and the presence of wide-field tangential neurons in the second neuropil of the larva of the whirligig beetle *D. sublineatus* (such neurons are similar to those found in the lobular plate of the higher Diptera).

The following question arises: How do we interpret the second row of neuropils in the optic lobe of a newly hatched larva of *P. niger*? In looking for the answer, we should probably consider two facts. First, the existence of two crossings of fibers connecting the optic ganglia of compound eyes is probably determined by the special packing of ganglia inside the optic lobes of insects, so that gradual addition of new neural elements in the course of growth of visual centers happens in opposite directions: anteromedial in the lamina (in accordance with the direction of eye growth), caudal in the medulla, and from the basal to peripheral (most remote from the protocerebral neuropil) part of the ganglion in the lobula (Panov, 1960; Meinertzhagen, 1973). The formation of the oligomerized larval visual system is probably rather rapid, and the anteroposterior gradient of differentiation of the embryonic epithelium is probably absent in the area in which stemmata are formed. It is possible that the laying of the visual neuropils also happens at one time. This is apparently the physical foundation of the absence of crossing of fibers between the first and second neuropils in the larval visual system.

Second, the key argument for solving the problem of the homologization of ganglia is the position of two neuroblast clusters from which the adult visual centers are formed. These clusters occupy a quite stable position in the optic lobe of holometabolous and hemimetabolous insects: the semicircular external cluster lies near the lamina, while the internal cluster lies between the medulla and lobula (Bauer, 1904; Panov, 1960; Meinertzhagen, 1973). In a newly hatched larva of *P. niger*, the external cluster, as noted above, is situated between the first and second optical neuropils and the internal cluster neuropil of the protocerebral lobe. Therefore, the second neuropils in *P. niger* apparently correspond to the medulla of the compound eyes of the adult.

Antenna and antennal lobes. The antennae of carabid larvae bear a rich set of sense organs, which include at least ten types of sensilla; special among them is the so-called antennal cone (or antennal sensory appendage), situated on antennomere 3 (Sinitsyna and Chaika, 2003). The great number of chemoreceptory neurons present in the antennal cone gives evidence that the larvae could be capable of finely distinguishing between smells while looking for prey (Giglio et al., 2008). Therefore, it is no surprise that a newly hatched larva of *P. niger* already has well-developed antennal lobes with structured glomerular neuropil. Very little is known about the presence of glomerules in the antennal lobes of newly hatched larvae of other beetles. They were found in newly hatched larvae of *T. molitor*, but they are absent in newly hatched larvae of some other beetles and lepidopterans (Panov, 1961). In mature beetle larvae, glomerular antennal lobes are present in many species (Bretschneider, 1914; Jawlowski, 1936).

Central complex. In adults the central complex typically consists of four components: the protocerebral bridge, upper and lower parts of the central body, and nodules (Pfeiffer and Homberg, 2014). This entire set of structures has not been found in the larval brain of any holometabolous insect. Larvae have at most the protocerebral bridge and the upper part of the central body. Such a central complex has been found only in newly hatched larvae of *T. molitor* (Panov, 1959; Wegerhoff and Breidbach, 1992) and in the saturniid moth *Antheraea pernyi* (Panov, 1959), although it has not been found in newly hatched larvae of either *Pieris brassicae* (Hanström, 1925) or *Ephestia kuehniella* (Schrader, 1938) or *Archips podana* (Shirokov and Chaika, 2014).

The lower part of the central body is formed in holometabolous insects only during metamorphosis (Pfeiffer and Homberg, 2014). The only known exception is the calliphorid fly *Phormia regina*: the central complex is absent in newly hatched larvae, and during its formation in the course of larval and pupal development, the lower part of the central body, the ellipsoidal body, is formed first (Gundersen and Larsen, 1978).

Mushroom bodies. In newly hatched larvae of *P. niger*, mushroom bodies are probably much more strongly developed than in newly hatched larvae of other beetles studied earlier (Panov, 1957). They are very close in degree of differentiation to mushroom bodies of the adult insect, except, of course, for the considerably smaller number of Kenyon cells and, accordingly, the less strongly developed peduncular apparatus. A special characteristic feature of the peduncular apparatus of larvae is the strong development of the "core" in the pedunculus and lobes; this structure consists of sparsely set fibers separated in fixed material by large intervals. A similar, but less strongly pronounced pale core was previously found in the peduncular apparatus of juvenile adults (Panov, 2013) and was interpreted as the zone into which processes of newly differentiated Kenyon cells grow; such a zone was described in some insects (Strausfeld et al., 2003; Mashaly et al., 2008; Zhao et al., 2008).

It is easy to explain the absence of the so-called horn, the innermost part of the neuropil protruding beyond the vertical lobe, in newly hatched larvae. The horn is very typical of the mushroom body in adults (Panov, 2013), but it is apparently absent in newly hatched larvae because those Kenyon cells the processes of which will form this structure at later stages of ontogeny have not yet formed. The course of the growth of fiber layers in the peduncular apparatus was studied in detail in *Tribolium castaneum* (Zhao et al., 2008).

Comparison of the general structure of mushroom bodies with the number of neuroblasts that form these bodies in the most basal taxa within the family Carabidae leads to the conclusion that initially each mushroom body of carabids had three single neuroblasts, each of them giving rise to one of the three subgroups of Kenyon cells. In advanced carabid taxa, the number of Kenyon cells increases considerably, and the number of neuroblasts increases accordingly (Panov, 2013). It was found that the number of neuroblasts in newly hatched larvae of *P. niger* is as much as 6–7 times higher than their suggested initial amount, and this number slightly rises in the course of larval development. Considerable growth of the number of neuroblasts of mushroom bodies has been recorded so far only in honeybees (Malun, 1998; Farris et al., 1999) and ants (Ishii et al., 2005), but it takes place only at postembryonic stages.

There are no answers yet to the following two questions: How do polyneuroblast proliferation centers form? Do they initiate at once as multicellular formations or are they formed as a result of division of few neuroblasts? It was observed in honeybees that neuroblasts divided evenly, resulting in an increase in their numbers (Malun, 1998). The chance to observe such divisions was apparently determined by the great number of neuroblasts in mushroom bodies and by the intensity of the general development of honeybee larvae and pupae. In larvae of *P. niger*, the number of neuroblasts in mushroom bodies is considerably smaller and the duration of development of these larvae is great. This is probably what explains the fact that the pattern of even division of neuroblasts could not be seen in the preparations.

REFERENCES

Bauer, V., Zur inneren Metamorphose des Zentralnervensystems der Insekten, *Zool. Jb. Anat.*, 1904, vol. 20, pp. 123–152.

Bretschneider, F., Über die Gehirne des Goldkäfers und des Lederlaufkäfers, *Zool. Anz.*, 1914, vol. 43, no. 11, pp. 490–497.

Farris, S.M., Robinson, G.E., Davis, R.L., and Fahrbach, S.E., Larval and pupal development of the mushroom bodies in the honey bee, *Apis mellifera, J. Comp. Neurol.*, 1999, vol. 414, pp. 97–113.

Friederichs, H.F., Beiträge zur Morphologie und Physiologie der Sehorgane der Cicindelinen (Col.), *Z. Morphol. Ökol. Tiere*, 1931, vol. 21, nos. 1–2, pp. 1–172.

Giglio, A., Brandmayr, P., Ferrero, E.A., Giulianini, P.J., Perrota, E., Talarico, F.F., and Zetto Brandmayr, T., Ultrastructure of the antennal sensorial appendage of larvae of *Ophonus ardosiacus* (Lutshnik, 1922) (Coleoptera, Carabidae) and possible correlations between size and shape and the larval feeding, *Zool. Anz.*, 2008, vol. 247, pp. 209–221.

Gilbert, C., Form and function of stemmata in larvae of holometabolous insects, *Ann. Rev. Entomol.*, 1994, vol. 39, pp. 323–349.

Gundersen, R.W. and Larsen, J.R., Postembryonic development of the central complex and protocerebral bridge of *Phormia regina* Meigen (Diptera: Calliphoridae), *Int. J. Insect Morphol. Embryol.*, 1978, vol. 7, nos. 5/6, pp. 455–465.

Hanström, B., Comparison between the brains of the newly hatched larva and the imago of *Pieris brassicae* L., *Entomol. Tidskr.*, 1925, vol. 46, pp. 43–52.

Ishii, Y., Kubota, K., and Hara, K., Postembryonic development of the mushroom bodies in the ant, *Camponotus japonicus*, *Zool. Sci.*, 2005, vol. 22, pp. 743–753.

Jawlowski, H., Über den Gehirnbau der Käfer, *Z. Morphol. Ökol. Tiere*, 1936, vol. 32, no. 1, pp. 67–91.

Lin, Ch. and Strausfeld, N.J., A precocious adult visual center in the larva defines the unique optic lobe of the split-eyed whirligig beetle *Dineutus sublineatus*, *Frontiers Zool.*, 2013, vol. 10, no. 10, pp. 1–10.

Malun, D., Early development of mushroom bodies in the brain of the honeybee *Apis mellifera* as revealed by BrdU incorporation and ablation experiments, *Learn. Mem.*, 1998, vol. 5, pp. 90–101.

Mandapaka, K., Morgan, R.C., and Buschbeck, E.K., Twenty-eight retinas but only twelve eyes: an anatomical analysis of the larval visual system of the diving beetle *Thermonectus marmoratus* (Coleoptera: Dytiscidae), *J. Comp. Neurol.*, 2006, vol. 497, pp. 166–181.

Mashaly, A., Winkler, M., Frambach, I., Gras, H., and Schürmann, F.-W., Sprouting interneurons in mushroom bodies of adult cricket brains, *J. Comp. Neurol.*, 2008, vol. 508, pp. 153–174.

Meinertzhagen, I.A., Development of the compound eye and optic lobe of insects, in *Developmental Neurobiology of Arthropods*, Young, D., Ed., Cambridge: Cambr. Univ. Press, 1973, pp. 51–104.

Panov, A.A., The structure of the brain of insects at successive stages of postembryonic development, *Entomol. Obozr.*, 1957, vol. 36, no. 2, pp. 269–284.

Panov, A.A., The structure of the brain of insects at successive stages of postembryonic development. II. The central body, *Entomol. Obozr.*, 1959, vol. 38, no. 2, pp. 301–310.

Panov, A.A., The structure of the brain of insects at successive stages of postembryonic development. III. Visual lobes, *Entomol. Obozr.*, 1960, vol. 39, no. 1, pp. 86–105.

Panov, A.A., The structure of the brain of insects at successive stages of postembryonic development. IV. The olfactory center, *Entomol. Obozr.*, 1961, vol. 40, no. 2, pp. 259–271.

Panov, A.A., Histological structure of tripartite mushroom bodies in ground beetles (Insecta, Coleoptera: Carabidae), *Biol. Bull.* (Moscow), 2013, vol. 40, no. 5, pp. 455–462.

Pfeiffer, K. and Homberg, U., Organization and functional roles of the central complex in the insect brain, *Ann. Rev. Entomol.*, 2014, vol. 59, pp. 165–184.

Romeis, B., *Mikroskopicheskaya tekhnika* (Microscopic Techniques), Moscow: Izd. Inostr. Lit., 1953.

Sbita, S., Morgan, R., and Buschbeck, E., Eye and optic lobe metamorphosis in the sunburst diving beetle *Thermonectus marmoratus* (Coleoptera: Dytiscidae), *Arthr. Struct. Dev.*, 2007, vol. 36, pp. 449–462.

Schrader, K., Untersuchungen über die Normalentwicklung des Gehirns und Gehirnexplantationen bei der Mehlmotte *Ephestia kühniella* Zeller nebst einigen Bemerkungen über das Corpus allatum, *Biol. Zl.*, 1938, vol. 58, pp. 52–90.

Sharova, I.Kh., *Zhiznennye formy zhuzhelits (Coleoptera, Carabidae)* (Life Forms of Ground Beetles (Coleoptera, Carabidae)), Moscow: Nauka, 1981.

Shirokov, V.N. and Chaika, S.Yu., The structure of the head ganglia in the larva and pupa of the budworm *Archips podana* Scopoli (Lepidoptera, Tortricidae), *Entomol. Obozr.*, 2014, vol. 93, no. 2, pp. 390–401.

Sinitsina, E.E. and Chaika, S.Yu., Receptor organs of the larvae of ground beetles (Carabidae, Coleoptera), *Entomol. Obozr.*, 2003, vol. 82, no. 2, pp. 276–288.

Strausfeld, N.J., Sinakevitch, I., and Vilinsky, I., The mushroom bodies of *Drosophila melanogaster*: an immunocytological and Golgi study of Kenyon cell organization in the calyces and lobes, *Microsc. Res. Techn.*, 2003, vol. 62, pp. 151–169.

Toh, Y. and Mizutani, A., Structure of the visual system of the larva of the tiger beetle (*Cicindela chinensis*), *Cell Tiss. Res.*, 1994, vol. 278, pp. 125–134.

Wegerhoff, R. and Breidbach, O., Structure and development of the larval central complex in a holometabolous insect, the beetle *Tenebrio molitor*, *Cell Tiss. Res.*, 1992, vol. 268, pp. 341–358.

Zhao, X., Coptis, V., and Farris, S.M., Metamorphosis and adult development of the mushroom bodies of the red flour beetle, *Tribolium castaneum*, *Dev. Neurobiol.*, 2008, vol. 68, no. 13, pp. 1487–1502.

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