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FEATHER MITES, FEATHER LICE, AND THANATOCHRESIS

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ABSTRACT: Unrelated taxa of feather mites use exuviae of their own, or closely related, species for molting within quills or on feather surfaces of diverse groups of birds. On the Orange-fronted Conure [*Aratinga canicularis* (L.)] and other parrot species, feather mites and mallophagan eggs coinhabit the same feather area, mites molt within the exuviae of other mites within the mallophagan egg shells. Molting within exuviae and within egg shells are examples of thanatochresis (the use of dead parts of one animal by living individuals of a second species, but not for food); this phenomenon may be common among feather mites and other Astigmata.

Thanatochresis (from the Greek *thanatos,* death; and *chresis,* use) is the utilization of cadavers, secretions, skeletal pieces, excrements and other products of one species by living individuals of a second species, but not for food (Margalef, 1977). A familiar example would be the use of shells of univalve mollusks by hermit crabs (Paguridae). Under special circumstances, the definition should be modified to include utilization of cadavers by living individuals of the same or different species, but not for food.

Quill inhabiting feather mites (Syringobiidae: Syringobiinae) molt within exuviae of their own species as do species of Pyroglyphidae. A few feather mites living outside the quills also molt within the exuviae of their own species, an event often taking place within egg shells of feather lice (Mallophaga). Egg shells and/or exuviae are apparently not necessary in the life cycles of the mites; thus, the mites are opportunistic and the phenomenon might be termed "facultative thanatochresis".

When feather mites molt, the ecdysial line is Y-shaped with the stem of the Y beginning near the prodorsal shield and the arms of the Y directed posterolaterally behind setae *d 2* and *l 2,* then posteriorly along the opisthosomal margins to meet above the anus (Oudemans, 1908; Figs. 2, 3). The section of the tegument posterior to the second row of setae (in essence an operculum) is pushed off as a new instar emerges; the resultant cast skin is a hollow shell with a large dorsoposterior opening. In some species, these empty "shells" are used by other individuals of the same or related species for molting in such a fashion that "chains" of "telescoped" exuviae can be formed (Figs. 1, 4).

Charadriiform mites

Exuvial chains have been reported for several species of Syringobiinae occurring in the quills of charadriiform birds; through time there have been various interpretations and speculations about this phenomenon. Trouessart (1887) in his description of *Anoplonotus* (=*Pterolichus*) *semaphorus* noted that 3 or 4 exuviae could accumulate, *one on top of the other,* which to him indicated that the mites underwent numerous molts in the same place, or at least, kept the old skins on their backs as sort of a mantel.

Trouessart (1894a) observed the same phenomenon in *Syringobia chelopus* (Trouessart and Neumann) and mentioned that he could count up to 6 skins, *one over the other,* and that the skins were of the same individual. Later (1894b), he modified his concept of exuvial chains, stating that the cast skins interlocked or fitted into each other in such a manner that the largest skin is the most exterior and the smallest is inside all of the others. Furthermore, the skins belonged to different individuals with the age and size regularly decreasing from the first to the last. Trouessart suggested that molting inside cast skins was a stratagem for the avoidance of predaceous Cheyletidae. The part of the mite covered by old exuviae would have the appearance of dead skin void of flesh and blood; the exposed opisthosoma would be protected by repugnant secretions of the opisthonotal glands analogous to certain Myriapoda.

Dubinin (1956), in discussions about life cycles of *Anoplonotus semaphorus* and *Thecarthra theca* (Mégnin and Trouessart), stated (and illustrated) that mites molting on top of cast skins would result in conservation of space within the quill. As a casual aside, he said that the series of skins looked almost as if one skin was within another.
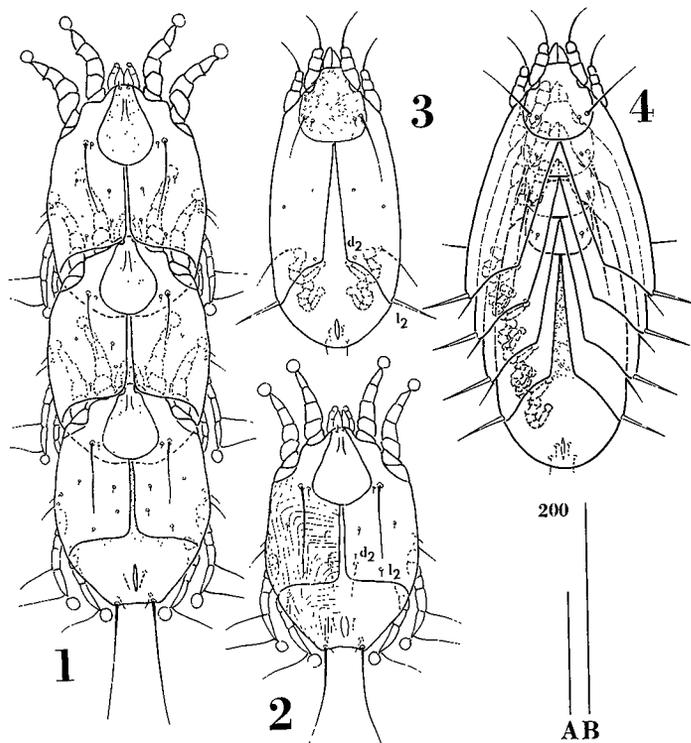
FIGURES 1–4.   *Chiasmalges* Gaud and Atyeo, sp. n., protonymphs. **1.** Exuvial chain. **2.** Cast skin. *Syringobia* Trouessart and Neumann sp. (from *Charadrius vociferus* (L.), protonymphs. **3.** Cast skin. **4.** Exuvial chain with legs deleted from right side. Scale in micrometers: A, Figures 3, 4; B, Figures 1, 2. Setae: *d 2 l 2*, second row of hyperstomals.

From a few specimens of field-collected Charadriiformes we have quills of flight feathers containing Syringobiinae. From museum skins we have taken syringobiid species from the abortive flight feathers of Kiwis. The mites studied and their hosts are listed; all shore birds are from North America.

Kiwilichus cryptosikyus Gaud and Atyeo, from the Kiwi (*Apteryx australis* Shaw), New Zealand.

Phyllochaeta Dubinin species from the Spotted Sandpiper [*Actitis macularia* (L.)]

Syringobia Trouessart and Neumann species from the Willet [*Catoptrophorus semipalmatus* (Gmelin)] and the Killdeer (*Charadrius vociferus* L.)

Thecarthra theca (Megnin and Trouessart) from the Black Tern [*Chlidonias niger* (L.)]

The Kiwi material was collected in the mid-

1960s and information on the condition of the quills was not taken. It can only be assumed that the observations to be given for the North American shore birds might be similar for Kiwis.

The quill is hollow and is regularly divided into compartments by pulp caps. Each cap is a thin convex/concave partition with the convex surface away from the feather base. Feather mites move in and out of the quill through the superior umbilicus. In all of the charadriiform quills observed, the pulp caps were intact and mites were in most of the compartments; presumably small holes had been created by the mites for passage up and down the quill length, but these were not seen.

Eggs are laid on the convex surface of the pulp cap (*Syringobia*) or in rows around the quill wall immediately above the pulp caps (*Thecarthra*). As mites within a compartment prepare to molt, they move along the quill wall and wedge themselves head downward between the wall and the convex surface of the pulp cap. Thus, above each pulp cap there can be an incomplete circle (or row) of ecdysing mites composed of larvae, protonymphs and/or tritonymphs (thigmotactic stereokenetic response?). Later developing individuals can either wedge between the wall and a pulp cap, or they can enter old exuviae. As the space between the wall and the pulp cap fills, options as to sites for molting become limited. Individuals within a compartment tend to be in similar developmental stages. Thus, chains of primarily protonymphs and later chains of primarily tritonymphs are formed (larval chains have not been observed). Whether the first or the last in a chain, each individual has the same appearance with the anterior legs (I and II) bent downward (Figs. 3, 4) and after the molt, the dorsum lacks the dorsoposterior tegument. If there are size differentials (i.e., different stadia), the degree of penetration by an active instar into exuviae is thus conditioned.

In *Syringobia*, as an active protonymph forcibly enters PN exuviae, the exuviae are distended laterally as can be determined by the expansion of the V-shaped opening along the dorsum (Fig. 4). As each successive protonymph enters the chain, the existing exuviae cannot be distended as much as the previous ones; the series of Vs formed by the dorsal splits become narrower and narrower with each skin. In *Syringobia* tritonymphs, the individuals have a different body conformation such that an active tritonymph can penetrate the exuvial cavity to

the same degree as the protonymphs, but the exuviae are not distended laterally. Tritonymphal chains are parallel-sided and the dorsal splits are equal for all individuals.

In species in which there is probably not such a synchrony of age classes, short exuvial chains occur with various instars in each chain (e.g., *Kiwialges*) without any particular sequence. Larvae are completely inside tritonymphal exuviae and conversely, tritonymphs molting in larval exuviae, because of the size differentials, have only their gnathosomata inserted in larval exuviae.

Except for one "curious" slide containing a short exuvial chain of *Struthiopterolichus sculpturatus* (Hirst) (Pterolichidae) from an Ostrich, we thought that ecdysing within exuviae only occurred in certain syringobiid taxa. However, in our microhabitat segregation studies with Mexican parrots (Pérez and Atyeo, 1984), we discovered that this phenomenon is common among diverse and unrelated groups of feather mites.

Psittaciform mites

From this point, information to be presented is for the Orange-fronted Conure [*Aratinga canicularis* (L.)] for which we have the best data; the same phenomena have been observed for species of feather mites from other *Aratinga* Spix, and from *Amazona* Lesson and *Forpus* Boie.

Two new species of *Paralgopsis* Gaud and Mouchet (Pyroglyphidae) are in the larger quills of *A. canicularis*, a large species (A) and a small species (B). When the 2 species inhabit the same quill, the exuvial chains can contain both species. The longest chain observed consisted of 5 protonymphs in the sequence of species A/A/B/B/B; however, any combination can occur. Occasionally in tritonymphal exuviae or in protonymphal A exuviae 2 or 3 protonymphs and/or larvae can be inside exuviae side-by-side and each of these can be beginnings of short exuvial chains.

All life stages of *Paralgopsis* species are concentrated around the pulp caps and in the space surrounding the superior umbilicus; sometimes they destroy a small portion of the medulla and enter the rachis. *Paralgopsis* species are small relative to the diameter of the superior umbilicus; they are able to leave the quill in any life stage. Presumably the dispersal stage, as in the Syringobiinae, are adult males and females or fertilized females.

comm., new observations) and pieces of mites in the alimentary tracts of both Amblycera and Ischnocera are common (Nelson, 1972; Marshall, 1981; Rothschild and Clay, 1952; Emerson and Dalgleish, pers. comms.). As regards feather mites, both predation and scavenging of egg shells and exuviae by the feather lice are probably true. Whether the predation is active or accidental and whether it is important to the Mallophaga are problematical.

DISCUSSION

Why have the stratagems of using old exuviae and mallophagan egg shells for molting evolved? For quill inhabiting Syringobiinae, Dubinin (1956) suggested that molting "on" old exuviae conserved space within the quill, but space does not seem to be a limiting factor. For the same mites, Trouessart (1894b) suggested it was a protection against predaceous Cheyletidae, but cheyletids within the quills are uncommon, at least today. Finally, both stratagems have evolved in unrelated groups of mites associated with diverse groups of birds.

We envision a different scenario involving both space conservation and protection. During the molt, mites are vulnerable to predation and/or the elements. By taking refuge in available protected area (i.e., egg shells) during these periods of vulnerability, the life expectancy would be increased. Because the egg shells are small and variable in number, ecdysing within old exuviae would conserve space, allowing more individuals to be protected in a given space. As feather mites secondarily invaded quills, it would be expected that molting within exuviae would be continued. Whether this evolutionary sequence is correct is immaterial in one sense. If some Mallophaga are actively predaceous on feather mites, then, the mites are using the egg shells of their predators for protection from these predators.

The use of exuviae and mallophagan egg shells for molting may be common among feather mites and other Astigmata. Egg shells filled with exuviae have been collected from museum skins of diverse orders of birds, namely, *Crypturellus cimmamomeus* (Lesson) with a species of Crypturopidae (Pterolichoidea), *Eudocimus albus* (L.) (Ciconiiformes) with a species of *Scutomegninia* Dubinin (Avenzoariidae: Bonnetellinae),

Phloeoceastes guatemalensis (L.) (Piciformes) with a species of Pteronyssinae (Avenzoariidae), and *Zenaidura macroura* (L.) (Columbiformes) with a *Falculifer* Railliet species (Falculiferidae).

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Molting within mallophagan eggs

Each of the 11+ species of feather mites living outside the quills of *A. canicularis* have discrete distributions on the feathers (Pérez and Atyeo, 1984). In establishing these sites, it was noted that there were mallophagan eggs on different parts of the feathers. Mallophagan eggs are known to have different shapes and different chorion sculpturing (Balter, 1968a, b) so to facilitate identification; eggs from different sites were prepared on microscope slides. We were very surprised to find that many eggs shells were filled with exuvial chains reminiscent of the Syringobiinae and *Paralgopsis* found within quills. The feather mites were molting in protected areas provided by the feather lice. These initial observations lead into a study of feather mites, feather lice, and thanatochresis.

Eichler (1954), working with slide mounted specimens, first reported mites in mallophagan eggs from the Buccerotidae and suggested that as the mites usually occurred in pairs within the eggs that each egg might be using an egg as a love nest (*Liebesnest*). Later (1956) he suggested other possibilities: the mites accidentally enter the eggs during preparation in Canadian balsam, the eggs could be hiding places for the mites, the eggs could be used for mite oviposition, and finally, the mites might be predaceous on the eggs.

We now know that Eichler's suggestions were not correct; the louse eggs are used by the feather mites for molting. As a distinct relationship exists between the feather mites and the eggs, the next questions involved the association of the eggs with the species of Mallophaga and to determine which mites were using the different eggs.

Eventually the distribution of 3 types of eggs were established (similar to Nelson and Murray, 1971) and each egg type was associated with a species of feather louse. For the lice, site preferences for oviposition seem to be conditioned more by feather structure than by topographical positions of the feathers.

On *Aratinga canicularis* there were 2 species of Amblycera [Menoponidae: *Psittacobrosus anduzei* (Stafford) and *Heteromenopon* Carriker, sp. n.] and 1 species of Ischnocera (Philopteridae: *Paragoniocotes venezolanus* Stafford); all are new host records. The quill inhabiting *Heterokodeia* Carriker (Menoponidae), known from species of *Ara* Lacépède, *Brotogeris* Vigors, and other species of *Aratinga*, have not been collected from *A. canicularis*.

Heteromenopon eggs are found between the superior umbilicus and the skin surface on all feathers except those of the body and lesser wing coverts (Figs. 5, 6); *Paragoniocotes venezolanus* eggs are attached to the plumulaceous barbs of all feathers (Figs. 5, 8); and *Psittacobrosus anduzei* eggs are restricted to the pennaceous barbs of the primaries, secondaries, primary coverts, alula and tail feathers (Figs. 5, 7).

The feather mites (all new species), using mallophagan egg shells for molting, are those that occur in the same sites as the eggs. *Chiasmalges* Gaud and Atyeo (Psoroptoididae) are concentrated around the superior umbilicus; they are the only mites entering the egg shells of *Heteromenopon* and they form exuvial chains. For these the ecdysial position is such that the anterior legs are not bent downward as in the Syringobiinae (Figs. 1, 2).

The eggs of *P. anduzei* are used by a number of species, each of which forms exuvial chains. Egg shells on the primaries are entered by *Protolichus* Trouessart (Pterolichidae) and *Eurydiscalges* Faccini, Gaud and Atyeo, species A (Psoroptoididae); those on the secondaries by *Aralichus* Gaud, species A (Pterolichidae) and *Eurydiscalges*, species B; those on the alula and primary coverts are used by *Eurydiscalges*, species A and *Protonyssus* Trouessart (Xolalgidae); and eggs on the tail feathers by *Aralichus*, species C. Where 2 mite species are present in 1 site, both can enter the same mallophagan egg and both form exuvial chains within the egg (up to 4 or 5 chains containing 20+ exuviae have been observed in one egg shell). The third species, *Paragoniocotes venezolanus*, attaches eggs to the plumulaceous barbs, the site occupied by 1 to 3 species of *Fainalges* Gaud and Berla (Xolalgidae). These eggs are not used by *Fainalges* or by any other feather mite species.

When mallophagan eggs are not present on an individual feather of *A. canicularis*, the acarofauna is unchanged on that feather. Short exuvial chains of mite exuviae can be seen in the sites normally occupied by mallophagan eggs. As stated earlier, egg shells are not obligatory for the mite life cycle.

On *Aratinga canicularis* there are 15+ species of feather mites and 3 species of Mallophaga. Whether the relationships between the 2 groups is predator-prey or whether the lice are only scavengers in unknown. Some Mallophaga are predaceous on other Mallophaga and/or on their own species (Nelson, 1971; Dalgleish, pers.
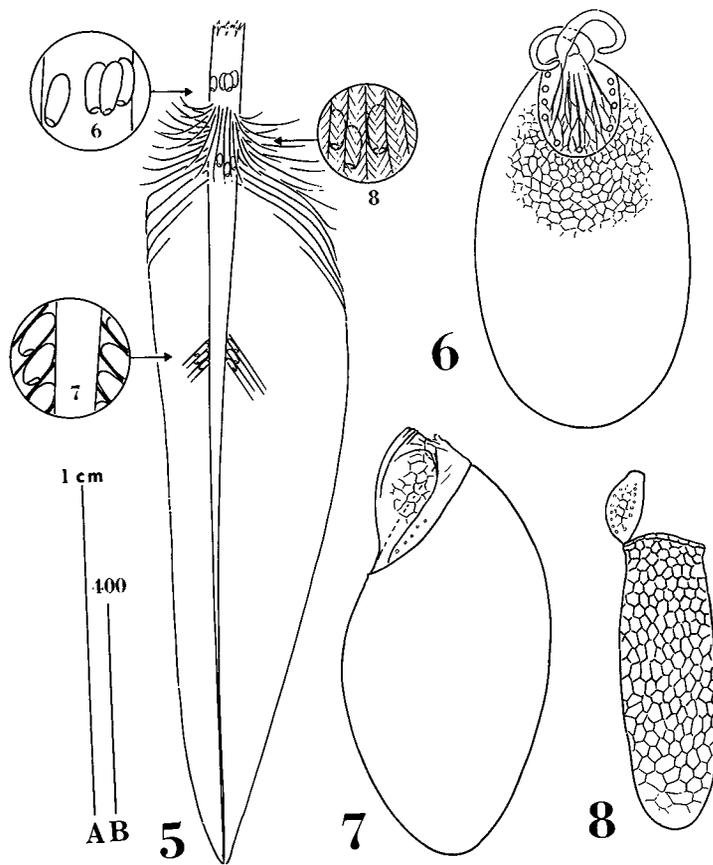
FIGURES 5–8.   5. Alula of *Aratinga canicularis* (L.) showing positions of mallophagan eggs. Mallophagan eggs. 6. *Heteromenopon* Carriker, sp. n. 7. *Psittacobrosus anduzei* (Stafford). 8. *Paragoniocotes venezolanus* Stafford. Scale A. Figure 5; scale B (in micrometers), Figures 6–8.

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