CLASS CHILOPODA:
EVOLUTION AND ENVIRONMENT ADAPTATION

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A reconsideration of the first theory about the linear evolution of the Class Chilopoda (Prunescu, 1965a), from the short to long chilopods was presented. The most important arguments were proved by the new anatomical structures discovered in the representatives of certain actual orders of Chilopoda. A careful analysis was undertaken about the main characters of the present orders of chilopods, related to the adaptation to distinct environments of life, their hunting peculiarities and their behaviors bound to the brood care or the lack of the brood care (Subclass Ovoconecta, Subclass Ovodispersa). These arguments led to the conclusion that the chilopods evolution developed along two distinct branches, starting from a common ancestor.

Key words: Chilopoda, Subclass Ovoconecta, Subclass Ovodispersa, environment adaptation, evolution.

INTRODUCTION

The biological adaptation is the process through which an organism is integrated in its own environment of life. The adaptation is the result of the action of natural selection concerning the inherited variations. The adaptation refers to the modifications of the structure, physiology, manners of attack and defense, reproduction and the development of the organism involved, related to the specificity of the environment. Some of these characters are considered as pre-adaptation traits; they can bring occasionally advantages for the organism. The study of the organism existence in relation with its environment defines more accurately its adaptation capacity.

The representatives of the Class Chilopoda express very stable relations with their environments of life.

The representatives of the order Geophilomorpha live in the profound levels of the litter and/or soil. Occasional the litter or soil may be replaced by big or medial size stones or the rotten bark of the fallen trees. In these two types of environment of life were found also the representatives of the orders Scolopendromorpha and Lithobiomorpha. The representatives of these two orders are frequently found in the superficial levels of the litter under medial or small size stones, etc.

The species of the order Scutigeromorpha live in the free spaces, open or close, anywhere in the world in a warm and wet atmosphere. In Europe, *Scutigera coleoptrata* is found in the terrestrial regions around Mediterranean Sea and/or around Black Sea and Romanian Danube.

ROM. J. BIOL. – ZOOL., VOLUME **55**, N° *2*, P. 113–127, BUCHAREST, 2010

The differences among these environments of life seem not to be very great. However, when we consider their hunting possibilities imposed by the environment conditions, these differences become very important. A geophilomorph blind, long and coiled, with the displacement by winding which is more frequent than the displacement based on the locomotion by articulated legs, hunts easily owing to a well developed sense of touch. Owing to its length, this chilopod controls an important area of the surrounding soil. The representatives of the order Scolopendromorpha namely the blind and pale Cryptopidae shorter than geophilomorphs and the stout and pigmented *Scolopendra*, with a fixed number of ocelli, hunt in the less deep levels of the soil. Their hunting is more active being based on the displacement by articulated legs. This fact is valid also for the representatives of the order Lithobiomorpha, which for the hunting displace more rapidly than the representatives of the order Scolopendromorpha.

In contrast to all these chilopods, the representatives of the order Scutigeromorpha present compound eyes placed on the important surfaces of the cephalic capsule, long antennae with segments multi-fragmented and legs with tarses formed of many articles. These characters facilitate an extremely rapid displacement during the hunting. The chilopods body structure is correlated with a particular organization of the displacement based on the segmented body and articulated appendages.The manner of hunting bound to the specific character of the displacement has important implications in the reproduction and development the chilopods.

The chilopods with long or very long body like the representatives of the orders Craterostigmomorpha, Scolopendromorpha and Geophilomorpha present the physical possibility to maintain and care the brood housed on the mother body till after the hatching. The chilopods orders of which individuals care their brood were grouped in the subclass Ovoconecta (Prunescu, 2006).

The chilopods with short body formed of 15 leg-bearing segments and with rapid displacement during the hunting, namely the representatives of the orders Scutigeromorpha and Lithobiomorpha cannot preserve the brood on their body during the embryonic and larval development. The eggs are deposed on the soil one by one or in small groups. The larvae which hatch with relative small number of leg-bearing segments will displace independently in their natural environment, will grow and develop adding leg-bearing segments by successive moults. These two orders were grouped in the subclass Ovodispersa (Prunescu, 2006).

SHORT REVIEW ABOUT THE CHILOPODS EVOLUTION CONCEPTIONS

At the beginning, the researchers tried to classify the chilopods in the natural taxonomic units.

To the end of the 19-th century was proposed the chilopods division in the Subclasses Epimorpha and Anamorpha (Haase, 1880, 1881). This classification was taken over by Attems (1926) and by other myriapodologists during the 20-th century.

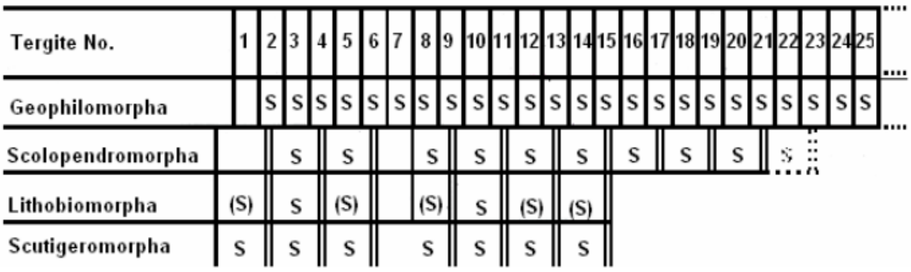
Pocock (1893; 1895-1896; 1902) divided the chilopods in the Subclasses Pleurostigmophora and Notostigmophora. This classification was adopted by Verhoeff (1902-1925) and by other researchers.

In the first part of the 20-th century a conception general accepted considered that the chilopods ancestor was an arthropod presenting the homonomous segmentation of the body. By this point of view, the chilopods with heteronomous segmentation must derive from the first ones. This theory supposed that the ocelli and compound eyes represented latter acquirements during chilopods evolution. The majority of myriapodologists and zoologists adopted this theory about the chilopods evolution (Broleman, 1930; Demange, 1967; Kästner, 1963; Manton, 1965).

In 1938, Fahlander realized a complex anatomical and histological study on the chilopods. This author signaled the massive accumulations of the primitive traits in the representatives of the order Scutigeromorpha and in the same time he observed the difficulties to assign the primitive traits to the chilopods on the basis of the organization plan of the representatives of the order Geophilomorpha, In his opinion the ancestor of the present chilopods could be similar to actual genus *Plutonium* (ord. Scolopendromorpha).

At the beginning of the sixty's years, Prunescu initiated a comparative study on the anatomy of the genital system and other internal organs of chilopods (Prunescu, 1965a). The data accumulated and the critical revision of the knowledge about the chilopods morphology and evolution led to the materialization of a new concept about the evolution of these arthropods.

The author analyzed the heteronomy of the tergal segmentation of the body consisting of the alternation of the long tergites with short tergites, with the defect of alternation at the level of the leg-bearing segments 7-8. This alternation is homologous for the majority of the chilopods orders: Lithobiomorpha, Scutigeromorpha, Craterostigmomorpha, Scolopendromorpha with one exception: the order Geophilomorpha (Fig. 1). Since the alternation long tergite-short tergite had the tendency to be attenuated in the frame of the orders Craterostigmomorpha and Scolopendromorpha and disappeared completely in the order Geophilomorpha, we considered to have arguments to sustain the idea of a linear evolution starting from the orders Lithobiomorpha, Scutigeromorpha through the orders Craterostigmomorpha, Scolopendromorpha till the order Geophilomorpha. In this way, we presented the first phylogenetic tree for the actual orders of the Class Chilopoda (Prunescu, 1965a) (Fig. 2). According to this theory, the chilopods evolution started from the short ancestors presenting tergal heteronomy of the body and was continued with the appearance of the long or very long chilopods presenting attenuated heterosegmentation till the homonomous segmentation of the body. It must be noted that the respiratory stigmata on the body of these chilopods are always placed on the leg-bearing segments with long tergites. In the representatives of the order Scutigeromorpha the respiratory stigmata are placed on a dorsal-median body line of the body and are always localized on the long tergites.



Tergite No. 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Geophilomorpha S S S S S S S S S S S S S S S S S S S S S S S S
Scolopendromorpha S S S S S S S S S
Lithobiomorpha (S) S (S) (S) S (S) (S)
Scutigeromorpha S S S S S S S

Fig. 1. Dorsal segmentation and stigmata repartition in Chilopoda (Prunescu 1965a). S: stigmata, (S): stigmata can be absent in certain types. Craterostigmophora presents stigmata distribution and tergites alternation similar to the orders Lithobiomorpha and Scolopendromorpha.

Numerous other internal or external morphological traits of the representatives of present orders of Chilopoda were enclosed in this phylogenetic tree (Fig. 2). The content of the paper “Contributions to the study of chilopods evolution” (original in French: “Contributions à l’étude d’évolution des Chilopodes”) (Prunescu, 1965a) was resumed by Shinohara (1970) who published the essence of our paper in a Japanese version.

Dohle (1985) published a theory about the Chilopoda evolution, starting from the idea that the order Scutigeromorpha presented the majority of its morphological and physiological traits like the common ancestor of chilopods. This author took over much from the ideas and the content of Prunescu’ paper (1965a), but he quoted Prunescu’s contribution limited only to the option for the division of the Class Chilopoda in Subclasses Notostigmophora and Pleurostigmophora (!).

Dohle’s theory was applied by Shear and Bonamo (1988) who described the fascinating fossil group *Devonobius delta* found in a Devonian stratum from New York zone. After the years 1990 and 2000, Prunescu’ original contribution concerning the chilopods evolution was quoted with formal attitude.

A new manner of chilopods evolution research consisted in the adoption of modern cladistic practices: there were selected hundreds of external and internal characters in association with some data of molecular biology of respective organisms (Edgecomb & Giribet, 2004).

Recently, an important monography about Class Chilopoda (Rosenberg, 2009) was published. The data and the new opinions on the chilopods evolution will be discussed in a future paper.

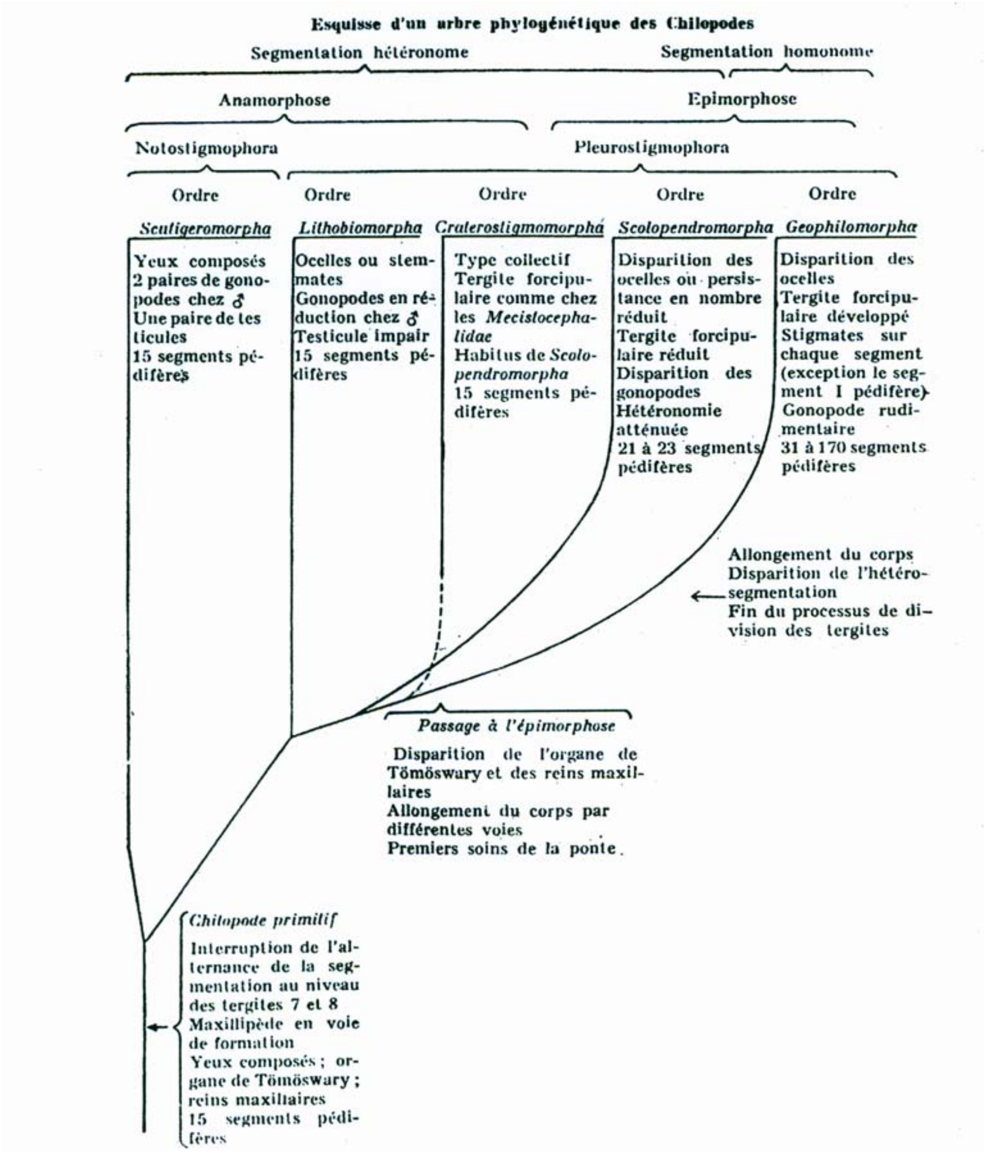


Fig. 2. Phylogenetic tree of the linear evolution of the Class Chilopoda (Prunescu, 1965a).

ADAPTATION AND EVOLUTION IN THE CLASS CHILOPODA

The discovery of new anatomical structures offered us the possibility to attain new insights about the chilopods evolution. The old phylogenetic tree presenting the linear evolution of the class Chilopoda was analyzed again in the light of these new data.

According to the old theory (Prunescu, 1965a) the last common ancestor of Chilopoda was an organism similar to those of the order Lithobiomorpha, presenting stigmata in pleural position and a male genital system similar or identical to genital system of the order Scutigeromorpha (Bouin, 1934; Fahlander, 1938; Prunescu, 1969) (Fig. 3). In 1969, was described for the first time the male genital system of *Anopsobius neozelandicus*, a species of subfamily Anopsobiinae (fam. Henicopidae, ord. Lithobiomorpha) (Prunescu & Johns, 1969).

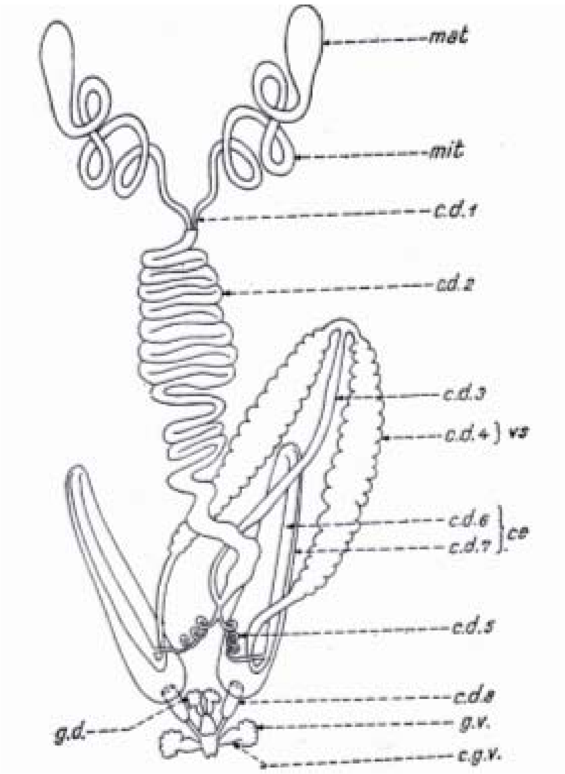


Fig. 3. Male genital system in *Scutigera coleoptrata* (Prunescu, 1969), mat: macro-testis; mit: microtestis; cd1: anterior deferens segments; cd2: epididymal duct; cd3: median channel; cd4: seminal vesicles; cd5: contorted channels; cd6: ascending ejaculatory channels; cd7: descending ejaculatory channels; cd8: terminal ejaculatory segments; gd: dorsal glands; gv: ventral glands; cgv: channel of the ventral gland.

This male genital system was formed of two gonads. On a side of body there was a functional genital tract constituted of an apical vesicle named macro-testis which was continued in the caudal extremity by a long and flexible canal named micro-testis. Each of these testicular segments was populated by a seminal line of macro-spermatogenesis type in the macro-testis and of micro-spermatogenesis type in micro-testis. Between the two types of spermatogenesis the difference was only by the dimensions of the spermatocytes, spermatides and spermatozoa. The two types of spermatogenesis were complete and seemed functional. On the other side of the body, there was a rudimentary gonad of small dimensions, populated with undifferentiated spermatogonies (Prunescu & Prunescu, 2001) (Fig. 4).

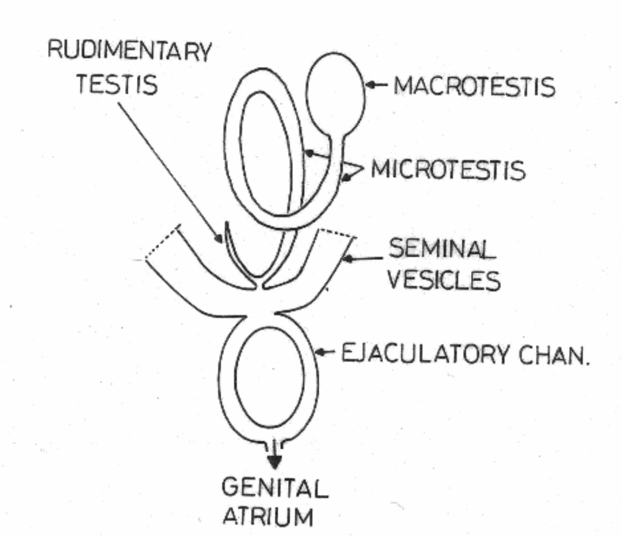


Fig. 4. Male genital system in *Anopsobius neozelandicus* (Prunescu & Prunescu, 2001).

This original genital system was found again in other two representatives of the subfamily Anopsobiinae: *Dichelobius bicuspis* (Prunescu, 1992) and *Anopsobiella dawydoffi* (Prunescu & Prunescu, 2004). It is important to remember that the family Henicopidae contains chilopods presenting macro- and micro-testis in the structure of their male genital system (subfamily Anopsobiinae) and chilopods presenting a median unique testis (subfamily Henicopinae) (Prunescu *et al*., 1996; Prunescu & Prunescu, 1999). These two subfamilies present numerous details of extern morphology almost identical. These two subfamilies were enclosed in the order Lithobiomorpha, near the family Lithobiidae which present also a median unique testis (Prunescu, 1964; Zerbib, 1966) (Fig. 5).

The existence of a double spermatogenesis based on the macro and micro-testis in the order Scutigeromorpha creates a link extremely important between subclass Notostigmophora and a subfamily of the order Lithobiomorpha from the Subclass Pleurostigmophora (!). This close similitude annihilates the distance between the two subclasses (Prunescu & Prunescu, 2001) and rise serious questions on the quality of archetype of the tracheal lungs system of the subclass

Notostigmophora. In the same time, was proposed the statute of the absolute plesiomorphic character to the respiratory system starting from pleural stigmata (Prunescu, 1965a).

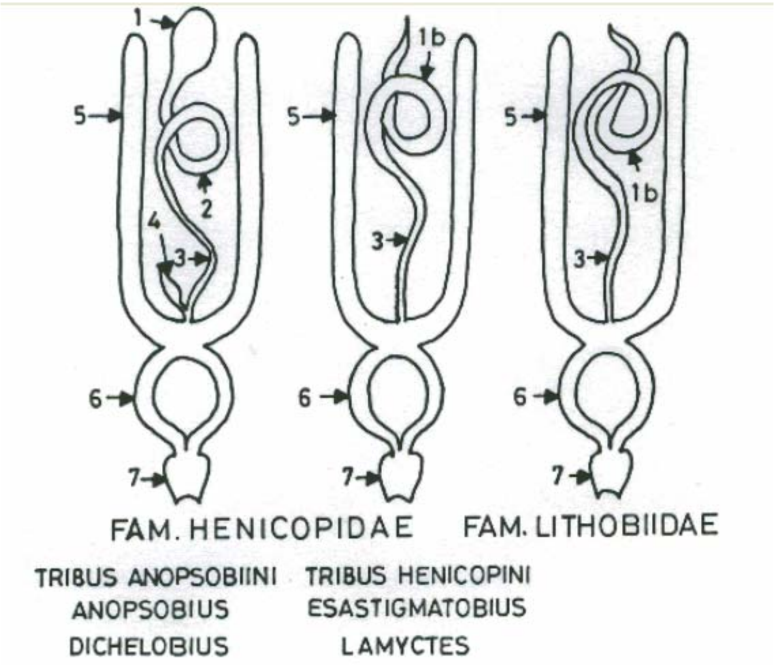


Fig. 5. Male genital system in the order Lithobiomorpha (Prunescu & Prunescu, 1999). 1: macrotestis; 1b: median testis; 2: microtestis; 3: deferens duct; 4: rudimentary gonad; 5: seminal vesicles; 6: ejaculatory channels; 7: genital atrium.

The appearance of the median stigmata and the grouping of the tracheae in form of tracheal lungs (Fig. 6) could be the result of the adaptation to the open air environment for the organisms of the order Scutigeromorpha which cannot preserve the body humidity like pleurostigmophoran chilopods which live in wet environment (Prunescu, 1996).

The comparative studies on the tracheal systems in pleurostigmophoran chilopods demonstrated the existence of the interconnections of the tracheae starting from the paired stigmata and/or from the stigmata situated at successive segments of the body (Manton, 1965; Hilken, 1997). Such interconnections were observed especially in the orders Scolopendromorpha and Geophilomorpha (Kaufman, 1960, 1962; Hilken, 1997) and seemed to form a true internal "skeleton" for the maintaining the body shape. The un-anastomosed tracheal structures were found in the tracheal lungs from the order Scutigeromorpha (Haase, 1884; Prunescu & Prunescu, 1996; Hilken, 1997) and in the tracheal system from the order Craterostigmomorpha (Prunescu, 1965b).

It must be admitted that, at the beginning of its adaptation to the terrestrial life, the last common ancestor of Chilopoda used for respiration numerous thin tracheae un-anastomosed, starting from the pleural stigmata.

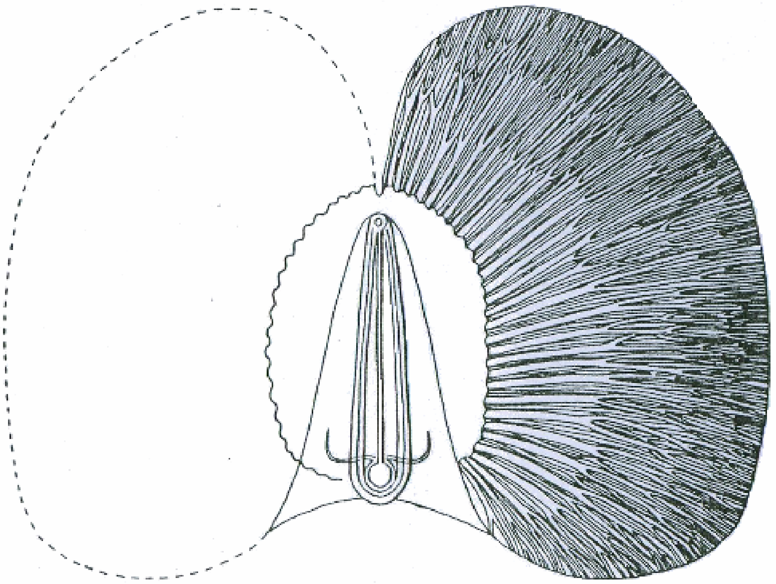


Fig. 6. Pair of tracheal lungs and median stigmata of *Scutigera coleoptrata* (Haase, 1884). Note the thin un-anastomosed tracheoles.

In the representatives of the order Lithobiomorpha, from the stigmata started main tracheae which gradually branch out in numerous tracheoles (Kaufman, 1961; Hilken, 1997). Consequently, the tracheal system of the order Craterostigmomorpha which is more simple and primitive cannot be derived from the tracheal system of the order Lithobiomorpha. The connections between the tracheal and the circulatory systems in Tracheata seem not to be sufficiently elucidated. The presence of the respiratory pigment haemocyanin in the haemolymph of some representatives from all groupes of Tracheata was demonstrated (Burmester, 2001; Kusche & Burmester, 2001; Kusche *et al.*, 2003). These discoveries indicated that the haemolymph carrying haemocyanin pigment is used in all these cases for the tissue respiration although, as a rule the Tracheata are endowed with tracheal systems which displace the gases exchange to every cell of the organism.

Coming back to the ancestor of the order Scutigeromorpha, the numerous thin un-anastomosed tracheoles starting from the stigmata initially in pleural position, had direct access in the pericardial sinuses located in their vicinity. The gases exchange realized at the haemolymph level from these sinuses, reduced the humidity lost by the organism (Prunescu, 1996).

The unification of the pair of stigmata located on the median dorsal zone of long tergites brought a contribution for the resistance increase of the tergal plates and body stability useful in the obtaining of a great speed necessary for the hunting in open space (Manton, 1965; Prunescu, 1996).

The research on the Malpighian tubules presenting lateral insertion in the terminal zone of the medial intestine in *Scutigera coleoptrata* led to the discovery of a second pair of Malpighian tubules of smaller dimensions and functional (Fig. 7). This second pair of Malpighian tubules opened in the same zone of the mid-gut having dorsal-ventral insertion (Prunescu & Prunescu, 1996). The study of the mid-gut terminal zone of the representatives from all other orders of chilopods, showed that only in *Craterostigmus tasmanianus* was present the second pair of Malpighian tubules with dorsal-ventral insertion (Fig. 8). It is particularly interesting the fact that these supplementary Malpighian tubules have been observed in individuals of *Craterostigmus tasmanianus* belonging to the two known populations (Tasmania and New Zealand) (Prunescu & Prunescu, 2006).

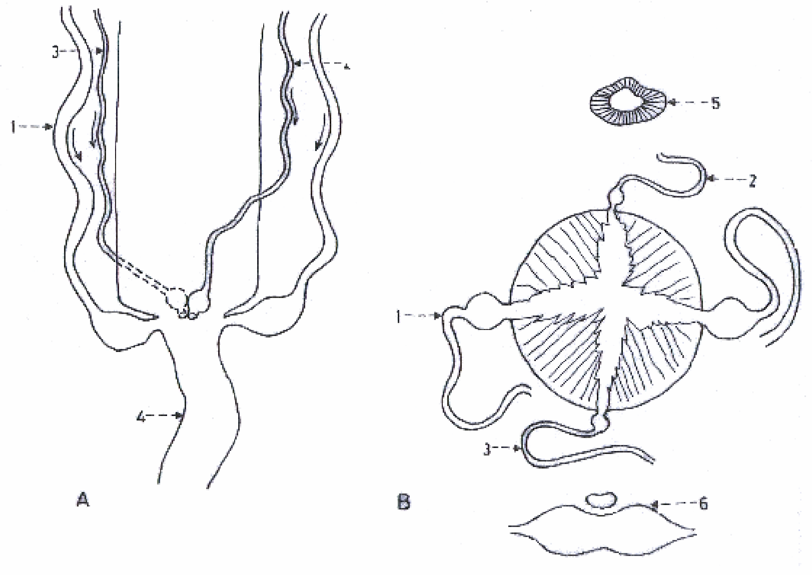


Fig. 7. Malpighian tubules in *Scutigera coleoptrata* (Prunescu & Prunescu, 1996). A: dorsal view; B: transversal section; 1: lateral (main) Malpighian tubule; 2: dorsal Malpighian tubule; 3: ventral Malpighian tubule; 4: hind gut; 5: vas dorsalis; 6: ventral nerve ganglia.

This character: **the second pair of Malpighian tubules with dorsal-ventral insertion in the terminal zone of the mid-gut** pointed a sure relationship between the orders Scutigeromorpha and Craterostigmomorpha and attested the existence of a common ancestor.

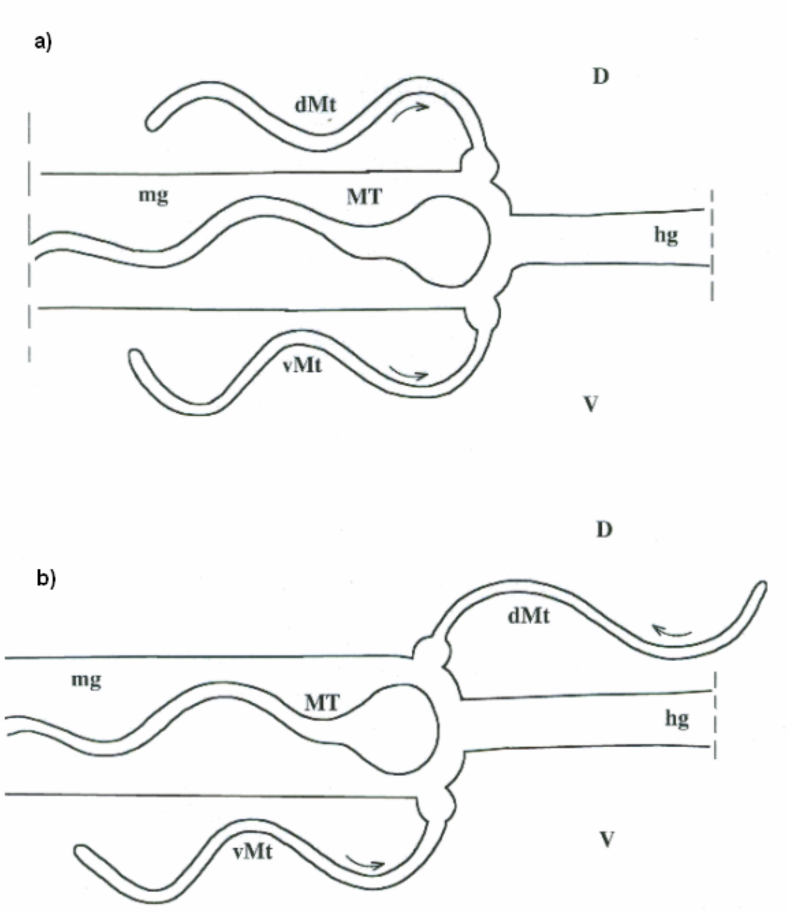


Fig. 8. Malpighian tubules in *Craterostigmus tasmanianus* (Prunescu & Prunescu, 2006). a) *C. tasmanianus* from New Zealand; b) *C. tasmanianus* from Tasmania; dMt: dorsal Malpighian tubule; vMt: ventral Malpighian tubule; MT: main (lateral) Malpighian tubule; mg: mid gut; hg: hind gut; D: dorsal; V: ventral.

According to the arguments presented in this paper, the chilopods evolution was not linear but took place simultaneously on two distinct lines detached from a common ancestor (Fig. 9). The last ancestor of the chilopods presented the first pair of legs transformed in forcipules endowed with poison glands. The leg bearing segments in number of 15, presented an alternation defect consisting of succession of two long tergites at the segments 7 and 8. These characters maintained on the both evolution lines detached from this ancestor.

Before leaving the aquatic medium the chilopod ancestor could protect and care his brood exactly like the great majority of Crustacea. The common ancestor of the orders Lithobiomorpha and Scutigeromorpha, made the option for the active seeking of the prey and for the rapid displacement into a terrestrial superficial environment. As a consequence it could not preserve the brood on its body. This fact led to the solution of laying down the eggs on the soil. The absence of the brood care by the mother favored the maintaining of the postembryonic development by anamorphosis and the capacity of the larva to feed independently. In this way, the main traits of the chilopods enclosed in the Subclass Ovodispersa (Prunescu, 2006) were established (Fig. 9).

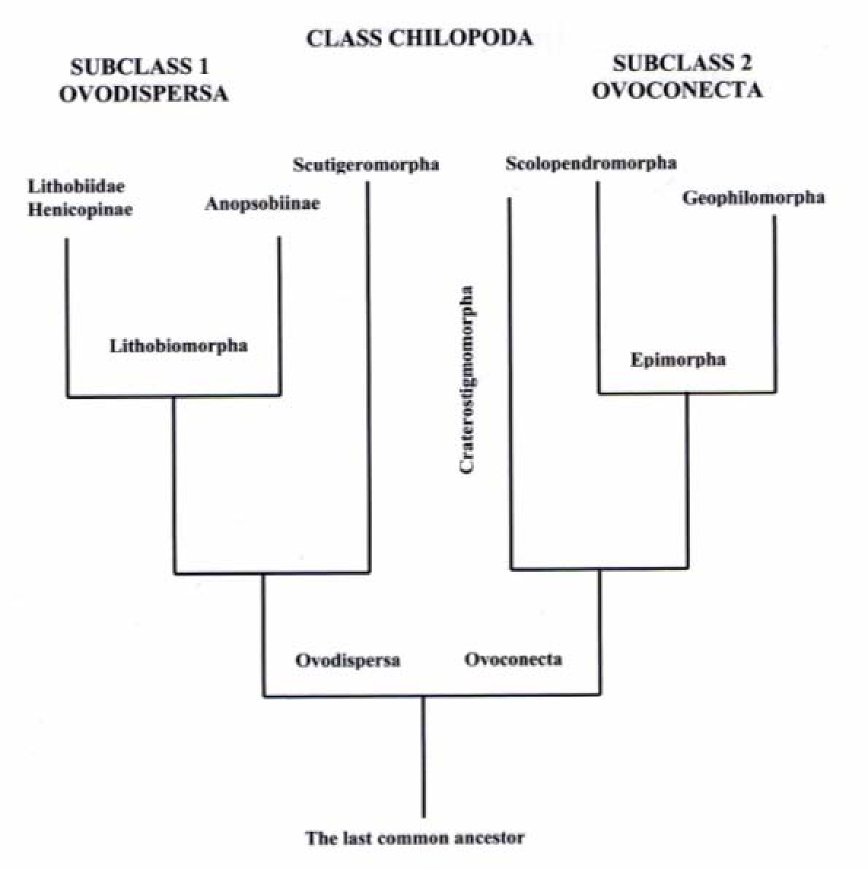


Fig. 9. The new phylogenetic tree of Class Chilopoda (Prunescu, 2006).

The other line of evolution detached from the last common ancestor of chilopods could maintain the brood on the body surface, in conditions in which the active pursue of the prey tended to be replaced by the waiting of the prey in the deeper levels of the litter or soil.

It would be a causal determination between the brood care and the prolongation of the period of embryonic development. This is the case of the orders Craterostigmomorpha which preserve a rudimentary anamorphosis and also in the other two orders with epimorphic development, which are grouped in Subclass Ovoconecta (Prunescu, 2006) (Fig. 9). The reduction and/or the disappearance of the ocelli, the diminution of the organ of Tömösvary in the order Craterostigmomorpha and the disappearance of this organ in the epimorphic chilopods are other morphological modifications correlated with a manner less active of the prey capture.

According to the current views, the evolution represents the assembly of the changes supported during the geological periods by the representatives of the animal and plant kingdoms having as the result the appearance of the new forms.

In the Class Chilopoda case this process of selective accumulation of some new characters led to the appearance of five orders of chilopods, each adapted for characteristic environment of life.

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Received October 1, 2010

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