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OF THE GENUS *SCHIZOCARPUS* TROUESSART, 1896
(ACARI, CHIRODISCIDAE)
FROM ALASKA AND INDIANA, USA

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MITES OF THE GENUS *SCHIZOCARPUS* TROUESSART, 1896 (ACARI, CHIRODISCIDAE) FROM ALASKA AND INDIANA, USA

BY A. FAIN¹ and John O. WHITAKER, Jr²

MORPHOLOGY
SCHIZOCARPUS
PARASITES
OF BEAVERS
GEOGRAPHICAL
DISTRIBUTION
HOST-PARASITE
PARASITE
LOCATIONS
ON BODY HOST
MULTISPECIATION
ALASKA
INDIANA

SUMMARY : Mites of the genus *Schizocarpus* Trouessart, 1896 (Acari, Chirodiscidae) parasitic on *Castor canadensis* from Alaska, USA were studied as compared with those from Indiana. Nine new species are described, three in the *mingaudi* group : *Schizocarpus paramingaudi* n. sp., *S. alaskensis* n. sp., and *S. reductus* n. sp. ; four in the *indianensis* group ; *S. postannulatus* n. sp., *S. centralis* n. sp., *S. contrarius* n. sp., and *S. distinctus* n. sp. ; and two in the *virgulatus* group : *S. protinus* n. sp. and *S. posticus* n. sp. These data support previous conclusions on European and Indiana Beavers concerning multispeciation in the genus *Schizocarpus* related to isolation of the Beaver populations in separate areas and relative confinement of the mites to definite areas of the Beaver. Observed differences in this genus are in the males ; it is suggested that multispeciation evolved as a means of species recognition.

MORPHOLOGIE
SCHIZOCARPUS
PARASITE
DES CASTORS
RÉPARTITION
GÉOGRAPHIQUE
HÔTE-PARASITE
DISTRIBUTION
SUR LE CORPS
DE L'HÔTE
MULTISPÉCIATION
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INDIANA

RÉSUMÉ : Les acariens du genre *Schizocarpus* Trouessart, 1896, parasites de *Castor canadensis* en Alaska, USA ont été étudiés et comparés à ceux récoltés sur le même hôte mais en Indiana. Neuf espèces nouvelles sont décrites, dont trois dans le groupe *mingaudi* : *S. paramingaudi* n. sp., *S. alaskensis* n. sp., et *S. reductus* n. sp. ; quatre dans le groupe *indianensis* : *S. postannulatus* n. sp., *S. centralis* n. sp., *S. contrarius* n. sp., et *S. distinctus* n. sp. ; et deux dans le groupe *virgulatus* : *S. protinus* n. sp. et *S. posticus* n. sp.

Ces nouvelles données confirment les observations faites précédemment sur les castors d'Europe et d'Indiana USA concernant la multispeciation dans le genre *Schizocarpus*, attribuée d'une part à l'isolement des populations de castors dans les régions bien séparées géographiquement et d'autre part au confinement des diverses espèces d'acariens dans des zones bien définies du corps des castors. Les différences observées chez les diverses espèces de *Schizocarpus* intéressent essentiellement les mâles, ce qui suggérerait que la multispeciation est peut-être un moyen de reconnaissance spécifique utilisé par l'acarien pour prévenir des hybridations stériles.

INTRODUCTION

In the U.S.S.R., mites of the genus *Schizocarpus* were studied by DUBININA (1964), who examined 22 Beavers (*Castor fiber* L.). She found 12 species

of *Schizocarpus* of which 11 were new. All the Beavers examined by DUBININA originated from the Voronesh State Reservation, along the river Voronesh which is a tributary of the main river Don, which flows into the Azov Sea.

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FAIN *et al.* (1984) studied fur mites of the genus *Schizocarpus* Trouessart parasitic on 11 American Beavers *Castor canadensis* from Indiana, U.S.A. They found eight species, of which the previously described *S. mingaudi* was found, whereas the other seven were new and entirely different from the Eurasian species. DUBININA had identified one as *S. mingaudi*, but FAIN and LUKOSCHUS (1985) believe DUBININA's *S. mingaudi* to be a new species, but close to *S. mingaudi*. It is our belief that *S. mingaudi* forms a link between *Schizocarpus* of Eurasia and of North America, and that probably one species, a *S. mingaudi* progenitor, was present at the time of separation of *Castor canadensis* and *C. fiber*.

Studies on the genus *Schizocarpus* from European Beavers were continued by FAIN and LUKOSCHUS (1985). These authors examined four Beavers, among which two originated from the basin of the river Elbe in D.D.R., one was from a river in Mongolia, and one was from an unknown locality, but the authors surmised that it came from southern Europe. They found a total of 25 species, of which 21 were new and four had been previously described by DUBININA. These 21 new species plus the 12 species described by DUBININA bring to 33 the number of species of *Schizocarpus* from Eurasian Beavers from different geographical areas.

Such extreme speciation is probably unique in parasitology. The cause of this phenomenon is not known but FAIN and LUKOSCHUS (1985) supposed that it results from the combination of two different mechanisms. The first process is isolation of the various populations of Beavers living in separated areas. This hypothesis is indirectly supported by the great differences in the composition of the mite communities between areas. The second mechanism is the microisolation resulting from the existence on the Beaver of various microhabitats which differ from each other by the texture and the thickness of the hair, the differences in the skin secretions, etc. The hypothesis that the different mite species select the different microhabitats is suggested by the relative confinement of most of the *Schizocarpus* species to a definite area on the Beaver. This confinement tendency is clear through all of these studies.

This paper presents information on beaver mites from Alaska, and also some new information on *Schizocarpus* from Indiana. Additional investigations are underway on Beavers from several other areas in the United States. Nine new species are described; as usual in this genus the new species are based only on male specimens.

Reexamination of the mites recorded from Indiana in our previous paper has shown that some of the new species found in Alaska and described herein were also represented in Indiana but were not then recognized as separate.

In Alaska we have found several closely related forms occurring together, and we considered designating them subspecies. However, subspecies should not occur together and maintain their distinctness. Those forms we have named as separate species we have found on the same beaver, and even in the same sample from beavers, yet they are maintaining their distinctness. Thus the test of the biological species is complete, although sometimes a few intermediate individuals, apparently hybrids, are found in our samples.

The holotypes of the taxa described here are deposited in the U.S. National Museum, Washington. Paratypes are deposited in the Institut royal des Sciences naturelles de Belgique, Bruxelles.

All the measurements are in micrometers (μm). The length of the opisthogastric shield is taken along its median axis. The length of the opisthotal shields is taken in the midline; the width is the maximum width in the median part of the shield.

MATERIALS AND METHODS

Beavers were skinned and samples of mites were taken from 2×2 inch squares in each of 23 different areas of the beaver, as described by FAIN, WHITAKER and SMITH (1984). Estimates were made of the number of mites in each sampling area and male mites were mounted and identified from each sample. In samples which contained males of only one species, more mites were mounted on the assumption that all of the mites were likely the same species, and the mites within each life stage were compared to assess whether all likely did

indeed belong to one and the same species. However, only the male mites are being reported upon here, except for one uncommon species, *S. spinifer*, in which the females are easily identified, and are included with the males.

LOCATION OF THE MITES ON THE BEAVERS

Most of the species described by DUBININA (1964) and FAIN *et al.* (1984) from *Castor fiber* or *C. canadensis* occupied different specific microareas on the host. We have also observed this specificity for definite areas in the new material described herein, but by species groups, not by individual species. We summarize observations on North American Beavers as follows :

Group *mingaudi* (*S. mingaudi*, *S. paramingaudi*, *S. alaskensis*, *S. reductus*) : primarily on the head, the anterior dorsum and outside of the front legs.

Group *indianensis* (*S. indianensis*, *S. tetrapilis*, *S. postannulatus*, *S. centralis*, *S. contrarius* and *S. distinctus*) : primarily on the posterior dorsum and outside of the hind legs.

Group *virgulatus* (*S. virgulatus*, *S. subvirgulatus*, *S. inversus*, *S. furcatus*, *S. protinus*, *S. posticus*) : primarily on the venter and inside of the legs.

Group *spinifer* (*S. spinifer* only).

Members of the *spinifer* group are very different from members of the other groups morphologically (they have no pattern of suckers on sucker plates), they occur in small numbers, and they so far do not seem to be restricted to any one part of the body. Females can be identified in this group since they have large spines like the males and since there is only one species in the group.

ORIGIN OF THE BEAVERS

Eurasian Beavers move long distances along the rivers where they are born but apparently seldom leave the basin on which the river depends. Some authors believe that the strict confinement of the Beaver populations has resulted in subspeciation in this animal. One can surmise that isolation of the host has tended to favor multiple speciation.

We therefore think it is important to take into consideration not only the locality where the Beaver was captured but, in Eurasian Beavers, also the river where it lived as well as the main river and the basin on which this river depends.

In North America this confinement to river basins is not as well developed. Beavers are in a number of aquatic habitats often ranging throughout the area between major river systems. In Indiana, for example, there are two drainage systems ; drainage in northern Indiana is to the north into the Great Lakes-St. Lawrence River, whereas through most of Indiana it is to the south through the Wabash-Ohio and Mississippi drainages. Beavers occur continuously between these two drainage basins, but all Indiana material is from the latter drainage. Even though the river drainages are apparently not as important in North America as in Eurasia, isolation is important. Because of this importance we have sought out beavers from distant parts of North America.

The beavers from Alaska (JOW No's 12667, 12668, 12669, 12670, and 12671) are from the Chena River Drainage, 35 mi E. Fairbanks, 15-30.XII.1985, in the Yukon River basin.

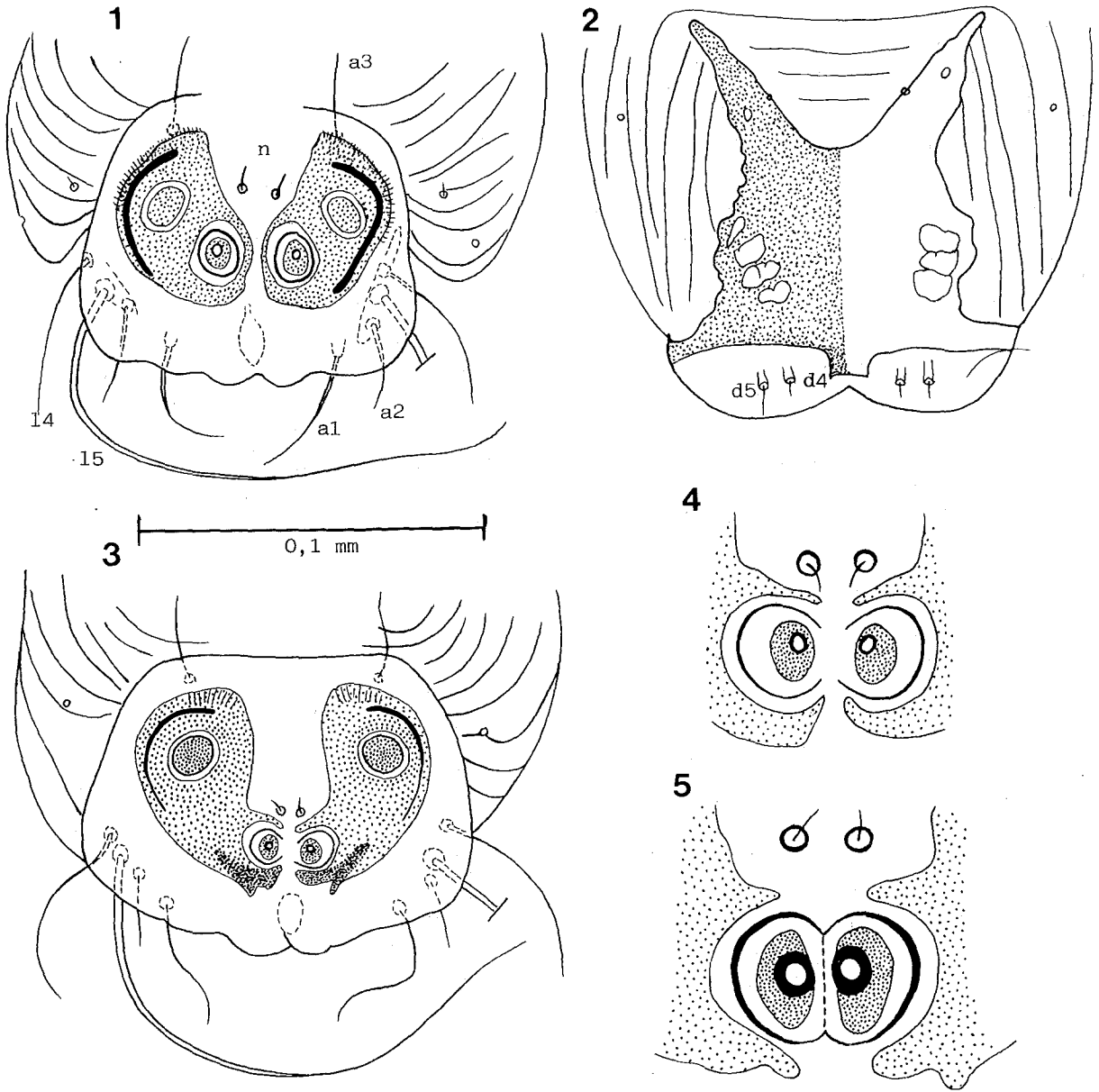
STUDY OF THE SPECIES

1. *Schizocarpus mingaudi* Trouessart, 1896

A lectotype of this species has been designated and described by FAIN *et al.* (1984). This species is very common on Beavers from Indiana, but we have not found it in Beavers from other states. In Alaska we found three new species of the *mingaudi* group (i.e., *paramingaudi*, *reductus* and *alaskensis*) but not the typical species. In Oregon and Massachusetts (unpublished) this species is replaced by *S. paramingaudi* n. sp., and in Maine we collected *S. reductus* n. sp. but not *S. mingaudi*.

2. *Schizocarpus paramingaudi* nov. spec.

Male holotype (figs. 1-2) : Idiosoma 350 long and 160 wide (in ventral view). Length and width in



FIGS. 1-2 : *Schizocarpus paramingaudi* n. sp. male
Opisthogaster (1), opisthonotal shield (2).

FIGS. 3-5 : *Schizocarpus alaskensis* n. sp. male
Opisthogaster (3), two aspects of suckers B and setae *n* (4 and 5).

4 paratypes in ventral view : 360 × 190 ; 352 × 175 ; 348 × 171 ; 342 × 180. Opisthonotal shield 75 long and 80 wide. With same shape as in *S. mingaudi*. Length and width in 4 paratypes : 87 × 91 ; 86 × 89 ; 85 × 92 ; 81 × 87. The internal anal sclerite is small. Opisthogastric shields more obliquely

oriented than in *S. mingaudi* : they are 57 long and 36 wide. Setae *n* situated in front of the suckers B, but difficult to see. Suckers B completely situated on the shield, the two shields approaching very close to each other in the midline. Suckers A oval, surrounded by an oval ring whose diameters are

18 × 12. Length and width of tarsi III 29 × 12, of tarsi IV 13 × 11. Length of setae : *a1* 55 ; *a2* 16 ; *a3* 33 ; *l4* 66 ; *l5* 165. Distance *a3-a3* 51.

Hosts and localities

Holotype male from Beaver no. 12668. *Paratype male* : from beavers no. 12667 (3 males), no. 12669 (5 males), no. 12671 (1 male) all from Alaska ; no. 12674 from Massachusetts, 30.VII.1984 (15 males), no. 12708 from Oregon, Wallowa Co., 1985, River basin (15 males), no. 11736 from Indiana, Daviess Co., Glendale Fish and Wildlife Area (5 males).

Remarks

This species differs from *S. mingaudi* by the greater size of the body, the more anterior situation of setae *n* (in front of suckers B), the placement of the shields closer to each other in their posterior part, the more oblique orientation of these shields and their slightly different shape.

S. paramingaudi resembles the species recorded by DUBININA (1964) as *S. mingaudi* ; however, our species differs from it by several characters, e.g. the different shape of the opisthonotal shield with much longer anterior arms, the situation of the opisthogastric shields closer to each other and the shape of the opisthogastric shields.

3. *Schizocarpus alaskensis* nov. spec.

Male holotype (figs. 3-5) : Idiosoma 363 long and 182 wide (in ventral view). Measurements of four paratypes (in ventral view) : 361 × 180 ; 360 × 178 ; 355 × 175 ; 338 × 174. Opisthonotal shield 80 long and 78 wide. Opisthogastric shields 63 long and 36 wide, with their median axis angulate and their internal margins straight and nearly parallel. Setae *n* as in *S. paramingaudi* but closer to suckers B ; these setae very small and difficult to distinguish. Suckers B are smaller than in *S. paramingaudi* and generally more elongate and not situated on the shields. These suckers are partly surrounded by a sclerotized ring open internally (fig. 4). In some specimens the two rings are fused in the midline

(fig. 5). Suckers A oval, their maximum diameter 15 × 16 and 18 × 15, in holotype. Length and width of tarsi III and IV 30 × 12 and 15 × 12. Length of setae : *a1* 45 ; *a2* 21 ; *a3* 35 ; *l4* 60 ; *l5* 170. Distance *a3-a3* 58.

Variations : The shape of the opisthogastric shields may vary. In some specimens the internal margins are divergent and suckers B are slightly larger and strongly elongate (fig. 5).

Host and locality

This species is known only from Alaska. *Holotype male* from Beaver no. 12670 from Alaska, Chena River drainage, 35 mi E Fairbanks, 15-30.XII.1985, in the Yukon River basin. *Paratype males* : From the same Beaver as the holotype (6 males), from Beavers no. 12667 (12 males), no. 12668 (4 males), no. 12669 (5 males), no. 12671 (4 males), all with same data as holotype.

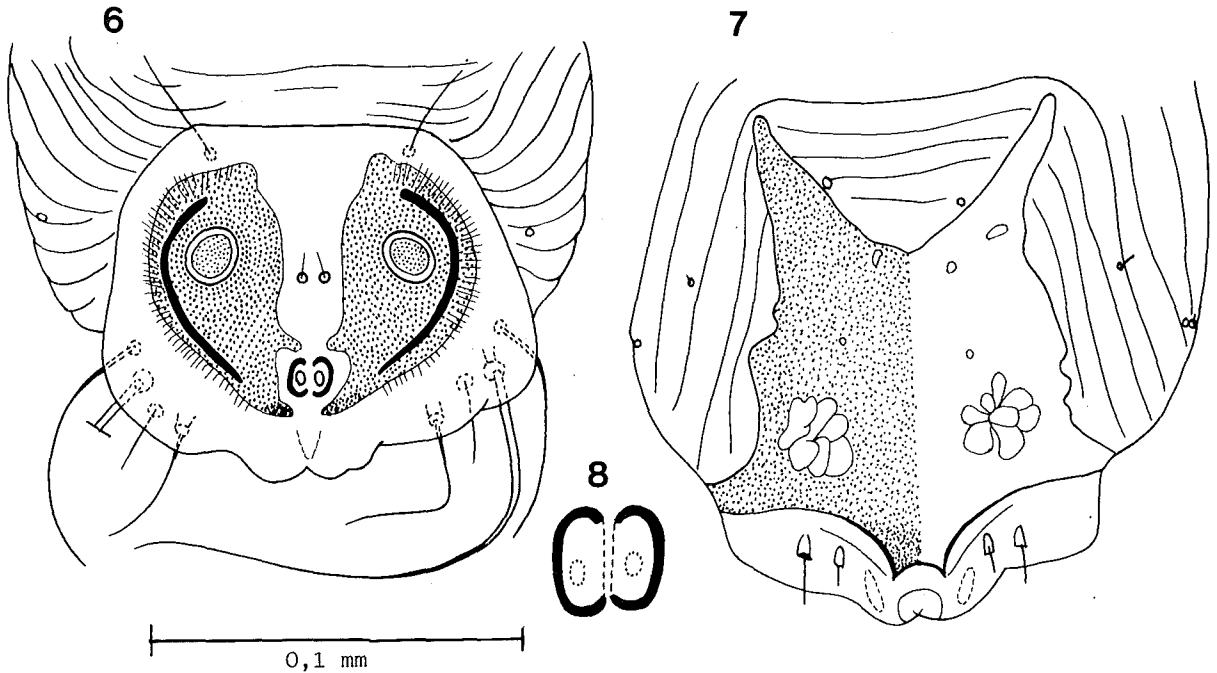
Remarks

This species differs from *S. paramingaudi* by the different shape of the opisthogastric shields (wider anteriorly and narrower posteriorly, and with an angulate axis). Moreover, suckers B are not situated on the shield. They are smaller, more elongate and incompletely surrounded by a ring open inside and fused or lacking the opposite ring.

This species is somewhat intermediate between *S. paramingaudi* and *S. reductus*.

4. *Schizocarpus reductus* nov. spec.

Male holotype (figs. 6-8) : Idiosoma 366 long and 182 wide (in ventral view). Length and width of 4 paratypes : 365 × 170 ; 360 × 182 ; 351 × 159 ; 342 × 160. Opisthonotal shield 87 long and 87 wide. Shape similar to that of *S. mingaudi*. Opisthogastric shields longer than in *S. mingaudi* : 71 long and 35 wide. Posteriorly these shields are excavated inside for the suckers. Setae *n* very small. Suckers B not situated on the shields and strongly reduced (hence the name of the species). They consist of two small elongate and sclerotized incomplete rings



Figs. 6-8 : *Schizocarpus reductus* n. sp. male
Opisthogaster (6), opisthonorotal shield (7), suckers B (8).

almost fused in the midline. The true suckers inside the rings are very small and indistinct. The rings are free rather than being included in the shields. Suckers A oval or more or less triangular, their maximum diameters 16×14 and 15×14 . Length and width of tarsi III 30×12 , of tarsi IV 15×12 . Lengths of setae : a_1 60 ; a_2 18 ; a_3 37 ; l_4 90 ; l_5 120. Distance a_3 - a_3 54.

Hosts and localities

Holotype male from Beaver no. 12669, Alaska, Chena River drainage, 35 mi E Fairbanks, 15-30.XII.1985, in the Yukon River basin. *Paratype males* : With the same data as the holotype, Beaver no. 12668 (8 males) and no. 12715 from Maine, Dexter, Penobscot Co., 26-29.IV.1986 (11 males).

Remarks

S. reductus resembles *S. alaskensis* but differs from it by the strong reduction of suckers B and the ring surrounding these suckers. This ring is much smaller and is elongate and strongly sclerotized.

5. *Schizocarpus spinifer* Fain, Whitaker & Smith, 1984

We report here two additional males of this species from Beaver 12671 from Alaska.

6. *Schizocarpus indianensis* Fain, Whitaker & Smith, 1984

This species was found in Beavers from Indiana but was not found in Alaska. A second species, *S. postannulatus* n. sp., closely related to *S. indianensis*, was recognized from both Indiana and Alaska. We have observed some variability in the position of the small subcuticular ring situated on the opisthogastric shields close to the suckers C. Two species closely related to *S. indianensis* have been recognized, and since they occur together with *S. indianensis* but maintain their distinctness, we have to describe them as separate species. In *S. indianensis*, the subcuticular ring is situated in front of the suckers C (FAIN *et al.* 1984, figs. 29-32).

7. *Schizocarpus postannulatus* nov. spec.

This species is very similar to *S. indianensis*, but the subcuticular ring is situated behind sucker C, either outside (form *pl*, fig. 9) or inside (form *pm*, fig. 11) of the sucker, while in *S. indianensis* it is situated in front of sucker C (FAIN *et al.*, 1984, Figs. 29-32). The holotype is of the *pl* type. This species resembles *S. tetrapilis* but differs from it by the absence of *na* setae. It was present in 9 Beavers from Indiana and three Beavers from Alaska. Form *pl* was found in 6 Beavers from Indiana, and 2 from Alaska. Form *pm* was found on one Beaver from Indiana and on three from Alaska.

Male holotype (form *pl*) (figs. 9-10) : Idiosoma 375 long. Length in three paratypes : 360 to 380. Opisthonotal shield 99 long and 87 wide. Opisthogastric shield 55 long and 36 wide. The small subcuticular ring is situated behind sucker C either outside (form *pl*, fig. 9-10) or inside the sucker (form *pm*, fig. 11-12). Tarsi III and IV 33 and 19 long and 17 and 12 wide respectively.

Hosts and localities

Holotype male (form *pl*) from Beaver no. 11887, Indiana, Newton Co., Willow Slough Fish & Wildlife Area, 2 May 1983. *Paratype males* : From the same Beaver as holotype (43 males, form *pl*) ; from Beaver no. 11349 from same locality (2 males form *pl*) ; from Beaver no. 11350 from Indiana, Lake Co., La Salle Fish and Wildlife Area, taken Nov. 1981 (6 males, form *pl*) ; from Beaver no. 11439 from Indiana, Laporte Co., Kingsbury Fish and Wildlife Area (2 males, form *pl*) ; from Beaver no. 11736 from Indiana, Glendale Fish & Wildlife Area, Daviess Co., XI.1982 (1 male form *pl* and 1 male form *pm*) ; from Beaver no. 11886 (1 male, form *pl*) ; from Beaver no. 12667 (5 males of form *pl* and 1 male of form *pm*) ; from Beaver no. 11668 (1 male of form *pm*) ; from Beaver no. 12670 (7 males, form *pm* and 2 males form *pl*) ; from Beaver no. 12671 (2 males form *pm*).

8. *Schizocarpus tetrapilis* Fain,
Whitaker & Smith, 1984

This species had been recorded from two Beavers in Indiana, but it is more widespread than previously noted. Closely related to it are three distinct and stable forms to which we give specific rank : *S. centralis* n. sp., *S. distinctus* n. sp., and *S. contrarius* n. sp.

S. tetrapilis : In this species the subcuticular ring is situated behind sucker C, the setae *na* are situated far in front of *np* and at the level of the anterior margins of suckers C (specimens from Indiana, see FAIN *et al.*, 1984, fig. 33) or slightly more posterior though distinctly separated from setae *np* (specimens from Alaska).

This species was found on four Beavers from Indiana (no. 11348, Potato Creek, St. Joseph Co., 3.XII.1981 ; no. 11350, La Salle Fish & Wildlife Area, Lake Co., IX.1981 ; no. 11439, Kingsbury, Laporte Co. Fish and Wildlife Area ; and no. 11736, Glendale Fish & Wildlife Area, Daviess Co., XI.1982) and in two Beavers from Alaska (no. 12667 and 12669, Chena River drainage, 35 mi. E Fairbanks, 15-30.XII.1985, in the Yukon River basin).

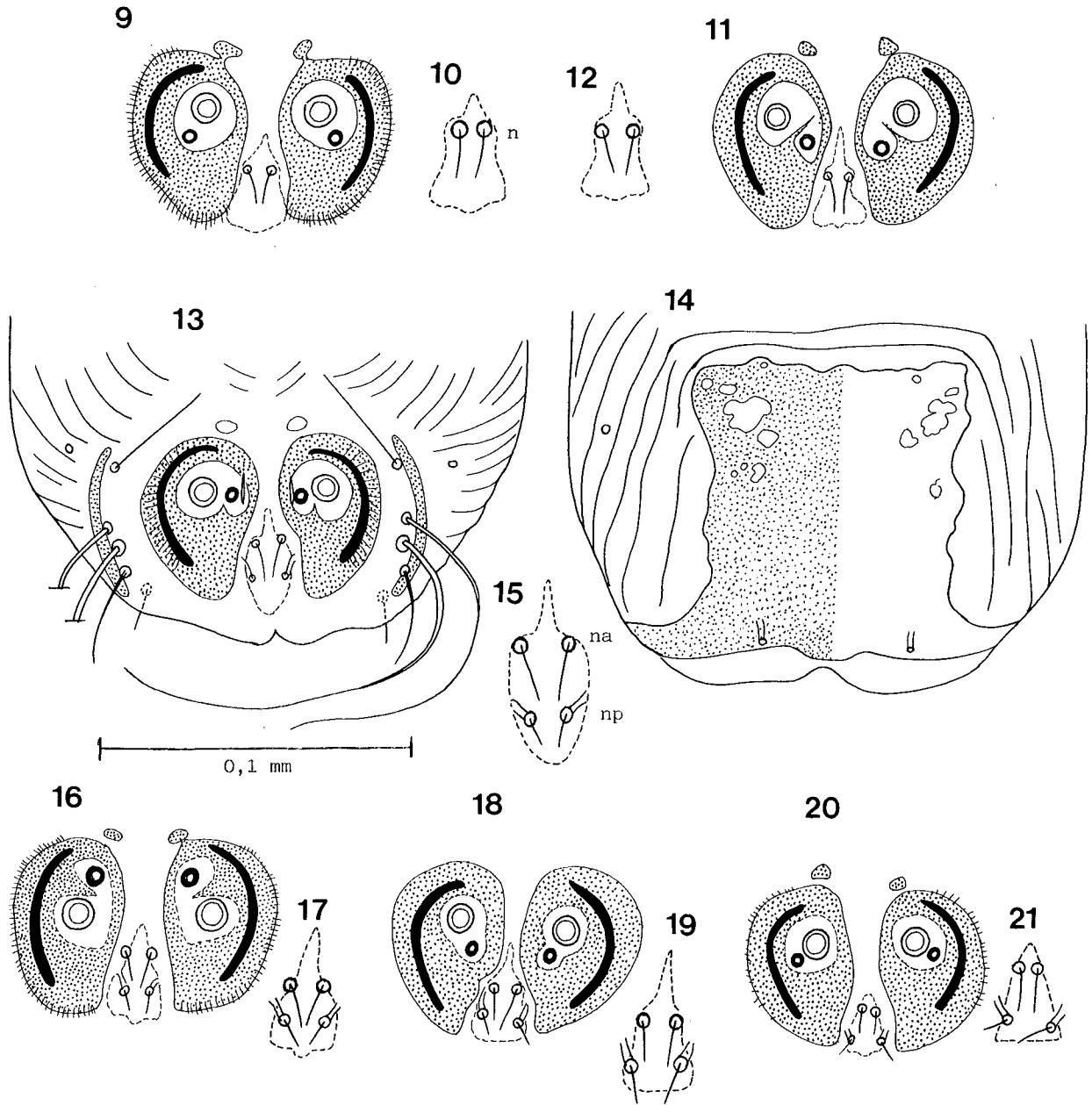
9. *Schizocarpus centralis* nov. spec.

Very similar to *S. tetrapilis* but the subcuticular ring is inside sucker C and at the same level with it ; setae *na* and *np* are in the posterior half of the shield and close together, moreover the bases of the setae *np* are connected at each side with a small canal directed anterolaterally. This form was found in two Beavers from Alaska (figs. 13-15).

Male holotype (figs. 13-15) : Idiosoma 369 long and 210 wide (in ventral view). Opisthonotal shield 90 long and 81 wide. Opisthogastric shields 53 long and 34 wide. Length and width of tarsi III and IV 31 × 16 and 19 × 12.

Hosts and localities

Holotype male from Beaver no. 12669, Alaska, Chena River Drainage, 35 mi. E Fairbanks, 15-



FIGS. 9-12 : *Schizocarpus postannulatus* n. sp. male
Opisthogastric shields and setae *n* enlarged in males of form *pl* (9-10) and form *pm* (11-12).

FIGS. 13-15 : *Schizocarpus centralis* n. sp. male
Opisthogastric shields (13), opisthonotal shield (14), setae *na* and *np* enlarged (15).

FIGS. 16-17 : *Schizocarpus contrarius* n. sp. male
Opisthogastric shields (16), setae *na* and *np* enlarged (17).

FIGS. 18-21 : *Schizocarpus distinctus* n. sp. male
Two different aspects of opisthogastric shields and setae *na* and *np* in form F (18-19) and in form B (20-21).

30.XII.1985, in the Yukon River basin. *Paratype males* : From the same Beaver as holotype (4 males); from Beaver no. 12670 with same collecting data (11 males).

10. *Schizocarpus distinctus* nov. spec.

Very close to *S. tetrapilis* but the subcuticular ring is situated behind sucker C and either outside (form B, fig. 20) or inside (form F, fig. 18) of this sucker. Setae *na* and *np* as in *S. centralis*. This species is known from there Beavers from Alaska.

Male holotype (figs. 20-21) : Idiosoma 410 long and 230 wide (in ventral view). Opisthonotal shield 85 long and 73 wide. Opisthogastric shield 51 long and 34 wide. Length and width of tarsi III and IV 30 × 16 and 18 × 12.

Hosts and localities

Holotype male from Beaver no. 12669, Alaska, Chena River Drainage, 35 mi. E Fairbanks, 15-30.XII.1985, in the Yukon River basin. *Paratype males* : From the same Beaver as the holotype (2 males); from Beavers no. 12667 (3 males) and no. 12668 (1 male), with same collecting data. All the specimens were of form B except 2 paratypes of form F (Beavers no. 12668 and 12669 with same collecting data).

11. *Schizocarpus contrarius* nov. spec.

Very close to *S. tetrapilis* but the subcuticular ring is situated in front of sucker C. Setae *na* and *np* as in *S. centralis*. This subspecies has been found

on one Beaver from Alaska and one from Indiana (fig. 16).

Male holotype (figs. 16-17) : Idiosoma 390 long and 205 wide (in ventral view). Hysterosomal shield 90 long and 82 wide. Opisthogastric shields 53 long and 39 wide. Length and width of tarsi III and IV 33 × 17 and 19 × 14.

Hosts and localities

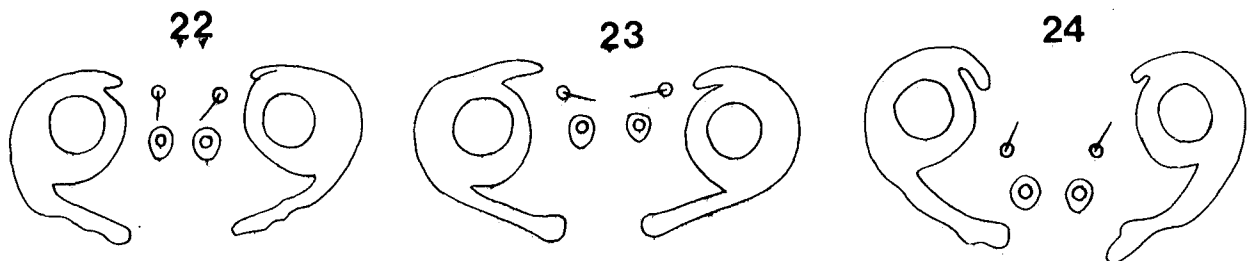
Holotype male from Beaver no. 12669, Alaska, Chena River Drainage, 35 mi. E Fairbanks, 15-30.XII.1985, in the Yukon River basin. *Paratype male* : 1 male from the same Beaver as the holotype and 1 male from Beaver no. 11394 from Indiana, Newton Co., Willow Slough Fish & Wildlife Area.

12. *Schizocarpus subvirgulatus* Fain, Whitaker & Smith, 1984

This species is found in Indiana and in Alaska. Typically setae *n* are slightly in front of the level of anterior suckers A, suckers *b* being behind the setae *n* at level of the posterior margins of suckers A and on the same longitudinal line as the *n* setae.

From the examination of numerous specimens of this species it appears that there is a high degree of variability in the relative situation of setae *n* and suckers *b*.

We found individuals from Indiana and Alaska which differed from the typical form by a more posterior position of both *n* and *b*. In some specimens from Alaska (fig. 24) setae *n* and suckers *b* are much more posterior than in the typical form, and intermediate forms exist between this and the typical form.



FIGS. 22-24 : *Schizocarpus subvirgulatus* Fain *et al.* male Variations in the situation of setae *n* and suckers *b* (22-24).

We also found a few specimens from Alaska with a slight anterior migration of the suckers *b* associated with a more external situation of setae *n* (fig. 23). In most specimens from Alaska setae *n* and suckers *b* are closer together and closer to the midline (fig. 22) than in the typical specimens.

All intermediate exist between these forms and the typical form. From both Indiana and Alaska we found specimens showing less variability in the situation of *n* and *b*, and we have separated these into two new species, *S. protinus* n. sp. and *S. posticus* n. sp.

S. subvirgulatus is known from Indiana and Alaska.

13. *Schizocarpus protinus* nov. spec.

Setae *n* and suckers *b* almost on a transverse line at the level of the anterior half of suckers A (fig. 25), *n* being inside of *b*. In some specimens *b* are slightly more posterior (fig. 30), in one specimen one seta *n* is more posterior than the other (fig. 29). This species is represented by 6 specimens (including holotype) from two Beavers from Alaska.

Male holotype (figs. 25-30) : Idiosoma 335 long and 165 wide. Length and width in 2 paratypes : 305 × 162 and 320 × 158. Opisthonotal shield 90 long and 90 wide. Opisthogastric shields as in *S. subvirgulatus* but setae *n* and suckers *b* are almost on a transverse line at the same level as the anterior half of suckers A. Length and width of tarsi III and IV 24 × 13 and 12 × 12.

Hosts and localities

Holotype male from Beaver no. 12668, from Alaska, Chena River Drainage, 35 mi. E Fairbanks, 15-30.XII.1985, in the Yukon River basin. *Paratype males* : From Beaver no. 12671 with same collecting data as holotype (5 males).

14. *Schizocarpus posticus* nov. spec.

Suckers *b* very lateral and posterior (close to the posterolateral arm of the shield), seta *n* more

internal and either on the same transverse line as *b* (fig. 33) or more anterior (fig. 31). This subspecies is represented in Indiana (mainly from Glendale Fish & Wildlife Area) and in Alaska (from 2 Beavers). We found also three specimens (from Beaver no. 11348) whose suckers *b* are slightly less lateral than in the typical form.

Male holotype (figs. 31-33) : Idiosoma 305 long and 170 wide. Length and width in two paratypes 308 × 165 and 290 × 158. Opisthonotal shield 75 long and 80 wide. Opisthogastric shields as in *S. subvirgulatus* but setae *n* are more posterior (at the level of posterior margins of suckers A) and suckers *b* are situated very laterally and close to the posterior arms of the shield.

Hosts and localities

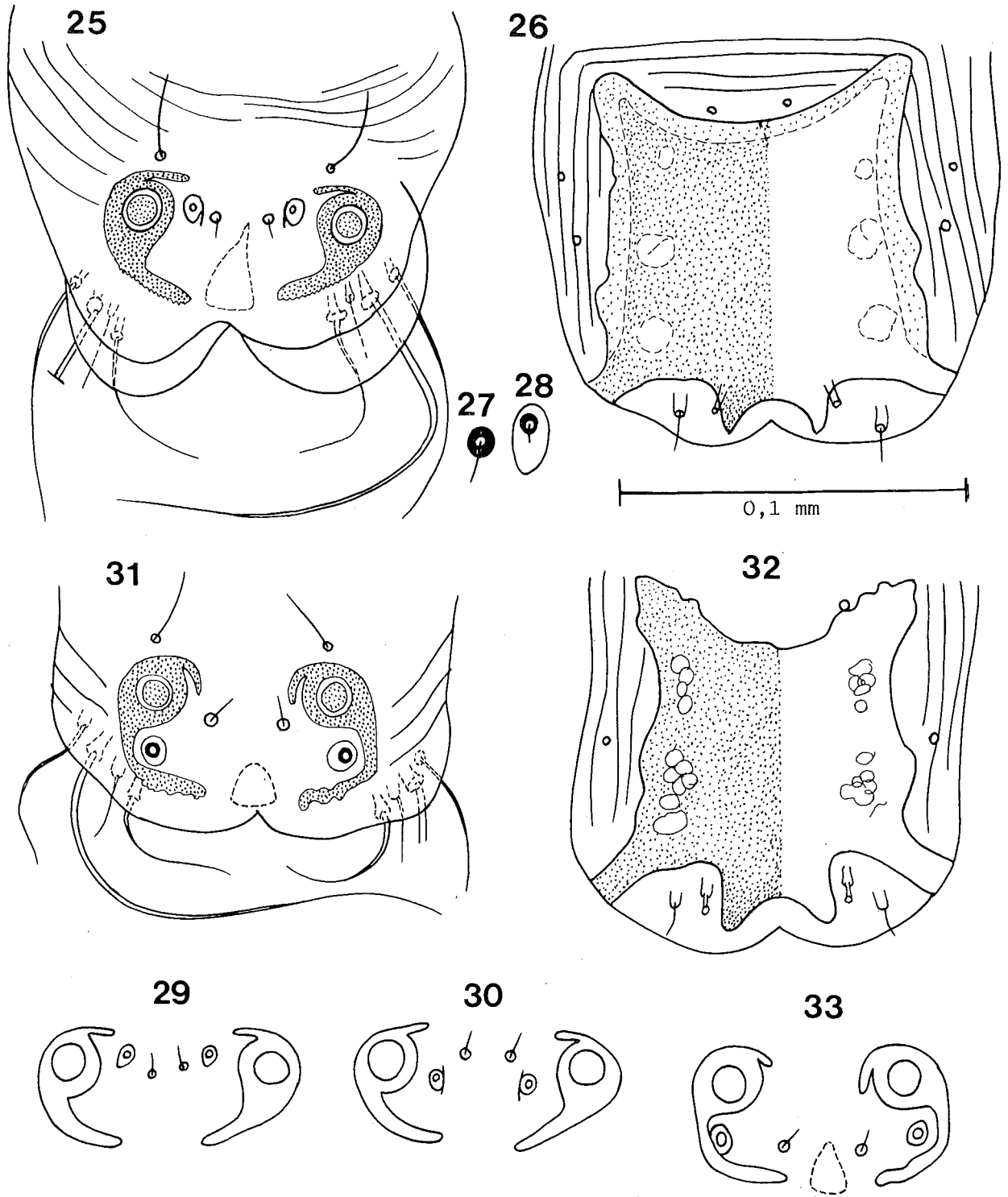
Holotype male from Beaver no. 11736, from Indiana, Glendale Fish & Wildlife Area, Daviess Co., XI.1982. *Paratype male* : From same Beaver as holotype (10 males); from Beaver no. 11348 (3 males slightly atypical); from Beaver no. 11734 from Indiana, La Salle Fish & Wildlife Area, Newton Co., X.1982 (1 male); from Beaver no. 12671 from Alaska, Chena River Drainage, 35 mi. E Fairbanks, 15-30.XII.1985, in the Yukon River basin (2 males); from Beaver no. 12667 (1 male).

15. *Schizocarpus inversus* Fain, Whitaker & Smith, 1984

This species differs from *S. subvirgulatus* mainly by the situation of suckers *b* which are in front of rather than behind seta *n* as in that species. Another difference is the more posterior situation of both *n* and *b* which are completely behind suckers A.

The typical form of *S. inversus* was described from Beaver no. 11736 from Glendale Fish & Wildlife Area, Daviess Co., Indiana.

In Alaska we found (Beaver no. 12671) 6 specimens with seta *n* and suckers *b* distinctly more posterior than in the typical form.



FIGS. 25-30 : *Schizocarpus protinus* n. sp. male

Opisthogastric shields (25), opisthonotal shield (26), seta *n* (27) and sucker *b* (28) enlarged, variations in the situation of *n* and *b* (29 and 30).

FIGS. 31-33 : *Schizocarpus posticus* n. sp. male

Opisthogastric shields (31), opisthonotal shield (32), variations in the situation of setae *n* and sucker *b* (33).

16. *Schizocarpus furcatus* Fain,
Whitaker & Smith, 1984

This species is close to *S. inversus*. It was previously recorded only from Indiana and from the same Beaver as *S. inversus*.

In Alaska (Beavers no. 12667 and 12671) we found 2 specimens of this species, but which differ slightly from the typical form by the shape of the posterior arms of the opisthogastric shields. In the typical series these arms are forked posteriorly. In the specimens from Alaska the anterior branch of the fork is poorly developed or absent.

THE SCHIZOCARPUS COMMUNITY

The text thus far has consisted of describing the new species and designating type material. Many more individuals were taken of most of the species than were involved in the original descriptions. Only the total numbers of males examined of each species from each of the five beavers during the descriptive phase of the work are given in Table 1 and compared with information for Indiana.

TABLE 1. — Beaver mites, genus *Schizocarpus*, from Alaska, as compared with those from Indiana. Data are expressed as total numbers of males identified of each species.

JOW Beaver #	Beavers from Alaska					Total	Beavers from Indiana
	12667	12668	12669	12670	12671		
S. MINGAUDI GROUP							
<i>S. mingaudi</i>							12619
<i>S. paramingaudi</i>	3	1	5		1	10	5
<i>S. alaskensis</i>	12	4	5	7	4	32	
<i>S. reductus</i>		8	1			9	
S. INDIANENSIS GROUP							
<i>S. indianensis</i>							226
<i>S. postannulatus</i>	6	1		9	1	18	57
<i>S. tetrapilis</i>	1		1			2	70
<i>S. centralis</i>			5	11		16	
<i>S. contrarius</i>			2			2	1
<i>S. distinctus</i>	3	1	3			7	
S. VIRGULATUS GROUP							
<i>S. virgulatus</i>							453
<i>S. subvirgulatus</i>	3	10	4	3	9	29	571
<i>S. protinus</i>		1			5	6	
<i>S. posticus</i>	1				2	3	15
<i>S. furcatus</i>	1				1	2	79
<i>S. inversus</i>					6	6	5
S. SPINIFER GROUP							
<i>S. spinifer</i>					2	2	3
No. species	8	7	8	4	9	14	12

A total of 14 species of *Schizocarpus* was found of the five beavers from Alaska as compared to 12 from the beavers examined from Indiana. The five Alaskan beavers had between 4 and 9 species of *Schizocarpus* each. The most important species of *Schizocarpus* were *S. alaskensis* in the *mingaudi* group, *S. postannulatus* in the *indianensis* group, and *S. subvirgulatus* in the *virgulatus* group. Only *S. alaskensis* and *S. subvirgulatus* were found on all five of the beavers from Alaska.

The most abundant Indiana species were *S. mingaudi* (*mingaudi* group), *S. indianensis* (*indianensis* group), *S. subvirgulatus* and *S. virgulatus* (*virgulatus* group). Thus all the most abundant of the Alaskan species differ from the most abundant of the Indiana species.

Five species were found in Alaska, not in Indiana, *S. alaskensis*, *S. reductus*, *S. centralis*, *S. distinctus*, and *S. protinus*. Three species, *S. mingaudi*, *S. indianensis* and *S. virgulatus* occurred in Indiana, but not in Alaska.

Schizocarpus spinifer is interesting in that it apparently is not found on any particular area but seems to occur anywhere on the Beaver.

DISCUSSION

Present data support our previous conclusions on European and North American Beavers concerning variability and multispeciation. As in Eurasia and Indiana, a number of species of mites are present on individual Beavers, and the major groups of mites are pretty much restricted to different parts of the Beaver's body.

The data we have been collecting also supports the idea of the species arising in different localities. For example, in Alaska, the *S. mingaudi* type has evolved into new species, by the movements together of the large suckers, and the movement forward of the small suckers in *S. paramingaudi*.

The mite fauna living on the Beavers in Alaska is quite different from that found on the Beavers in Indiana, both in relative abundance of the various species and in species composition.

Schizocarpus populations in Alaska appear to be undergoing rapid evolution, the *mingaudi* group on

the head, anterior dorsum, and outer portions of the front legs; the *indianensis* group on the posterior dorsum, and the *virgulatus* group on the abdomen. Most adult males are distinctly one species or another, but several individuals were found which appeared to be hybrids. These are currently under study, but so far all presumed hybrids have occurred in areas where both their presumed parental stocks occurred.

Mites of the genus *Schizocarpus* have several life stages. Descriptions of species are based on sucker plates of the adult males. These sucker plates vary between species. The immature females (embryo, larva, protonymph, and tritonymph) all have the sucker plate corresponding to that of the adult male and these immature female stages are fastened to the adult male during their development. The adult female, however, lacks the sucker plate. We suspect that mating occurs at the time of transformation to the adult. The immature male stages (embryo, larva, protonymph and tritonymph) also lack the sucker plate, and are exceedingly similar to the adult female. We are usually able to determine the group these stages belong to (published), but it is usually not possible for us to identify species within groups at least as yet. We are currently studying these stages.

FAIN and LUKOSCHUS (1985) suggested that multispeciation in *Schizocarpus* occurs through a combination of isolation of Beavers plus the restriction of the mites to various parts of the Beaver. The implication is that the mites then evolutionarily diverge to better fit these various habitats. This hypothesis creates some problems. If the mites are evolving differently in relation to various hair-related habitats, then wouldn't all life stages develop these adaptations? Why is it just in the sucker plates of the males and associated immature females? Why don't we see similar differences in the males and immature female stages which also live in the same habitat?

We do not question that there are separate biotopes on different parts of the Beaver. There are, as documented by KELLER (1983). Also there is no question but that the mites live on different parts of the Beaver, thus avoiding competition by partitioning the habitat. We do question whether the

differing habitats on the Beaver could serve as primary isolating mechanisms, thus allowing speciation to occur on individual Beavers or in individual Beaver populations. Individuals that have migrated to new biotopes on the Beaver are still genetically from the same stock as those in the previous area, and for that matter there presumably would be mites occurring in the intermediate areas. These factors, it appears to us, would practically preclude the formation of primary isolating mechanisms in this situation. We are not saying that it could not happen, but only that it is difficult to envision. This would be especially difficult at the time the mites disperse from one Beaver to another, since genetically, ecologically, and behaviorally, they are essentially identical with the parent stock. Why wouldn't they go right back to the ancestral habitat? What primary isolating mechanisms would keep them from merging with the ancestral population? About the only way we could see speciation of the mites occurring within Beaver populations is if a genetic change occurred (macromutation, if you will) in which the changes were large enough to immediately serve as secondary as well as primary isolating mechanisms.

We think that geographic isolation of the Beavers is very important and that this isolation constitutes the primary isolating mechanisms. When this isolation occurs, speciation can begin. The mites do tend to live on various parts of the Beaver. This is true at the group level, less true at the species level. For example, in Alaska, members of the *mingaudi* group, *paramingaudi*, *alaskensis* and *reductus*, occur on the head, anterior dorsum, and outside of the front legs. However, little separation has developed between these three species in that area, although any one particular sample location on any one Beaver often has only one species, or predominantly one species.

We think the situation here is more complicated than simply the geographic isolation of Beavers and the later partitioning of habitat by the mites, although both these processes are occurring. We here present some additions and modifications to these ideas.

The striking similarity between species in the adult females and immature males seems to indicate

that their respective microhabitats are very similar as far as the mites are concerned. That the species characters are almost entirely in the adult males (and associated sucker plates of the immature females) indicates to us that these differences are of significance in species recognition rather than directly in habitat segregation. We think that evolution is presently occurring at a rapid rate in *Schizocarpus*, especially in Alaska, that the various forms there originally evolved in different geographic areas (i.e., the primary isolating mechanisms are geographic), but that the original geographic isolating mechanisms have then broken down (either by natural movements of the Beavers or by reintroductions by man, or both). The Beaver mites in separate (isolated) populations start to evolve, but rather often come into contact with mites from other populations as the Beavers come back together.

We further think that this has caused strong competition between species especially within groups and that this, in turn, has led to habitat partitioning and to enhancement of the species recognition characters through selection against hybridization. Habitat partitioning is well developed between groups, but not within groups especially in Alaska. Species within groups are so closely related that hybrids can sometimes be formed. We have some evidence of hybridization and are carrying on further studies along these lines (unpublished). We suspect that, as competition among these mites continues in Alaska, the following three processes will occur :

1) that some of the forms will be outcompeted and disappear ;

2) that forms in which the secondary isolating mechanisms are not well enough established (i.e., the hybrids are not selected against) will merge with each other. This could be presently occurring with *posticus* and *subvirgulatus* in Alaska). This probably often happens in *Schizocarpus* which secondarily occur together before the secondary isolating mechanisms have completely formed ;

3) when the secondary isolating mechanisms are well formed, then the two will remain distinct, although occasional hybrids might occur if the

species are still closely enough related. Such hybrids would be selected against, since the secondary isolating mechanisms are generally working. If the hybrids are selected against, then also the parents that formed the hybrids would be selected against. The tendency would be for the two to diverge still further, by the selection for divergence of those characters (the differing sucker plates of *Schizocarpus* in this case) that allowed the "right" versus the "wrong" choice. Further partitioning of the habitat would also be selected for as an additional aid in making the correct choice.

All of this is similar to the situation in two groups of birds, the dabbling ducks, Anatidae, and the wood warblers, Parulidae (SIBLEY, 1961).

Once the secondary isolating mechanisms are in place, then it would be beneficial for the mites to separate or partition themselves on the Beaver. For example, *S. paramingaudi*, *alaskensis*, and *reductus* might now be tending to partition the head and anterior dorsum area. The divergent sucker plates would generally keep them from interbreeding, but spatial separation on the Beavers would help them to keep from "wasting time and energy" by attempting interbreeding. If these ideas are correct, the mites are not selecting different parts of the Beaver because of differential microhabitats, but because of competitive exclusion.

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