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Feather mites of the Common Sandpiper *Actitis hypoleucos* (*Charadriiformes*, *Scolopaci*) - an attempt at a reconstruction of acarofauna origin (*Acari*: *Astigmata*)

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ABSTRACT. Feather mites (*Astigmata*) of Common Sandpiper (*Actitis hypoleucos* (*Charadriiformes*; *Scolopaci*) are analyzed. Recent acarofauna of Common Sandpiper is a heterogenous assemblage of mites that belong to five distinct groups: mites related to those of Arenarine Sandpipers (*Scolopaci*; *Scolopacidae*; *Arenariini*) and Calidrine Sandpipers (*Scolopaci*; *Scolopacidae*; *Calidridini*), mites characteristic of Tringine Sandpipers (*Scolopaci*; *Scolopacidae*; *Tringini*), "old invaders" from Oystercatchers (*Charadrii*; *Haematopodidae*) and "recent invaders" from Charadrine Plovers (most probably from Little Ringed Plover *Charadrius dubius* (*Charadrii*; *Charadriidae*). The mechanism of replacement of the Common Sandpiper's own acarofauna by new mites is proposed. A systematic position of the host based on the composition of its feather mite acarofauna is suggested.

INTRODUCTION

A very close association between feather mites and birds seems to suggest a general coevolutionary pattern of phylogenies of both animal groups. Indeed, there exist some conspicuous examples of feather mites-birds coevolution (e.g. DUBININ, 1949, GAUD, 1978, GAUD & ATYEO, 1979, MIRONOV, 1982, 1991, DABERT, 1991). The major feather mite lineages and orders of birds evolved probably in parallel (ATYEO & GAUD, 1979), but cases of discordance between phylogenies of mites and their hosts are very frequent. For instance, cases of acarofauna exchange, secondary cospeciation after recolonization, geographic (allopatric) speciation or independent mite speciation are observed (literature data review see MIRONOV, 1982). Sometimes old and new components of bird acarofauna make it difficult to recognize a "mixture". The origin of acarofauna of Common Sandpiper *Actitis hypoleucos* is such a case.

SYSTEMATIC POSITION OF THE HOST SPECIES

The systematic position of the Common Sandpiper is clear for most contemporary ornithologists. It is a member of the tribe *Tringini* of the family *Scolopacidae* (*Charadriiformes*; *Scolopaci*) (GOCHFELD et al., 1984). The genus *Actitis* (i.e. Common Sandpiper and Spotted Sandpiper *A. macularia*) is closely related to the genus *Tringa* and sometimes considered to be its synonym. Only some authors (STRAUCH, 1978) place *Actitis* in the Calidrine Sandpipers, together with the genera *Aphriza*, *Calidris*, *Eurynorhynchus*, *Limicola*, *Micropalama*, *Philomachus* and *Tryngites*.

FEATHER MITE ACAROFAUNA OF COMMON SANDPIPER

The feather mites from plumage of *Actitis hypoleucos* are listed in table 1.

Tab.1 Feather mites of *Actitis hypoleucos*.

Mite species	Habitat	Data source
Alloptes orthogrammae	Ex, In	2, 4, 7, 8, 9
Avenzoaria totani	In	2, 4, 7, 8, 9
Bychovskiata charadrii	In	1, 2, 3, 7, 8, 9
Montchadskiana minuta	In	3, 6
Dichobrephosceles actitidis	In	1, 3, 4, 5, 7, 8, 9
Phyllochaeta interfolia	Qu	1, 2, 3, 4, 5, 6, 7, 8, 9
Ingrassia forcipata	Dw	1, 7, 10

Ex - external vane surface, In - internal vane surface, Dw - threads of down feathers, Qu - inside the quills. 1 - GAUD, 1972, 2 - DABERT, 1991, 3 - VASJUKOVA & MIRONOV, 1990, 4 - VASJUKOVA & MIRONOV, 1991, 5 - DUBININ, 1951, 6 - DUBININ, 1956, 7 - MIRONOV, 1981, 8 - PETERSON & ATYEO, 1968, 9 - VASJUKOVA & MIRONOV, 1986, 10 - DABERT, unp. data.

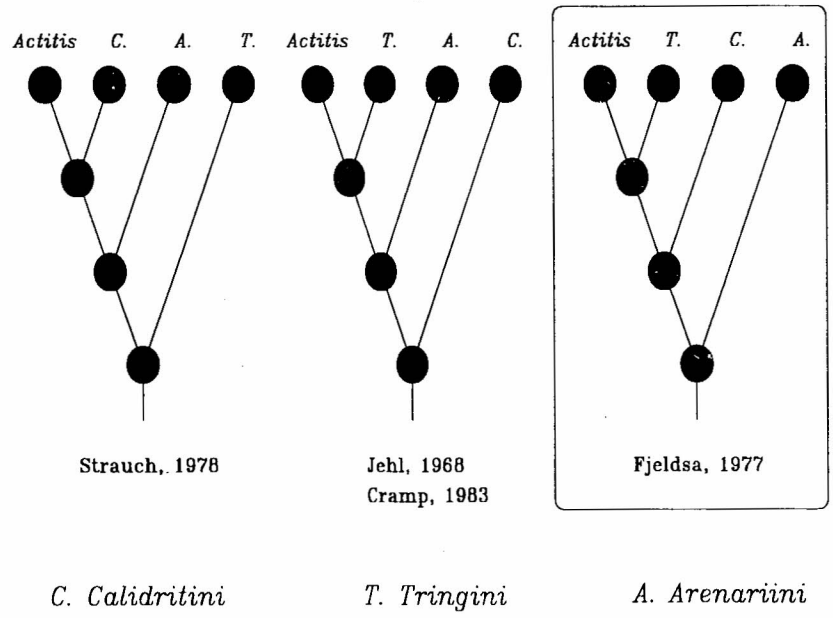
It is a heterogenous assemblage of mites which are specific (or closely related to specific mites) for several host groups. Short characteristics of systematic position and host-parasite relationships of particular mite species are given below.

ANALGOIDEA

Avenzoariidae; *Avenzoariinae*

1. *Avenzoaria totani* is a typical mite of several species of the genus *Tringa* (*Scolopacidae*, *Tringini*). It is most closely related to *Avenzoaria calidris* from the Calidrine Sandpipers (*Scolopacidae*; *Calidridini*).

2. Six species of the genus *Bychovskiata* are restricted to plovers of the family



. Simplificied cladograms for possible intermediate hosts of the Common Sandpiper's acarofauna. Cladogram in frame is the most consistent with the relative age of coexistence of particular mite groups (only familiar parasites) with *Actitis hypoleucos*

Charadriidae. *Bychovskiata charadrii* occurs regularly exclusively on feathers of *Actitis* and some plovers of the genus *Charadrius* (*Charadriidae*, *Charadriinae*). It is found irregularly but relatively often on some wader species of the suborder *Scolopaci* (VASJUKOVA & MIRONOV, 1990, DABERT, 1991) and even on members of other orders (DUBININ, 1956).

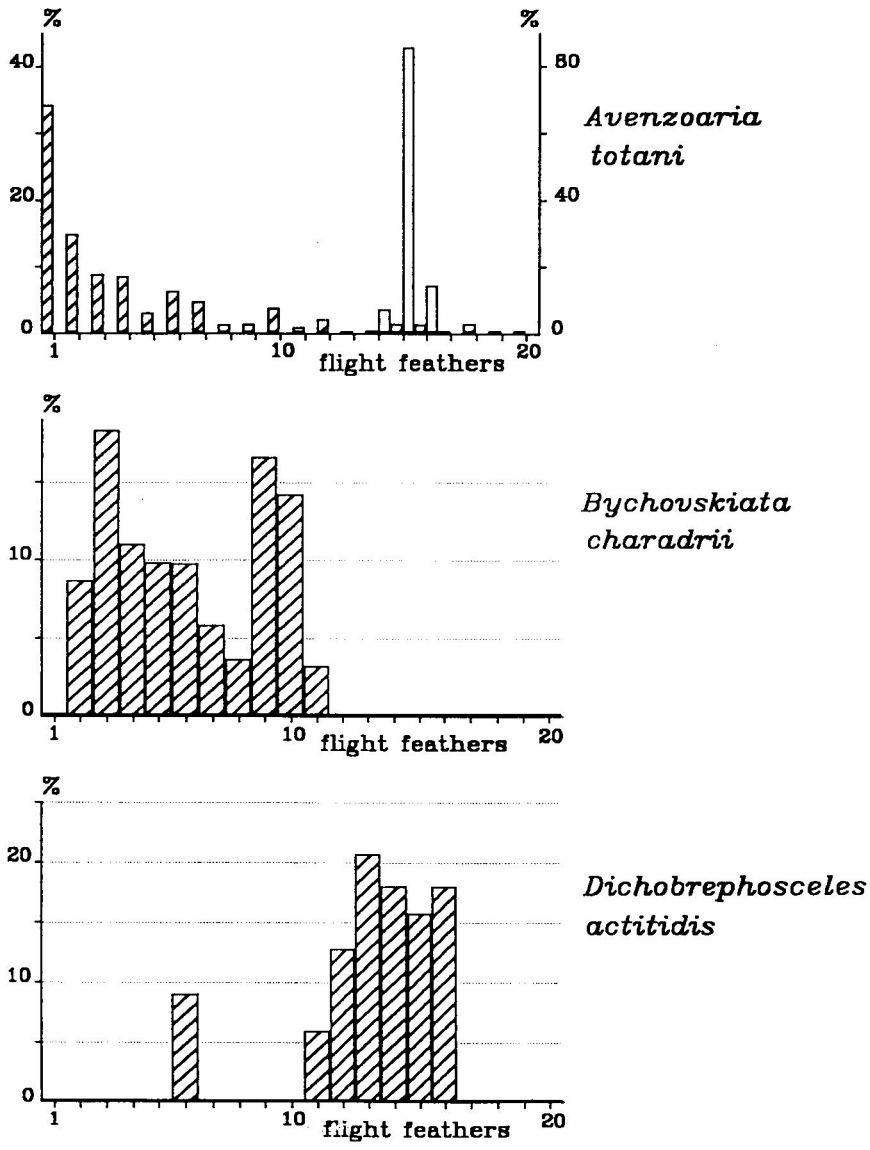
Alloptidae; *Alloptinae*

3. Monoxenic *Dichobrephosceles actitidis* - its only congenere *D.eroliae* is a parasite of the Calidrine Sandpipers (*Scolopacidae*, *Calidridini*).

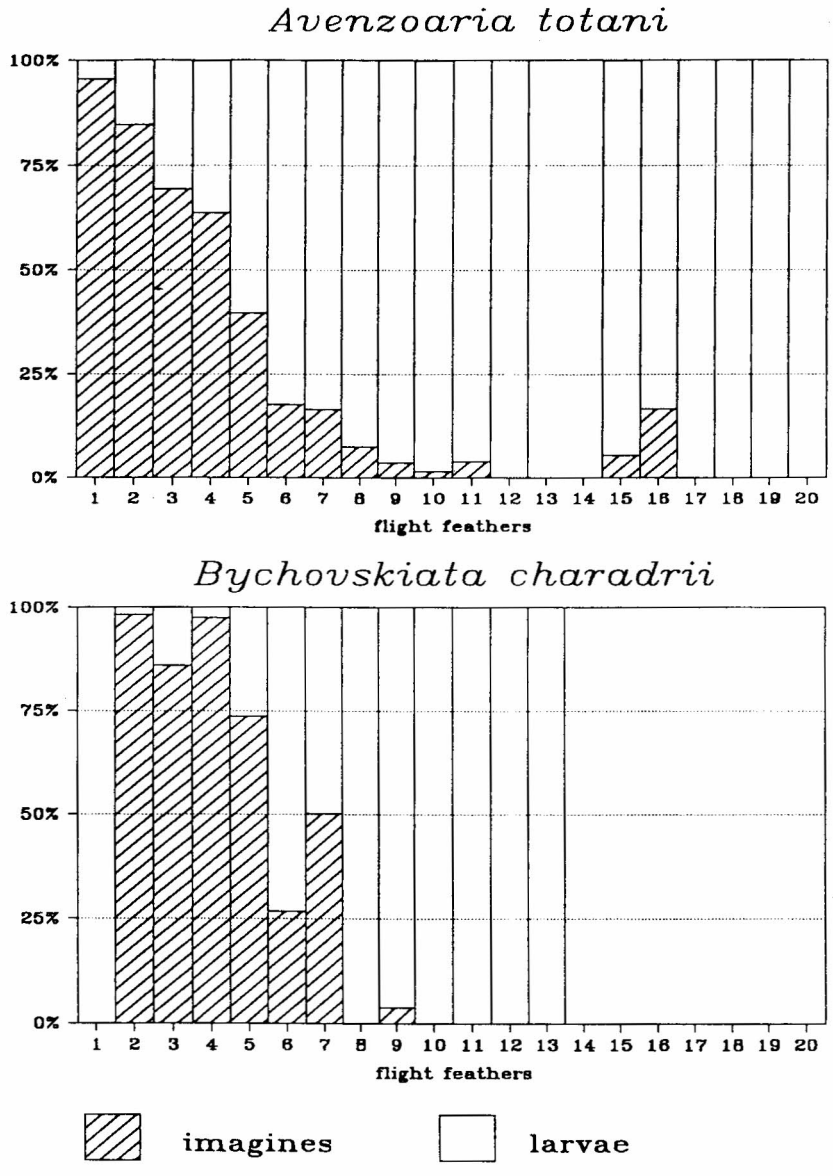
4. The subgenus *Alloptes* (*Apodalloptes*) comprises only two species. *Apodalloptes orthogrammae* is known only from the Common Sandpiper. Its sibling-species *A.curtipes* inhabits feathers of Oystercatcher *Haematopus ostralegus* (*Haematopodoidea*, *Haematopodidae*).

Xolalgidae; *Ingrassiinae*

5. About 25 species of the genus *Ingrassia* are found on water birds of five orders:



2. Distribution of three competitive feather mite species inhabiting the internal vane surface of primaries in Common Sandpiper (from DABERT, 1991). Hatched bars - situation in *Actitis hypoleucos*, empty bars - situation in *Tringa* spp.



3. Spatial age structure of populations of *Avenzoaria totani* (from *Tringa* spp.) and *Bychovskiata chardrii* (from *Actitis hypoleucos*) on primaries

Anatiformes (1 species), *Charadriiformes* (over 15), *Pelecaniformes* (1), *Podicipitiformes* (1) and *Procellariiformes* (4). *Ingrassia forcipata* [1] inhabits only birds of the genus *Actitis* (*A.hypoleucos*, *A.macularia*). Its systematic relationships to other members of the genus are uncertain. The shape of epimeres III (males) and concave terminal margin of hysterosomal shield (female) indicate that it is related to species of "*tringae*" group which inhabit plumage of *Calidris*, *Philomachus* and *Limnodromus* (DABERT & EHRNSBERGER, in press), but some other features (shape of opisthosomal lobes, terminal membranes, absence of fusion between sclerites of scapular setae with scapular shields) resemble species of "*veligera*" group specific to birds of the genus *Tringa*.

PTEROLICHOIDEA

Pterolichidae; *Magimeliinae*

6. *Montchadskiana minuta* inhabits plumage of several species of the Tringine Sandpipers (*Actitis*, *Tringa*). The occurrence on the Knot *Calidris canutus* (DUBININ, 1956 and other data cited by this author) needs to be confirmed. This mite is closely related to *M.fascigera*, parasite of *Arenaria interpres* (*Scolopacinae*; *Arenariini*) and to *M.phalaropus*, parasite of *Phalaropus fulicarius* and *Ph.lobatus* (*Scolopacinae*; *Phalaropodini*).

Syringobiidae; *Syringobiinae*

7. The genus *Phyllochaeta* was reported from the Charadrine Plovers (*Charadriidae*), Calidrine Sandpipers (*Scolopacidae*, *Calidridini*), Turnstones (*Scolopacidae*, *Arenariini*) and Dowitchers (*Scolopacidae*, *Limnodromini*). *Phyllochaeta interfolia* inhabits only members of the genus *Actitis* [2] and is most closely related to *P.trouessartii* from *Arenaria interpres* (DABERT, 1991).

Therefore particular mite groups of the Common Sandpiper's acarofauna have different origin. At least five such groups can be distinguished:

1. "arenarine" feather mites - *Phyllochaeta interfolia*.
2. "calidrine" feather mites - *Dichobrephosceles actitidis*.
3. "tringine" feather mites - only *Avenzoaria totani* is the fully tringine species in the Common Sandpiper's acarofauna. At present *Avenzoaria totani* is dying out and being replaced by *Bychovskiata charadrii*. *Montchadskiana minuta* occurs probably both on the Calidrine and Tringine Sandpipers and is relatively seldom in Common Sandpiper's plumage.

Ingrassia forcipata could be included in "calidrine", "arenarine" or "tringine" group.

4. "haematopodoide" feather mites - *Alloptes* (*Apodalloptes*) *orthogrammae* is

[1] The second species *Ingrasia centrotibia* (GAUD, 1972) was reported from Common Sandpiper. This species lives in down feathers of Black-winged Stilt *Himantopus himantopus* (*Haematapodoidea*, *Recurviristridae*) and its occurrence on Common Sandpiper was probably an accidental contamination.

[2] Acarofauna of *Actitis macularia* is poorly known. This bird is inhabited by another subspecies of *Phyllochaeta interfolia* (unp. data).

clearly a well-adapted invader from the Oystercatchers, and most likely replaced another *Alloptes* species of the subgenus *Conuralloptes* and evolved into a separate species. *Conuralloptes* is a common mite for the order *Charadriiformes*, especially the suborder *Scolopaci*, inhabiting the same niche as *Apodalloptes*.

5. "charadrine" feather mites - *Bychovskiata charadrii* is the newest element of acarofauna of *Actitis hypoleucos* . This mite replaces *Avenzoaria totani*. It seems that speciation is not initiated yet.

RECONSTRUCTION OF ACAROFAUNA ORIGIN

The recent acarofauna of Common Sandpiper has resulted partly from an evolutionary parallelism of mites and host, and partly from invasions of feather mites from other waders and, in some cases, secondary cospeciation. In my opinion the "arenarine", "calidrine" and "tringine" mites are examples of the coevolution, while the "haematopodoide" and "charadrine" mites are invaders.

The mites of the native part of acarofauna show different degrees of specialization and host-parasite relationship. *Dichobrephosceles actitidis* and *Phyllochaeta interfolia* are the highest specialized, monoxenic (see footnote No2) species in this group. *Dichobrephosceles* lives only on birds of the order *Scolopaci* but is closely related to the genus *Brephosceles* and related genera from the order *Charadrii* and other waterfowl. Both *Phyllochaeta interfolia* and its common relative *Ph.trouessarti* occur only on *Scolopaci* but other species inhabit the Charadrine Plovers. At the moment it would be risky to state which species is older, *Dichobrephosceles actitidis* or *Phyllochaeta interfolia*. *Ingrassia forcipata* is an intermediate form between "*tringae*" group (from *Calidridini*, *Limnodromini* and *Phalaropodini*) and "*veligera*" group (from *Tringini*), inhabiting only two host species: *Actitis hypoleucos* and *A.macularia*. Contrary to them *Avenzoaria totani* and *Montchadskiana minuta* show a moderate degree of morphological specialization compared with their congeneres. *Montchadskiana minuta* inhabits several bird species and genera of the tribe *Tringini* and one of the tribe *Calidridini*; *Avenzoaria totani* lives exclusively on the Tringine Sandpipers. Provisionally the above mentioned mites can be arranged according to their decreasing evolutionary age: *Dichobrephosceles actitidis*, *Phyllochaeta interfolia* - *Ingrassia forcipata* - *Montchadskiana minuta* - *Avenzoaria totani*. It is noteworthy that such a sequence seems to suggest the systematic position of hosts:

- *Actitis* should be included in the tribe *Tringini*,
- *Tringini* are a sister-group for *Calidridini*[3],
- *Arenariini* could be the out-group for *Tringini* and *Calidridini* or these two lineages had a common ancestor.

Such a phylogenetic relationship between these host groups was postulated by some ornithologists (FJELDSÅ, 1977) (see fig.1).

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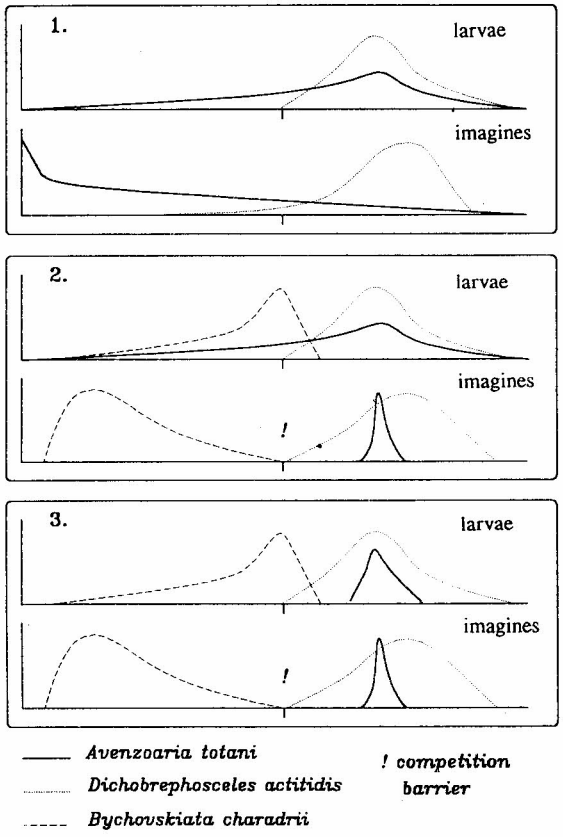
[3]Studies of FJELDSÅ (1977) on downy plumage patterns in young of shorebirds and my analysis of morphology of the genus *Avenzoaria* from genera *Tringa* and *Calidris* (DABERT, 1991) confirm this suggestion.



4. Hypothetical mechanism of replacement of *Avenzoaria totani* by *Bychovskiata charadrii* in the Common Sandpiper's acarofauna. 1 - possible situation before invasion of *B. charadrii*, 2 - the first generation after invasion, 3 - present situation

The origin of the other components of acarofauna of the Common Sandpiper is two-grade. The older "invaders", like *Alloptes (Apodalloptes) orthogrammae* had come from the Oystercatchers and evolved into a separate species. Conditions of such a transfer are at present difficult to explain. Circumstances of the second transfer of *Bychovskiata charadrii* are possible to reconstruct. This happened probably relatively recently because speciation of *Bychovskiata charadrii* has not started yet. I suppose that the transfer took place from the Little Ringed Plover *Charadrius dubius*. The Common Sandpiper and Little Ringed Plover have the same breeding biotopes. The probability of nesting adoption during the breeding season between these two birds and acarofauna exchange between new parents and "orphans" is relatively high (P. CHYLARECKI, pers. com). The invasion was unidirectional, from *Charadrius dubius* to *Actitis hypoleucos*. Compared with *Avenzoaria totani*, its closest evolutionary and biological relative in the

Common Sandpiper's acarofauna, *Bychovskiata charadrii* is a very expansive species (broad constant and accidental host range, even outside the waders). It shows a low degree of morphological and biological specialization: absence of particular morphological adaptations, the most primitive idiosoma chaetotaxy in the subfamily, relatively frequent primitive way of precopulatory coupling between male and female (not tritonymph).

It is not clear if *Bychovskiata charadrii* has displaced another species *Dichobrephosceles actitidis* to the forearm flight feather. Mites of *Brephosceles*-like group inhabit the secondaries during moderate infestation or the whole wing and tail feathers during heavy infestation (DUBININ, 1949, 1951, PETERSON, 1971). It is possible that the presence of *Bychovskiata charadrii* reduces the population size of *Dichobrephosceles actitidis* which inhabits only the optimum microhabitats (secondaries). But it can not be excluded that *Dichobrephosceles actitidis* was forced to occupy the second flight feathers already during its coexistence with *Avenzoaria totani*.

The third species inhabiting internal vane surface, *Montchadskiana minuta*, does not compete for microhabitats with the native mites (*Avenzoaria totani*, *Dichobrephosceles actitidis*) or with the new invaders (*Bychovskiata charadrii*). Mites of the genus *Montchadskiana* are adapted to inhabiting the most distal part of the primaries (VASJUKOVA & MIRONOV, 1990, DABERT, unpublished). Other mites avoid this place because of its very severe aerodynamic and climatic conditions.

A question arises: If the concept of replacement of *Avenzoaria* by *Bychovskiata* is true, why is the first flight feather not occupied by *Avenzoaria*? (fig.2). *Avenzoaria totani* prefers most of all the first flight feather[4] while *Bychovskiata* never inhabits it. In my opinion this results from the specific spatial age structure of both mite populations (fig.3). Eggs are stuck mostly on the primaries near the vane bases. After hatching the larvae move first of all into secondaries where they are less exposed to aeration influence, and spatially separated from adults and nymphal stages (competition? cannibalism?). Even when adults and juvenile stages live on the same feather, larvae and nymphs inhabit mostly more distal or proximal parts of feather than the adult mites. As they grow up, the nymphs and adult mites move into the wing margin. Consequently on the one hand during its return to the primaries *Avenzoaria totani* meets the strong competitor and is not able to inhabit the preferred first flight feather, on the other hand it can survive in strongly reduced number in suboptimum microhabitat (secondaries) because of lack of *Bychovskiata charadrii* in that place. Figure 4. shows this hypothetical mechanism of competition between the examined mites that leads to elimination of the more specialized species. It is necessary to add that *Avenzoaria totani* shifted to suboptimum microhabitat is forced to compete with *Dichobrephosceles actitidis* inhabiting these feathers. But both species reduce the interactions due to occupying separate parts of the same feather; *Avenzoaria* occurs on dark parts of feather, *Dichobrephosceles* on white ones. It is not known if such a site selection took place before the invasion of *Bychovskiata charadrii*.

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[4]Data obtained by observation of this species from the genus *Tringa*: *T. glareola*, *T. totani* and *T. stagnatilis* (DABERT, 1991).

DISCUSSION

Using rigorous methodologies to examine the degree of parallelism of both feather mite and bird host phylogenies (e.g. PAGE, 1991) is sometimes difficult because of extreme heterogeneity of acarofauna. Numerous cases of acarofauna exchanges and secondary cospeciations, especially if they take place among closely related host taxa, may be misleading. For instance it is not impossible that a part of above mentioned native mites of the Common Sandpiper are invaders. Of course it was not my aim to perform a complex parasitophyletic analysis of both parasite and host phylogenies. First of all data about host-parasite relationships among the genus *Actitis* and its related genera are too incomplete. I would like to show only the potential implications resulting from detailed acarofauna analysis. It can give directions to studies on some elements of biology and evolution of both parasites and hosts. Because at present feather mite acarofaunae of various birds are known relatively unequally, the strict coevolutionary studies can be undertaken only in few cases. But there is no doubt that in the future these arachnids might be one of the best models for such studies.

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