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Diversity and trends of the evolution of testes in Psocidea

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Variation of the number and mutual position of seminal follicles in males of Psocidea is considered. Literature data on all taxa involved (Nitzsch, 1882; Snodgrass, 1899; Pavlovsky, 1907, 1922, 1923; Badonnel, 1934; Jentsch, 1939; Finlayson, 1949; Ferris, 1951; Klier, 1951; Mukerji & Sen-Sarma, 1955; Blagoveshchensky, 1956; Wong & Thorntom, 1968; Vishniakova, 1970; Saxena & Agarwal, 1981) and data on Psocoptera obtained by the second author (Golub, in press) have been used. Preparations of testes of Anoplura made by the late D.I. Blagoveshchensky and deposited at the Zoological Institute RAS in St.Petersburg have been also used.

Reasoning on the pathways of morphological evolution of different taxa of Psocidea is based upon phylogenetic schemes of Smithers (1972), Vishniakova (1964, 1987), and New (1987) regarding Psocoptera, and upon schemes of Königsmann (1960), Clay (1970), Kim and Ludwig (1978), and Lyal (1985) regarding Phthiraptera.

Female reproductive system of Psocidea was not considered specifically. It should be noted, however that in Psocoptera variations in the number of ovarioles are insignificant and have the character of a simple oligomerization and/or polymerization. In all three suborders of Psocoptera 5 ovarioles per female ovary occur. All studied species of the psocopteran suborders Trogiomorpha and Troctomorpha, as well as of Phthiraptera are characterized by five ovarioles per ovary. Only in the advanced psocopteran suborder Psocomorpha this number declines consecutively to 4 and 3.

The evolutionary changes of testes are much more remarkable and complicated. In Psocoptera there are several essentially different types of testes: (1) unifollicular, (2) trifollicular with consecutive arrangement of follicles (comb-shaped testes), and (3) trifollicular with fan-shaped arrangement of follicles (stems of all follicles converge at one point). Apart from these major types the only case of testes with 4 follicles is known in *Caecilioides* sp. (Caeciliidae, Psocomorpha), arrangement of follicles being consecutive as in variant 2 (Wong & Thornton, 1968). This is undoubtedly a secondary phenomenon.

Testes with two follicles have never been found in Psocoptera. Only unifollicular testes are known in Trogiomorpha. In Troctomorpha and Psocomorpha in several families (Liposcelidae, Caeciliidae, Peripsocidae) species with unifollicular and multifollicular testes occur. In case of multifollicular testes only fan-shaped arrangement is known in Troctomorpha, whereas both fan-shaped and comb-shaped arrangements are known in Psocomorpha. Thus, all variants occur in the order Psocoptera including the variant with four consecutive follicles, dispersal of variants on the phylogenetic tree being mosaic.

Fan-shaped and comb-shaped arrangements were found in different species of the genus *Stenopsocus* (data are available for 5 species). In the family Philotarsidae representatives of different genera have different arrangement (studied 2 genera, 2 species). In the family Caeciliidae in *Caecilius piceus* polymorphism in the follicle arrangement has been revealed: comb-shaped arrangement in the majority of males, however fan-shaped arrangement in single males. In the latter case the seeming fan-shaped arrangement may be the result of the too close location of follicles' bases to each other. In other species of this family only comb-shaped arrangement occurs, follicles are always situated at a long (the longest in Psocoptera) distance from each other.

Vishniakova (1970) observed at the larval stage of males (and females) in *Psococerastis gibbosus* concentration of follicles' bases (and ovarioles' bases accordingly) in one point and transferring from comb-shaped to fan-shaped arrangement (Figs 15a, b, c; 46a, b, c in cited work). The same process of concentration of ovariole bases in one point was observed by Blagoveshchensky (1956) in larval ontogenesis of Mallophaga and Anoplura. Vishniakova asserts that in Psocoptera fusion of three follicles into one is a continuation of concentration process, however this statement is conceptual and has not been supported by any real observations. It should be noted that no intermediate states, e.g. one follicle with three apices, or any others, have been found in any psocopteran species.

The suborders Troctomorpha and Psocomorpha include families characterized only by unifollicular or only trifollicular testes. In Elipsocidae, Mesopsocidae and Psocidae the pattern of follicle arrangement is a family character. All studied species of the first two families have comb-shaped testis pattern, whereas those of the third family have fan-shaped pattern, although data are still scanty.

Of Psocomorpha the family Caeciliidae includes one genus with 1 follicle, 3 genera with 3 and 1 genus with 4 consecutive follicles. However, with one exception, only one species in each genus was studied. The exception is the genus *Caecilius* all 8 studied species of which have 3 follicles. In

Caecilius piceus characterized by three consecutive follicles separate individuals have fan-shaped arrangement. In the family Peripsocidae the genus *Ectopsocus* contains species with 1 follicle and with 3 fan-shaped follicles. No other families, genera and, the more so, species that would be characterized at the same time by both unifollciular and multifollicular testes and in the latter case by comb-shaped and fan-shaped arrangement are known. It is remarkable that no groups of generic or higher level with only unifollicular or only comb-shaped testes are known. This suggests that these two forms are on the opposite ends of the morphogenetic row.

Psocoptera seems to display a pronounced "prohibition" of bifollicular structure of testes. This is particularly interesting because in Anoplura and in mallophagan Ischnocera testes are always bifollicular; bifollicular testes occur also in separate species of more primitive mallophagan Amblycera, characterized by trifollicular testes.

Testes and ovaries in insects were initially arranged by segment and on each side fell into a common seminal duct or oviduct. Thus, the initial number of follicles and ovarioles is equal to 7 (by the number of pregenital segments) and a primary variant of their arrangement is a consecutive one. The evolutionary morphological series of transformations of testes as applied to Psocoptera and their closest ancestors *a priori* looks as follows: 3 follicles – comb-shaped arrangement; 3 follicles – fan-shaped arrangement – 1 follicle; the preceding stage consisted in oligomerization of up to 3 follicles and stabilization of 3.

In *Caecilioidus* sp. (Caeciliidae) the stabilization block was supposedly partly overcome and the number of follicles was polymerized up to 4 (comb-shaped arrangement).

If we distract from Phthiraptera for a while and build phylogeny of Psocoptera based on the data on follicles alone, we will obtain a scheme directly opposite to the scheme of Smithers and contradicting the generally accepted ideas of primitive and advanced suborders of Psocoptera because the plesiomorphic state of testes (consecutive arrangement of follicles) occurs in Psocomorpha only. Troctomorpha and Trogiomorpha will be then joined by the lack of a consecutive arrangement because their follicles are fan-shaped or, in this context, degenerative fan-shaped, oligomerized to one. Trogiomorpha can be derived as a daughter group from those Troctomorpha groups, which always have only one follicle. Consistency of the scheme will be disturbed by unifollicular representatives of Troctomorpha: their repeated appearance will have to be regarded as a parallelism (= convergence), a parallel variant of extreme oligomerization.

The greater the number of such independent appearances the less plausible the interpretation of those as parallelisms. The data used in this publication imply that there are not less than 8 such cases.

With such an approach we will build a tree that would not resolve all the contradictions and, moreover, will turn upside down the generally accepted and sufficiently corroborated ideas of Psocoptera phylogeny. In any case it is impossible to build a tree resolving all contradictions without admitting numerous homoplasies.

As has been mentioned already variants of testes structure are arranged as alternating bands on the phylogenetic tree. A simple interpretation of such arrangement implies admitting multiple parallelisms that are far beyond the stochastically accepted norm. It appears that the most plausible explanation can be given based on the phylogenetical manifestations of the law of N.I. Vavilov's homological series, which the first author (Emelyanov, 2000) proposed to denote as morphocycles.

As applied to this particular case we observe a morphocycle of three successive states: 3 consecutive follicles – 3 fan-shaped follicles – 1 follicle, the states, which according to simple logic had stepwise development in the early phylogenesis of Psocoptera or their more remote ancestors. These changes arose by of a two-stage anaboly of ontogenesis, and in modern Psocoptera they occur by way of cancellation of one or two commands for anaboly. Thus, fan-shaped arrangement of follicles may be achieved by means of arrest and inverse development (concentration) of interfollicular parts of seminal ducts, i.e. areas lying higher (further distally) than the most posterior follicle; Vishniakova (1970) has shown that this occurs in larval ontogenesis.

Appearance of unifollicular testes can be achieved by command for fusion of follicles proper at the early stage of formation of gonad rudiments. Further it can be assumed that the factor responsible for concentration of follicles into a fan and the factor responsible for appearance of the only one follicle is the same factor (fusion factor), which in different representatives of Psocoptera starts acting at different moments of testes' ontogenesis: if it acts early 1 follicle arises, if it acts late a fan of follicles arises; if it acts very late or does not act at all a consecutive arrangement of follicles arises.

This hypothesis provides a plausible explanation of why in the evolution of Psocoptera from 1 follicle there evolved 3 fan-shaped follicles and only afterwards 3 comb-shaped follicles. This may be attributed to a progressive delay of action of the aforementioned hypothetical factor and enlarging range of its manifestation in time in ontogenesis.

In Phthiraptera two variants of testes structure are known: comb-shaped trifollicular and opposite bifollicular, i.e. appearing to be fan-shaped bifollicular.

Nusbaum (1882) examined postembryonic development of mallophagan species *Columbicola columbae* (= *Lipeurus bacilus*) and *Goniocotes hologaster*, which have bifollicular testes. He has shown that such testes arise from comb-shaped trifollicular ones by reduction of the apical follicle (as a late arrest of development and degeneration). Thus, it may be assumed that the psocopteran factor of follicles fusion is switched off in Phthiraptera. However a new morphogenetic factor (synapomorphy of Ischnocera and Anoplura) blocking development of apical follicle appears in this group.

According to Vishniakova (1980) and Lyal (1985), Phthiraptera originated from representatives close to the psocopteran fam. Liposcelidae. Among Mallophaga, Amblycera are characterized by the consecutive type of arrangement of follicles, the number 3 being retained. In two non-related representatives of the family Philopteridae (*Menacanthus pusillus* of Menacanthinae and *Myrsidea subaequalis* of Dennyinae) the number of follicles reduces to two, but follicles retain a former similar orientation characteristic of the consecutive type. Pathways of formation of bifollicular testes in these cases unknown. If they arise by a simple oligomerization (change in the number of elements during the early stage of formation) these are cases of simple convergence with Ischnocera. If they arise by reduction of the apical follicle as in Ischnocera this may indicate concrete ancestors of Ischnocera among Amblycera. Ischnocera and their derivatives Haematomyzina (= Rhynchophthirina) as well as Pediculina (= Anoplura) are characterized by bifollicular testes with opposite orientation of follicles: the anterior is directed with its apex orally, the posterior one – aborally (opposite testes). Thus, the main shift in the arrangement of testes in Phthiraptera occurred during formation of Ischnocera.

Opposite testes may be of two types – with follicles on stems and with follicles fused by their bases, without stems. These two variants form a two-step morphocycle, because they occur both among Ischnocera and among Anoplura. In Haematomyzina (1 genus, 2 species) follicles are stem-like. Here again we can assume action of the psocid factor of follicle fusion – switching on of the factor at the late stage of follicle development leads to fusion of their bases.

To summarize the aforesaid the following scenario of the evolution of testes in the superorder Psocidea can be proposed.

Phase A: Formation of psocid three-step follicular morphocycle

1. Stabilization of trifollicular state with comb-shaped arrangement of follicles.

2. Arrest and reversion of development of interfollicular parts of the seminal duct – concentration of follicles' bases into one point – formation

of fan-shaped arrangement of follicles. Appearance of the follicle fusion factor. Late action of follicle fusion factor.

3. Non-division of follicles – formation of the only follicle (in each testis). Early action of the follicle fusion factor.

Phase B: Stable existence of three-step morphocycle

4. Trogiomorpha. Stabilization of unifollicular state. Early action of follicle fusion factor.

5. Troctomorpha. Alternation of the moment of switching on of the follicle fusion factor. The factor switches either at the early stage of testes formation or at a later stage, already after separation of follicles. Accordingly unifollicular and fan-shaped trifollicular states occur.

6. Psocomorpha. The most variable action of follicle fusion factor – alternation of all three states: unifollicular, trifollicular fan-shaped and trifollicular comb-shaped. In the third case the fusion factor does not act (is delayed).

6a. *Caecilioidus* sp. (Caeciliidae). Overcoming the "block" for stabilization of trifollicular state (4 follicles) – the state beyond the limits of the standard psocid morphocycle.

Phase C: Appearance of a new two-step phthirapteran (Ischnocera – Anoplura) morphocycle instead of psocid three-step morphocycle

7. The common ancestor of Phthiraptera. Switching off of the psocid factor of follicle fusion.

8. Amblycera. Stabilization of a comb-shaped trifollicular testis.

8a. Oligomerization of comb-shaped testis up to two follicles during formation or by reduction of the apical follicle (*Menacanthus pusillus, Myrsidea subaequalis*). The latter is more probable.

9. The common ancestor of Ischnocera + Anoplura. Reduction of the apical follicle. Late (end of embryogenesis – beginning of postembryogenesis) blockage of the development of apical follicle. Formation of opposite arrangement of follicles.

10. Ischnocera, Rhynchophthirina, Anoplura. Fusion of two follicles by their bases (oppositely) and formation of Ischnocera – Anoplura two-step morphocycle: opposite follicles on stems – opposite follicles, fused by their bases. Possibly fusion of follicles by their bases is determined by restoring of psocid factor of follicle fusion switching on at a late developmental stage.

11. Rhynchophthirina. An incomplete manifestation of the morphocycle. It is only possible in connection with restricted diversity of the suborder – 1 genus, 2 species.

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