

Formation of Central Nervous System in a springtail,

Tomocerus ishibashii (Collembola: Tomoceridae) I

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SUMMARY: Formation of the central nervous system is described. Protocerebrum consists of three pairs of ganglia (Lobes 1-3). Deutocerebrum is derived from the antennal, and the tritocerebrum from the intercalary ganglia. The lobe 3 of the protocerebrum is regarded as the ganglion of the preantennal segment. The tritocerebrum retains the original postoral position throughout the life cycle. The ventral nerve cord consists of ten pairs of ganglia deriving from the mandibular to the fourth abdominal segments. The metathoracic and four abdominal ganglia fuse to form a synganglion during embryogenesis.

INTRODUCTION

The Collembola are generally regarded as one of the groups that first diverged from the other hexapods. The Collembola may be important not only to discuss the evolution of the entognathous insects but also to resolve the phylogeny of the Antennata.

Formation of central nervous system is one of the most important problem in the comparative embryology. On the formation of central nervous system in the Collembola, we have several works (1)(2)(3). However they are fragmentary and did not discuss the segmentaion of the Arthropoda. To resolve this problem, I describe details of the early formation of the central nervous system in the collembolan Tomocerus ishibashii, and compare and discuss our observations with the previous works.

MATERIALS AND METHODS

Adults of Tomocerus ishibashii were collected at Sugadaira and Ueda of Nagano Prefecture, Japan, in May and June. About ten insects were kept in a plastec case with pressed soil, and reared at room temprature. Each female laid 10 to 20 eggs in the laboratory condition. Eggs were transferred into another plastic case. The egg period lasted about 10 days at room temperature.

Eggs and first instar larvae were pricked by an fine needle and fixed in Carl's or Bouin's fluid for about 24 hours at room temperature. Fixed materials were stored in 70 % ethyl alcohol. For sectioning, the chorion and

vitelline membrane were partially removed from fixed eggs before processed for embedding. The eggs were dehydrated and cleared through an ethyl alcohol, methyl benzoate and benzene series, or a butyl alcohol, ethyl alcohol and water mixtures and butyl alcohol series. The normal paraffin embedding method was employed. Sections were stained with Delafield's or Heidenhain's haematoxylin or Mayer's acid haemalaun and eosin. Drawings were made with the aid of Abbe's camera lucida.

RESULTS AND DISCUSSION

a. Ventral nerve cord

In Stage 3 (4), neuroblasts differentiate at the both sides of the median line of the germ band. Their nuclei of the neuroblasts are larger than those of the other ectodermal cells, and are less stained with haematoxylin. At the same time when the neuroblasts appear, each anlage of appendages is formed. In this stage, the neuroblasts appear initially in the gnathal segments, and slightly later in the thoracic ones. They appear in the abdominal region in Stage 4. Each ganglion anlage has three to four neuroblasts in the cross section, and three to four in the longitudinal. Soon after the appearance, neuroblasts commence a series of unequal divisions to form daughter cells or ganglionic cells on their dorsal side. The nuclei of daughter cells are smaller and darker than those of neuroblasts. In this stage, the daughter cells are arranged in double straight rows above each neuroblast (Fig. 1). Until late Stage 4, four pairs of ganglia are formed in the intercalary to labial segments (Fig. 2), three pairs in the thoracic and four pairs in the abdominal (Fig. 1). In the fifth and sixth abdominal segments, the neuroblasts do not appear, and the ganglia are not formed.

In Stage 6, a pair of fibrous structures, i.e. neuropiles, begins to differentiate at the inner dorsal sides of each ganglion. Soon, paired neuropiles form two commissures, anterior and posterior ones in each ganglion. In the mandibular segment, however, only one commissure is recognized, and two commissures may be formed adjacent to each other in this segment. At the same time of the formation of the commissures, paired neuropiles in the intercalary to fourth abdominal segments are longitudinally connected with a pair of extending neuropiles, i.e. the connectives. At the beginning of the neuropile formation, the neuroblasts become indistinguishable, and a columnar arrangement of the ganglionic cells is obliterated. Degeneration figures of the neuroblasts are not observed, and the neuroblasts probably change themselves into the ganglionic cells. In the mandibular to fourth abdominal segments, a pair of nerve bundles is formed for both sides and runs from each ganglion to each

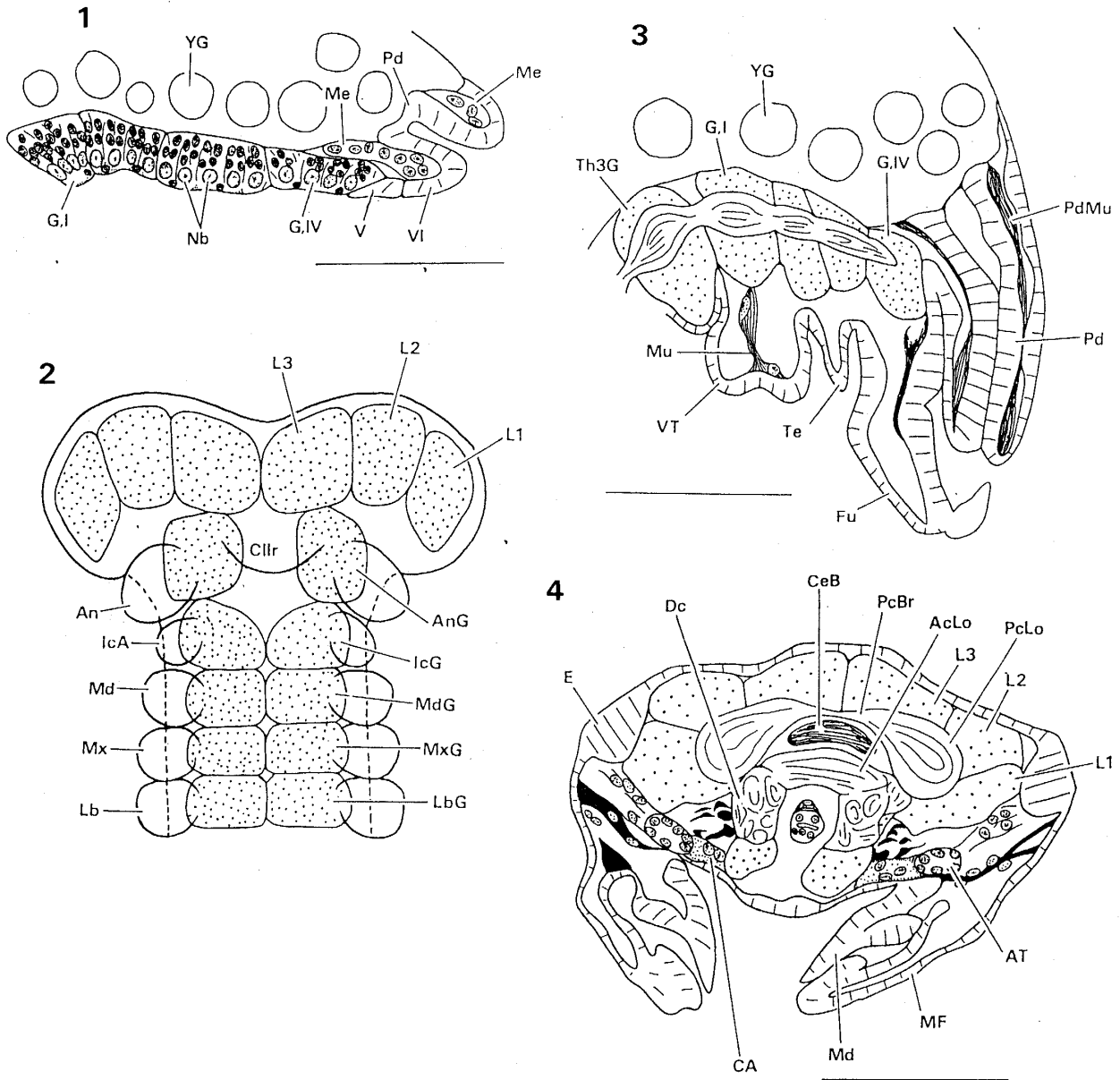


Fig. 1. Sagittal section of abdomen, late Stage 4. Scale = 50 μ m.
 Fig. 2. Diagram showing distribution of ganglia in cephalic region, Stage 3.
 Fig. 3. Sagittal section of metathorax and abdomen, Stage 6. Scale = 50 μ m.
 Fig. 4. Cross section of head through mandibular segment, Stage 8. Scale = 50 μ m.

AcLo, accessory lobe; An, antenna; AT, anterior tentorium; CA, corpus allatum; CeB, central body; Cllr, clypeolabrum; Dc, deutocerebrum; E, eye; Fu, furcula; G.I and G.IV, first and fourth abdominal ganglia; IcA, intercalary appendage; IcG, intercalary ganglion; Lb, labium; LbG, labial ganglion; L1-3, lobus 1-3; Md, mandible; MdG, mandibular ganglion; Me, mesoderm; MF, mouth fold; Mu, muscle; Mx, maxilla; MxG, maxillary ganglion; Nb, neuroblast; PcBr, protocerebral bridge; PcLo, protocerebral lobe; Pd, proctodaeum; PdMu, proctodaeal muscle; Te, tenaculum; Th3G, third thoracic ganglion; VT, ventral tube; YG, yolk globule; V and VI, fifth and fourth abdominal segments.

developing appendage. In the second abdominal segment which the well-developed appendage anlagen are not found, such nerve bundles do not arise.

In Stage 7, three pairs of ganglia in the three gnathal segments are fused to form the large suboesophageal ganglion. It is definitively situated in the region which is surrounded anteriorly with the hypopharynx and posteriorly with the postmentum. After the formation of the suboesophageal ganglion, the four abdominal ganglia shift anteriorly, fuse and form a large synganglion. In Stage 8, this synganglion is located in the first to third abdominal segments (Fig. 1). It shifts further anteriorly, and fuses with the third thoracic ganglion in Stage 9. The neuropile of the synganglion is thick in the anterior region and thin in the posterior one. The fusion of the metathoracic to fourth abdominal ganglia is also reported for Tetrodontophora bielensis (3).

The ventral nerve cord of T. ishibashii is composed of the suboesophageal ganglion, two thoracic ganglia and the synganglion consisted of the metathoracic and four abdominal ganglia. In later stages, these ganglia are sheathed by fine cellular membrane, i.e. neurilemma. It derives from the peripheral layer of ganglia.

b. Tritocerebrum

In Stage 3, the neuroblasts appear in the intercalary segment, and form a pair of ganglia. These ganglia are initially situated in the region posterior to the stomodaeum and come into contact posteriorly with the mandibular ganglia (Fig. 2). In Stage 6, the neuropile of this ganglia appears and two commissures are formed in the postoral region. In Stage 8, the intercalary ganglion or developing tritocerebrum is almost filled with the neuropile and the neuropile is surrounded by the thin layer of the ganglionic cells. The developing tritocerebrum never shifts anteriorly, and the definitive position is postoral unlike those of the other hexapods. In most of the other hexapods, of which intercalary ganglia further migrate anteriorly, the migration causes the remarkable extension of the suboesophageal commissures, while in T. ishibashii there is never found such an extension of the commissures. The circumoesophageal connectives also remain posterior to the stomodaeum and do not stretch. In Tetrodontophora bielensis (3), however, the tritocerebrum shifts and is situated at the lateral sides of the stomodaeum. The tritocerebrum retains its original or embryonic postoral position as the definitive. The postoral position of the tritocerebrum is generally accepted as one of the primitive characters of the hexapods.

The tritocerebrum innervates the frontal ganglion with a pair of nerve

bundles, i.e. nervus connectives, running by the both sides of the stomodaeum.

c. Deutocerebrum

In Stage 3, the neuroblasts appear in both the regions lateroanterior to the stomodaeal pit and form the antennal ganglia in both the lateral sides of the clypeolabral anlage. The deutocerebrum derives from the ganglia. The developing deutocerebrum comes into contact with the protocerebral lobes 3 anteriorly and with the developing tritocerebrum posteriorly (Figs. 2, 4). In Stage 6, just after the neuropile formation, the right and left ganglia fuse with each other by the commissure. The deutocerebrum innervates the antennae by the antennal nerves.

d. Protocerebrum

In Stage 2, the ectoderm of the protocephalon situated anteriorly to the antennal segment is divided into two layers. The outer layer develops into the future epidermis and ocelli, and the inner one develops into the anlagen of protocerebral ganglia. In Stage 2, the inner layer is divided into three paired parts (lobes 1, 2 and 3). The lobe 3 is located just anteriorly to the antennal segment, and the lobes 1 and 2 are situated in each side lateral to the lobe 3 (Fig. 2). The protocerebrum originates from these three paired lobes. The lobe 1 develops into the future optic ganglion. According to Tyszkiewicz (3), the lobe 1 is not formed in Tetrodontophora bielanensis. It may reflect the fact that the ocelli are lacking in this species.

The ganglionic cells produced by the neurogenic function of the neuroblasts of lobes 1, 2 and 3 do not show any regular arrangements, in a striking contrast to the case in the other ganglia, in which the ganglionic cells are arranged into columnar rows. In Stage 4, the epidermis of the lobe 1 begins to thicken, and assumes a lens-shape. In Stage 5, the lens-shaped epidermis, i.e. optic lobe, separates from the lobe 1 except for the median part. In Stage 6, the neuroblasts become undetectable and the neuropiles are formed in the lobes 1, 2 and 3. The neuropiles of the lobe 3 are larger, and the neuropiles of the right and left lobes 2, i.e. protocerebral lobes are connected with the protocerebral bridge. The central body deriving from the lobe 3 is situated posteriorly to the protocerebral bridge, and the accessory lobes differentiate in both the sides of lobe 3 posteriorly to the protocerebral lobes (Fig. 4).

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