

## NOTES ON SYSTEMATICS, DISTRIBUTION AND ECOLOGY OF MITES OF THE GENUS *FAGACARUS* (ACARIFORMES: ACARIDAE)

### ЗАМЕЧАНИЯ ПО СИСТЕМАТИКЕ, РАСПРОСТРАНЕНИЮ И ЭКОЛОГИИ КЛЕЩЕЙ РОДА *FAGACARUS* (ACARIFORMES: ACARIDAE)

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Ключевые слова: Acariformes, Acaridae, Fagacarini stat. n., *Fagacarus*, систематика, распространение, гипопус, Дальний Восток России

#### ABSTRACT

The external morphology of adults and unknown hitherto hypopi of *Fagacarus* Fain et Norton is studied. The subfamily Fagacarinae Fain et Norton is given the tribe status, Fagacarini stat. n. (Acaridae, Rhizoglyphinae). The genus *Fagacarus* is recorded in the Palaearctic region for the first time. It is hypothesized that the species of *Fagacarus* are the obligate mycetophagous inhabitants of decaying wood.

#### РЕЗЮМЕ

Изучено морфологическое строение взрослых и неизвестных ранее гипопусов рода *Fagacarus* Fain et Norton. Подсем. Fagacarinae Fain et Norton рассматривается как триба, Fagacarini stat. n. (Acaridae: Rhizoglyphinae). Род *Fagacarus* впервые указан для Палеарктики. Предполагается, что представители рода — облигатные мицетофаги, обитающие в мертвой древесине.

#### INTRODUCTION

Up to the present the genus *Fagacarus* Fain et Norton included the only species, *Fagacarus verrucosus* Fain et Norton, known by adults, which were collected in the decaying wood of *Fagus grandifolia* Ehrhart (Fagales: Fagaceae) in Indiana, USA [Fain & Norton, 1979]. When described the genus *Fagacarus*, Fain & Norton [1979] noted that the new genus combines characters of the subfamily Ctenoglyphinae (Glycyphagidae) and the genera *Rhizoglyphus* Claparede and *Schwiebea* Oudemans (Acaridae: Rhizoglyphinae). They proposed a new subfamily, Fagacarinae Fain et Norton. This taxon has been placed in the family Acaridae as the elements of legs were similar to those of the aforementioned genera [Fain & Norton, 1979].

The author studied *Fagacarus verrucosus* (adults, hypopus) from the USA (Indiana, Michigan), *F. sp. 1* (adults, hypopus) from the Russian Far East (first record of the genus in the Palaearctic), and *F. sp. 2* (hypopus) also from the USA (Colorado). Morphological data of adults and unknown hitherto hypopi of *Fagacarus* and 10 other genera of Acaridae were analyzed cladistically with the computer program PAUP\* Ver. 4.0b4a [Swofford, 1999] using the brand and bound approach. The analysis allows developing a new hypothesis concerning the phylogenetic relationships of *Fagacarus*. The subfamily Fagacarinae is considered to be the part of the subfamily Rhizoglyphinae (Fagacarini stat. n.). Terminology for designating the body parts and idiosomal chaetotaxy follows that of Griffiths et al. [1990], leg elements of Griffiths [1970], cheliceral setae of Grandjean [1947].

Voucher specimens are kept in the collections of the Institute of Biology and Pedology, Vladivostok, Russia (IBPV) and the Museum of Zoology, the University of Michigan, Ann Arbor, USA (UMMZ).

#### MATERIAL

*Fagacarus verrucosus* Fain et Norton. USA: 1 paratype ♂ — Indiana Wells Co., 8 mi East of Bluffton, ex frass in dead *Fagus*, 9.01.1973 (R.F. Wilkey) (IBPV); 15 ♀♀, 5 ♂♂, 11 teleonymphs, 10 protonymphs, 1 larva — Michigan, Michigan Lake Co., 3.5 mi WSW Irons, Driftwood valley, 44°07.8' N 85°59.9' W, ex rotten wood of deciduous tree, 1.10.2000 (B.M. OConnor) (UMMZ); 3 ♀♀, 4 ♂♂, 1 hypopus — Michigan, Washtenaw Co., Cedar Lake, black spots in core of *Populus grandidentata* Michx. (Salicales: Salicaceae) log with *Pleurotus ostreatus* (Jacq. ex Fr.) Kummer (Agaricales, Pleurotaceae), 10.10.2000 (B.M. OConnor) (UMMZ).

*Fagacarus* sp. 1. Russia, Primorskiy kray: 33 ♀♀, 22 ♂♂, immatures — Ussuriyskiy rayon, Kaymanovka, bank of Barsukovka river, rotten stump of deciduous tree, near white fungal mycelium, 7.10.1998 (P. Klimov) (6 slides); 2 ♀♀, 1 deutonymph, 3 protonymphs, 1 hypopus — Khasanskiy rayon, "Kedrovaya Pad'" Reserve, fallen trunk of deciduous tree with a colony of *Lasius niger* (Linnaeus, 1758) (Hymenoptera, Formicidae), 29.04.1999 (P. Klimov) (2 slides.); 1 teleonymph — same locality, log of deciduous tree with a colony of *L. niger*, 29.04.1999 (P. Klimov) (IBPV).

*Fagacarus* sp. 2. USA, Colorado, Boulder Co., Indian Peaks Wilderness Area Nitwot Ridge, 330 m., malaise trap residue, 22.07.1992 (G. Coolley) (UMMZ).

Data for other Acaridae mentioned in the paper were obtained from the following genera and species. The type species is underlined; if a species is represented by adults or hypopi only it is indicated in parentheses; IR = Russia: Irkutskaya oblast', PR = Russia: Primorskiy kray):

*Acarus* Linnaeus, 1758. *A. siro* (Linnaeus, 1758) — Uzbekistan (hypopi); *A. farris* (Oudemans, 1905) — IR, PR (adults); *A. immobilis* Griffiths, 1964 — IR, PR.

*Boletoglyphus* Volgin, 1953. *B. boletophagi* (F. Türk, S. Türk, 1952) — IR. *B. extremiorientalis* Klimov, 1988 — PR.

*Calvoliella* Samšinák, 1969. *C. laphriae* (Samšinák, 1956) — Russia: Khabarovskiy kray, Amurskaya oblast', PR, Kemerovskaya oblast', IR; Czech Republic (hypopi).

*Capillaroglyphus* Klimov, 1998. *C. polypori* Klimov, 1998 — PR; Japan.

*Carabidobius* Volgin, 1953. *C. sp.*, PR, ex *Harpalus* (*Pseudoophonus*) *ussuriensis* Chaudoir, 1863 (Coleoptera, Carabidae) (hypopi).

*Cosmoglyphus* Oudemans, 1932. *C. krameri* (Berlese, 1881) — South Korea: Suncheon (hypopi).

*Histiogaster* Berlese, 1883. *H. ornatus* Volgin, 1966 — PR; *H. sp. 1* — PR, rotten wood (adults); *H. sp. 2* — PR, ex flux of *Quercus* (adults).

*Horstia* Oudemans, 1905. *H. helenae* (Oudemans, 1903) — Japan: Ryukyu Is. (hypopi).

*Reckiacarus* Kadzhaja, 1972. *R. sp. 1* — IR, rotten wood; *R. sp. 2*. — PR, under bark of *Quercus* (adults).

*Rhizoglyphoides* Volgin, 1978. *Rh. nidicola* Volgin, 1978 — Kazakhstan: Alma-Atinskaya oblast' (adults); *Rh. sp.* — IR, PR.

*Rhizoglyphus* Claparede, 1869. *Rh. echinopus* (Fumouze et Robin, 1868) sensu Zachvatkin, 1941 — IR, PR.

*Sancassania* Oudemans, 1916. *S. chelone* Oudemans, 1916 — Russia: PR, Sakhalin, Bury-

atiya; Japan: Kyushu; Vietnam; *S. berlese* (Michael, 1903) — IR, PR; *S. geotruporum* (Zachvatkin, 1941) — Russia: Sakhalin, Kuril Is., Japan: Hokkaido, Honshu (hypopi); *S. mandzhur* (Zachvatkin, 1940) — PR; *S. sphaerogaster* (Zachvatkin, 1937) — PR; *S. spinatarsus* (Hermann, 1804) — PR (hypopi).

*Schwiebea* Oudemans, 1916. *S. talpa* Oudemans, 1906 — IR, PR (adults); *S. kurilensis* Bugrov, 1995 — Russia: Kuril Is. (female); *S. longibursata* Fain et Wauthy, 1979 — IR, PR; South Korea: Kyongsangnam-Do; *S. neomycolicha* Klimov, 1988 — PR; *S. parallela* (J. Müller) — Russia: PR, Kamchatka, Kuril Is.; *S. nova* (Oudemans, 1906) — Russia: Novosibirskaya oblast', IR, PR; *S. sakhalinensis* Bugrov, 1995 — Russia: Sakhalin (female); *S. sp. 1* — PR, subcortical habitats; *S. sp. 2* — PR, subcortical habitats.

*Thyreophagus corticalis* (Michael, 1885) — PR (adults).

*Tyrophagus* Oudemans, 1924. *T. putrescentiae* (Schrank, 1781) — IR, PR (adults); *T. longior* (Gervias, 1844) — PR (adults); *T. sylvester* Zachvatkin, 1941 — IR (adults).

*Umakefeq* Klimov, 2000. *U. macrophthalmus* Klimov, 2000 — PR; *U. mesoophthalmus* Klimov, 2000 — PR (hypopi); *U. microphthalmus* Klimov, 2000 — PR; Japan: Honshu (hypopi).

*Viedebantia* Oudemans, 1929. *V. egorovi* Klimov, 1998 — Russia: IR, Khabarovskiy kray, PR, Kuril Is.; Korea: Suwon; *V. sp. 1* — PR, ex *Silpha perforata* Gebler, 1832 (Coleoptera, Silphidae) (hypopi).

Undescribed genus of primitive Rhizoglyphinae related to *Viedebantia* — PR, ex *Lycoperdon* sp. (Basidiomycetes, Gasteromycetales) and *Lycoperdina koltzei* Reitter, 1887 (Coleoptera, Endomychidae).

Undescribed genus of advanced Rhizoglyphinae — PR, ex *Mycetina marginalis* (Gebler, 1830) (Coleoptera, Endomychidae) (hypopi).

Several state assignments were made with the help of description and figures in the literature: Cunliffe, 1964; Fain, 1982a; Fain, 1982b; Fain, Chmielewski, 1987; Fashing, 1974; Griffiths, 1970; Ho, 1993; Lombert et al., 1982; Manson, 1972; OConnor, 1996; Woodring, 1966; Wurst & Frank, 1998.

## ANALYSIS OF DIAGNOSTIC CHARACTERS OF THE GENUS *FAGACARUS*

Adults of Acaroidea are characterized by claws located on condilophores, ventral sejugal apodemes and tarsal suckers in males [Zachvatkin, 1941; OConnor, 1982, 1992]. Adults of Acaridae are characterized by asymmetrical setae *e* and *f*, with *f* longer than *e*, and ventral tarsal setae

*u* and *v*, which are longer than the lateral ones [OConnor, 1992]. Adults of *Fagacarus* possess all those characters. Thus, there is direct evidence that *Fagacarus* belongs to both this family and the superfamily as Fain & Norton [1979] suggested. Resemblance of *Fagacarus* and Ctenoglyphinae (Glycyphagidae), also indicated by these authors, is not supported by such important morphological characters as the leg and idiosomal chaetotaxy. This might be a result of the convergence that is not discussed in the present paper. Diagnostic characters originally proposed for the subfamily Fagacarinae (1–20) as well as several additional characters (21–33) are analyzed below with the genus *Tyrophagus* Oudemans, 1924 taken for the polarization of the character states. If the character is used in a phylogenetic analysis, then the number that refers to it is given in parentheses (Appendix 1):

#### Adults

1. Cuticle dorsally with raised protuberances ("warts"). Autapomorphy (3).
2. Ventrally raised protuberances present only on lateral area. This character state refers to characters ♂ 1 in this list.
3. Dorsal setae serrate (Fig. 1, A). Plesiomorphy (7).
4. Ventral setae short. In fact, ventral setae are following: *1a*, *3a*, *3b*, *4a*, and *g*. Apomorphy (8).
5. Setae *ve* absent. Apomorphy (9).
6. Setae *scx* represented by massive spine. Autapomorphy. (11).
7. Setae *c*<sub>3</sub> being absent. Apomorphy (14).
8. Adanal setae absent. Ancestrally, in the ontogenesis of Astigmata, when the hypopal stage is omitted, the adanal setae (or their alveoli) develop, first appearing in the teleonymph. In most Acaridae (Acarinae, Tyrophaginae, primitive Rhizoglyphinae), setae *ad* develops in females only. In derived Rhizoglyphinae, these setae being secondarily absent in all homeomorphic stages as a result of the paedomorphosis. *ad* transformed to suckers of the anal disk in the hypopi of Astigmata. Apomorphy (17).
9. Pseudoanal setae (*ps*) of female being absent. Apomorphy (18).
10. Male genital apparatus placed behind coxae IV and close to anus. Apomorphy (19).
11. Legs short and thick. Apomorphy (21).
12. Legs with several widened spines. In fact, those are *wa*, *la*, *ra* III–IV, *gTI*–IV, *hT*, *mG*, and *cG* I–II. Apomorphy (22).
13. Anterior part of dorsum forming a tegmen covering the gnathosomal base. Tegmen is absent in *F. verrucosus* and *Fagacarus* sp. 1 I studied. Probably, the presence of tegmen is a normal condition for Acaroidea, but appearance of the character depends on the degree in which the mites are pressed by a microscope cover glass.
14. Epimerae I Y shaped, other epimerae free. Synapomorphy or symplesiomorphy for Acaroidea.
15. Genital papillae well-developed. Symplesiomorphy for Acaroidea.
16. Setae *cp* absent. These setae are depicted in female of *F. verrucosus* (Fig. 1.4) and present in all instars of *Fagacarus* spp. I studied.
17. Atrium (=vulva) resembles inverted Y, situated between coxae IV. This character is synapomorphy or symplesiomorphic for Acaroidea.
18. Male anal suckers absent. Flattened and sclerotized fields with two alveoli are depicted on sides of posterior tip of anus in *F. verrucosus* [Fain & Norton, 1979]. The same structures present in *Fagacarus* sp. 1. As the male anal suckers bear *ad*<sub>1</sub> and *ad*<sub>2</sub> alveoli [Zachvatkin, 1953; Griffiths et al., 1990], and are often placed near posterior end of anus in Acaridae, the paraanal sclerites of *Fagacarus* should be considered as reduced and probably non-functional homologues of the anal suckers (autapomorphy). Thus, the anal suckers are secondarily absent in *Fagacarus*. Also the secondary absence of the anal suckers was recorded in *Neotropacarus* Baker, 1985 [Cunliffe, 1964] and *Sancassania anomala* (Nesbitt, 1944) [Nesbitt, 1944].
19. Legs with sessile claws. Synapomorphy (? symplesiomorphy) for Acaridae.
20. Male tarsal suckers developed. Synapomorphy for Acaroidea [OConnor, 1982]).
21. Chelicera with two setae (*cha* and *chb*). Two subequal cheliceral setiform setae are reported in oribatid mites [Shaldybina, 1975], which are considered as ancestors of the Astigmata [Zachvatkin, 1953; OConnor, 1982; Griffiths et al., 1990], and even in more primitive acariform mites, for example, *Terpnacarus* Grandjean, 1939 [Grandjean, 1939]. In Astigmata, the presence of two cheliceral setae was recorded only in *Ctenoglyphus canestrinii* (Armanelli, 1887) (Glycyphagidae: Ctenoglyphinae) [Akimov, 1985], *Viedebantia* (Acaridae: Rhizoglyphinae), and the related undescribed genus of primitive Rhizoglyphinae [Klimov, 1999]. Plesiomorphy (1).
22. "Additional" cheliceral seta (*chb*) short, placed slightly proximad to *cha* (Fig. 1, I). Proximal location of *chb* is registered in oribatid mites [Shaldybina, 1975] and in *Terpnacarus* [Grandjean, 1939]. In *C. canestrinii*, *chb* is placed as in *Fagacarus* (potential plesiomor-

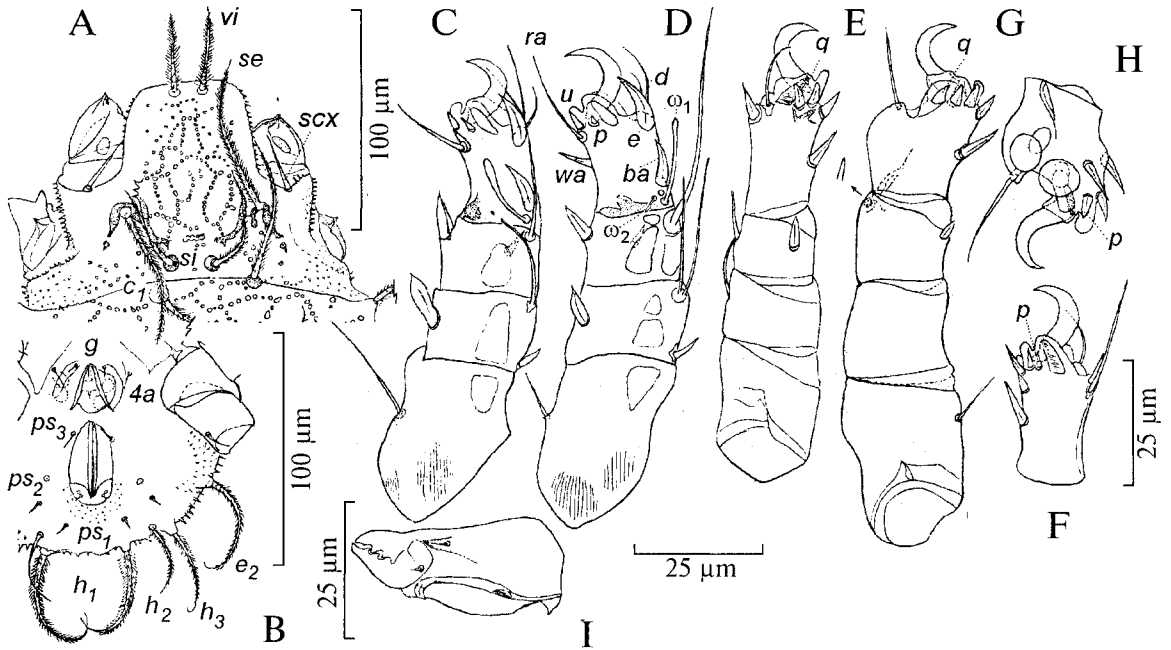


Fig. 1. *Fagacarus* sp. (adults): A — propodosoma, dorsal view, B — opisthosoma, ventral view, C–G — legs I–IV, respectively, F, H — tarsi III–IV, respectively, I — chelicera. A, C–E, F, I — female; B, G, H — male. Scale bars: A, B — 100  $\mu$ m; C–I — 25  $\mu$ m.

Рис. 1. *Fagacarus* sp. (взрослые): А — проподосома дорсально, В — опистосома вентрально, С–Г — ноги I–IV, соответственно, F, H — лапки III–IV, соответственно, I — хелицера. А, С–Е, F, I — самка; В, G, H — самец. Масштаб: А, В — 100  $\mu$ m; С–I — 25  $\mu$ m.

phy), while in *Viedebanttia* and the related genus this seta is long, placed distad to *cha* (potential apomorphy). Potential plesiomorphy (2).

23. Idiosomal setae  $f_2$  absent (Fig. 1, B). In ontogenesis, these setae appear starting with the protonymph in many astigmatid mites (including Acaridae: Acarinae, Tyrophaginae) and secondarily disappear in all homeomorphic stages of advanced Rhizoglyphinae (Naiadacarini, Thyreophagini) as a result of pedomorphosis [Klimov, 1999]. Apomorphy (15)
24. Solenidion  $\omega_3$  longer and thicker in males than in females. This character state occurs in *Boletoglyphus* Volgin and *Umakefeq*, while in *Thyreophagus* it is shorter in males than in females. Plesiomorphic condition of this character is the equal length and width of the solenidion in both sexes (Acarinae, Horstiinae, Caloglyphini, Rhizoglyphini, *Viedebanttia*, and *Histiogaster*). Apomorphy (24).
25. Ventroapical spines  $p$  and  $q$  I–IV developed. These spines are not depicted in *F. verrucosus* [Fain & Norton, 1979] and being present in material I studied (Fig. 1, E–H). Plesiomorphy.
26. Setae  $nG$  III absent. The seta  $nG$  III is perhaps the seta most prone to regression and is not

reliable synapomorphy as occurred in distant taxa independently, e.g. *Medeus ithacaensis* OConnor, 1997 (Acaridae: Horstiinae) [OConnor, 1996], *Histiostoma brevimanus* (Oudemans, 1914) (Histiostomatidae) [Bongers et al., 1985], *Boletoglyphus*, *Capillaroglyphus* [Klimov, 1998a], and *Thyreophagus* [Fain, 1982b].

#### Hypopus

1. Supracoxal organ (*scx*) with a bifurcate tip in *F. verrucosus* and *F. sp. 1* (Fig. 2, A) as in *Lasioacarus* Kadzhyaya et Sevastianov, 1967 (Rhizoglyphinae: Lasioacarini), an undescribed genus of the advanced Rhizoglyphinae, and *Horstia* (Horstiinae). The ancestral state of this character is setiform *scx* (most other Acaroidea, including Acarinae, Tyrophaginae, primitive Rhizoglyphinae, and *F. sp. 2*). Polymorphic. (32)
2. Idiosomal setae *se*, *si*,  $c_p$ ,  $d_p$ ,  $e_p$ , and  $h_1$  of median length, setiform, finely serrate in *F. verrucosus* and *F. sp. 1* (Fig. 2, A). Similar length of aforementioned setae is recorded in *Cosmoglyphus* (Rhizoglyphinae: Acotyledonini), *Capillaroglyphus* (Rhizoglyphinae: Boletoglyphini), *Acarus* (Acarinae) and some other genera. I consider this character state as a potential plesiomorphy. In *F. sp. 2* these setae are short. Polymorphic.

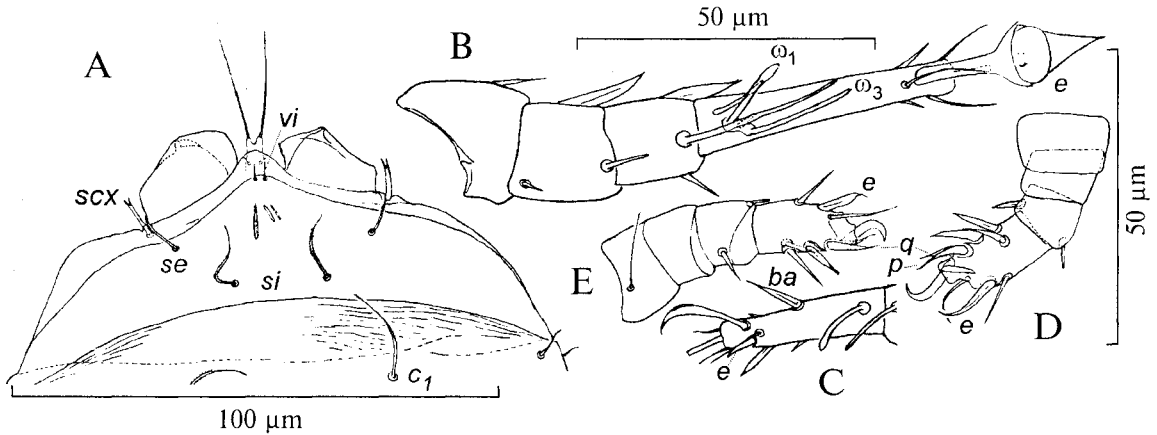


Fig. 2. *Fagacarus* sp. (hypopus): A — propodosoma, dorsal view, B — leg I, C — tarsus II, D, E — legs III–IV, respectively. Scale bars: A — 100  $\mu$ m; B–E — 50  $\mu$ m.

Рис. 2. *Fagacarus* sp. (гипопус): А — проподосома дорсально, В — нога I, С — лапка II, D — ноги III–IV, соответственно. Масштаб: А — 100  $\mu$ m; В–Е — 50  $\mu$ m.

3. “Saucer” [Zachvatkin, 1941] of *e* I very large, triangle, sharpened on tip (Fig. 2, B). Autapomorphy (35).
4. Solenidion  $\omega_3$  positioned adjacent to  $\omega_1$  on tarsus I (Fig. 2, B) as in undescribed genus related to *Viedebanttia*, *Capillaroglyphus*, *Schwiebea*, *Histiogaster*, and *Thyreophagus* (Rhizoglyphinae).  $\omega_3$  is remoted from  $\omega_1$  base in *Tyrophagus* (Tyrophaginae), *Acarus* (Acarinae), *Cosmoglyphus*, and *Sancassania* (Acotyledonini). Apomorphy (38).
5. Gnathosoma elongate, almost parallel-sided, with 1 pair of setae placed on basal palpomer as in some *Schwiebea* 1916 (*S. nova*, *S. longibursata*) and *Naiadacarus* Fashing, 1974 (*N. fashingi* OConnor, 1989). It is difficult to polarize this character state, as gnathosoma is non-functional in hypopi. Possibly this character state is a potential apomorphy. Gnathosoma is short in *F. sp. 2*. Polymorphic.
6. Ventoapical tarsal setae *p* and *q* III–IV and dorsoapical *e* III–IV spiniform, with attenuate tips (Fig. 2, D–E) as in several *Schwiebea*. Similar pattern is recorded for *Capillaroglyphus*, but *e* IV setiform. Apomorphy (39).
7. Leg setae *nG* III being absent. Apomorphy (see above for adults).
8. Dorsoapical tarsal seta *e* II spiniform (Fig. 2, C). Ancestral state of the character is setiform *e* II (*Carabidobius*, *Sancassania*, *Tyrophagus*, *Acarus*, and others). Apomorphy.

The placement of the genus *Fagacarus* within Acaridae is proven above. Thus, synapomorphies and symplesiomorphies of Acaridae, originally used to diagnose Fagacarinae (14, 15 17, 19, 20 from list above), should be excluded, as well as erroneously interpreted characters (13, 16). In order to substantiate the subfamily rank of Faga-

carinae it would be necessary to demonstrate that *Fagacarus* have a common ancestry with the most related subfamily of Acaridae (Rhizoglyphinae). Nevertheless, a number of character states (for example, 4–5, 7–11, 18, 23, 24) suggests that *Fagacarus* shares a more recent common ancestry with certain advanced genera within the Rhizoglyphinae. This hypothesis is discussed below, as well as the character states which may be accounted for its support or, vice versa, the rejection.

In Rhizoglyphinae, as well as in *Fagacarus*, there is a number of character states, which do not correlate to each other in homeomorphic and heteromorphic stages of the same species (polymorphic characters). As a rule, hypopi retain a plesiomorphic condition of the character whereas the adults (homeomorphic stages) have an apomorphic one. Prevalence of plesiomorphies in hypopi could not be explained by the ontogenetic aspect only as the homologous characters are represented by apomorphic condition in earlier instars. If the asymmetry of states of a homologous character is an ancestral characteristic for several groups, then following events are possible:

- 1) Plesiomorphic condition of a character in one stage transforms to an apomorphic condition in another stage (the character is completely presented by apomorphic condition in both hypopi and adults);

- 2) Apomorphic character state transforms to a plesiomorphic one (reverse of plesiomorphic state in both hypopi and adults).

The phylogenetic dendrogram for the family Acaridae, developed by OConnor [in litt.], partially supports an assumption about the cross changes in character states between hypopi and adults. In the lineage comprising genera *Schwiebea* — *Thyreophagus*, the transformation from

apomorphic to plesiomorphic condition promoted by morphology of the hypopus occurred at least two times, in *Calvoliella* (re-establishment of  $f_2$  in protonymphs-adults as in hypopi) and in *Lasioacarus* (re-establishment setiform *ba* II in homeomorphic stages as in hypopi). Presence of apomorphic state at least in one stage suggests that the group under question relatively more recent, whereas the reverse of plesiomorphic state throughout the ontogeny (case 2) can lead to an erroneous conclusion that the group is relatively more primitive. Lorenzen [1993, 1996] presented a method for selective seeking of cases of secondary absence of characters. This method also can be used for revealing a secondary reversion of an ancestral condition in Astigmata. Presence of the homologous characters in similar apomorphic conditions throughout ontogeny (case 1) may be a result of the evolutionary independent induction of morphology of adults to hypopi, or hypopi to adults in different derived groups (i.e. homoplasy). Thus, employing in phylogenetic analysis characters ancestrally represented by two conditions in adults and hypopi should be restricted in hypopi.

The diagnosis of the clade comprising *Schwiebea*, *Naiadacarus*, *Histiogaster*, and *Thyreophagus* [OConnor, 1989] is based on the characters existing in two conditions in both adults and hypopi, e. g. the presence of a posterior opisthosomal shield in male, the loss of 7 homologous pairs of dorsal setae (including  $f_2$ ) in adults, and the loss of *ve* in hypopi. It is also mentioned that this clade shares with *Rhizoglyphus* the loss of *aa* and the modification of setae *ba* I–II in homeomorphic stages. The latter character is also represented by two states in adults and hypopi. As there are no species within lineage *Rhizoglyphus*–*Thyreophagus*, in which seta *aa* being present throughout the ontogeny, it is possible that the loss of *aa* had occurred simultaneously in hypopi and adults and could be considered as the reliable synapomorphy, although the loss of *aa* had independently occurred in Horstiinae (*Medeus* Volgin, 1974 and *Horstia* Oudemans, 1905). The remaining characters of *Schwiebea*–*Thyreophagus* will be discussed below.

The presence of opisthosomal shield in male is recorded in Boletoglyphini, the more basal rhizoglyphine lineage [Klimov, 1998a]. This shield is absent in males of *Umakefeq* belonging to advanced Rhizoglyphinae. The complement set of dorsal setae was found in *Reckiacarus*, the genus that is closely related to *Histiogaster*. All dorsal setae, with the exception of  $f_2$ , were found in *Schwiebea cuncta* Ho, 1993 [Ho, 1993]. Similar modification of *ba* I–II in homeomorphic stages was recorded for *Rhizoglyphoides* Rhizoglyphinae:

Acotyledonini). Therefore, the reliable synapomorphy for this clade is the loss of *ve* only, a single character recorded for all hypopi of the clade *Schwiebea*–*Thyreophagus*. Although ancestrally some of previously mentioned character states probably were present such as the loss of  $f_2$  and spiniform *ba* I–II in adults, these characters can be considered as holapomorphies.

In *Fagacarus*, the following characters presented by two states in hypopi and adults (homeomorphic stages): all idiosomal setae with the exception of *ve* are developed in hypopi, whereas setae  $f_2$ ,  $c_3$ , and *ad* are secondarily absent in adults; solenidion  $w_3$  is located in common field with  $w_1$  in hypopi, whereas adults retain plesiomorphic condition of this character; solenidion *j* III is being present in feeding stages but secondarily absent in hypopi. Similar transformations were documented in several species of *Schwiebea*. I consider these character states as homoplasies, which appearance was promoted by the cross "influence" of hypopal and adult morphologies. Absence of the seta *nG* III in adults and hypopi of *Fagacarus* may suggest that this genus is more advanced with the respect to *Schwiebea* having several representatives (*S. nova*, *S. longibursata*) with this seta found to be well-developed [Klimov, 1998b]. However the loss of *nG* III appears to be an ancestral condition for *Fagacarus*, because in Boletoglyphini these setae are also lacking. The seta *nG* III is perhaps the seta most prone to regression. Loss of *nG* III has occurred in distant taxa independently, thus this character state is not being reliable synapomorphy.

*Fagacarus* spp. shares with the lineage *Rhizoglyphus*–*Boletoglyphus*–*Thyreophagus* the loss of setae *aa*, and spiniform *ba* I–II (holapomorphy) in adults and with *Schwiebea*–*Thyreophagus* lineage the loss of  $f_2$ , *ve*,  $c_3$  (holapomorphies), the reduction of Grandjean's organ (not indicated by OConnor [1989]) and several features of male genital apparatus in adults and the loss of *ve* in hypopi. The combination of several primitive characters [comparatively long dorsal setae, anterior position of  $ps_3$  in males (as in Boletoglyphini) and barbed setae] which are modified in the *Schwiebea*–*Thyreophagus* lineage suggests that the *Fagacarus* is a sister group with the clade comprising *Schwiebea* and related genera than with the Rhizoglyphinae as a whole.

Therefore, the subfamily Fagacarinae should be considered as a separate tribe in the subfamily Rhizoglyphinae.

The explanation for the development of most synapomorphies (symplesiomorphies) in adults of *Fagacarus* (the sculpture of idiosoma, heavily barbed dorsal setae and the development of crista

on tarsus IV in male) may lie in the microhabitat preferences and different feeding substrates exploited by the species of this genus (see below).

### THE PHYLOGENETIC ANALYSIS

Data for the phylogenetic analysis were obtained from the external morphology of adults and deutonymphs of the genus *Fagacarus* and 10 other genera of Acaridae, which are the type genera for the family group taxa, excluding *Lasioacarus* and several taxa known only from adults or hypopi. The out-group study involved a hypothetical ancestor and the genus *Tyrophagus*. Data were analyzed with the computer program PAUP\* Ver. 4.0b4a for 32-bit Microsoft Windows [Swofford, 1999] using the bootstrap with the branch and bound search (number of replicates was set to 400). Forty characters were included in the analysis (see Appendix 1). The characters are un-

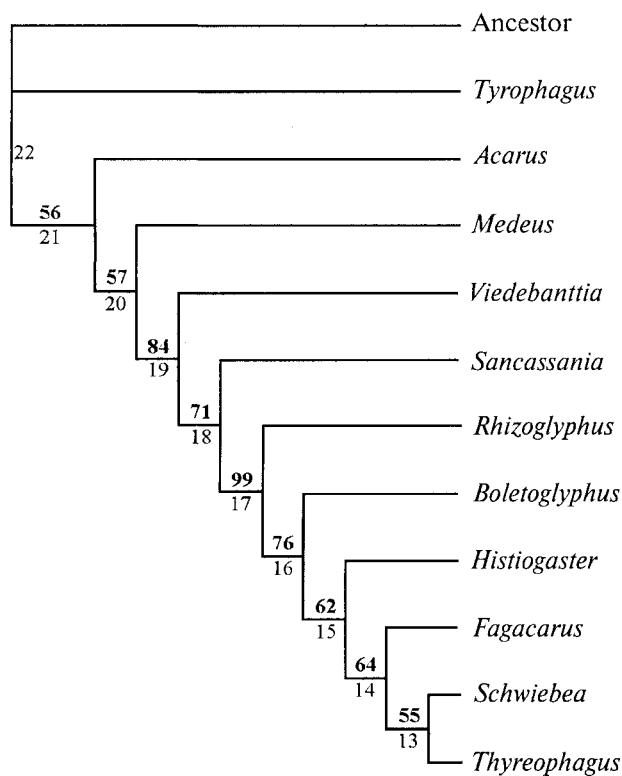


Fig. 3. Phylogenetic relationships between *Fagacarus* and related genera. The single most parsimonious tree found in bootstrap analysis using branch and bound searches. The numbers above branch correspond to bootstrap proportions of 50% or more, whereas the number below branches corresponds to the node numbers in Appendix 3. The clade at node 19 is comprised by genera of the subfamily Rhizoglyphinae.

Рис. 3. Филогенетические взаимоотношения *Fagacarus* и близких родов. Единственная кладограмма, найденная при помощи метода bootstrap (branch and bound search). Число над ветвью кладограммы соответствует соотношению 50% или больше этого метода, ниже — номеру ноды в Приложении 3. Клада у ноды 19 включает роды подсемейства Rhizoglyphinae.

weighted, ordered (beside 5, 12, 27, 28), and coded as binary or multistate. Multistate taxa are interpreted as polymorphic. Characters were optimized using the accelerated transformation method (ACCTRAN).

The analysis yielded a single most parsimonious cladogram (length 93, CI excluding uninformative characters 0.714, RI 0.774, RC 0.574). This cladogram (Fig. 3) differs from that of OConnor [in litt.] by the placements of the subfamily Acarinae, located more basally in OConnor's cladogram, and the genus *Histiogaster*, that forms a clade with *Calvoliella* and *Thyreophagus* in OConnor's cladogram. It is beyond the scope of the paper to provide the complete phylogenetic analysis of the family Acaridae. Thus I will discuss only the part of this cladogram, namely the clade comprising *Fagacarus*.

The cladogram supports the placement of the genus *Fagacarus* within Acaridae and shows that the genus *Fagacarus* shares the common ancestry with the advanced genera *Thyreophagus* and *Schwiebea* of the subfamily Rhizoglyphinae (Fig. 3). Those three genera share the following derived character states (only unambiguous apomorphies listed): the reduction of Grandjean's organ (5), the absence of setae  $c_3$  (14), and the placement of  $\omega_3$  (38). They share the absence of opisthosomal setae  $f_2$  in adults (15) and propodosomal setae  $ve$  in hypopi (33) with the genus *Histiogaster*. Thus, the hypothesis about the subfamily rank of *Fagacarus* is not substantial.

The tribe Naiadacarini, the clade *Schwiebea*–*Thyreophagus* sensu OConnor [1989] and OConnor [in litt.], includes the genus *Histiogaster*. This genus is placed in my diagram more basally (Fig. 3) that resulted from the structure of Grandjean's organs: stick-form in the genera *Histiogaster* and *Sancassania* and vestigial in *Fagacarus*, *Schwiebea* and *Thyreophagus*. Absence of several idiosomal setae in *Histiogaster*, *Schwiebea* and *Thyreophagus* adults is a character that is present in two states in both adults and hypopi (all hypopi of aforementioned genera have these setae), and probably cannot be considered as the valid synapomorphy for these genera. Nevertheless, this conclusion requires the more detailed analysis, and I have to leave this problem unsolved. Provisionally I exclude *Histiogaster* from Naiadacarini and consider the genus *Fagacarus* as a sister-group for Naiadacarini s. str. that justifies the separation of the monotypic tribe Fagacarini stat.n.

The clade comprising the genus *Fagacarus* is diagnosed by following apomorphies (i): cuticle

dorsally and in part ventrolaterally with raised protuberances (3), setae *scx* in form of massive spine (11), copulatory opening of female separated from anus by distance greater than half of the anus length (18), tarsus IV of male with a dorsal crista (30); ventroapical tarsal setae *p* and *q* III–IV and dorsoapical *e* III–IV spiniform, with attenuate tips (39); and reversals (ii): chelicera with 2 setae (1), dorsal setae serrate (7), setae *si* long (12); setae *c*<sub>1</sub> present (13), retinae absent in hypopi (34); saucer of *e* I in hypopi very large, triangle, sharpened on tip (35).

### SYSTEMATIC POSITION OF THE GENUS *FAGACARUS*

On the basis of above arguments, the following diagnosis for this monobasic tribe is proposed:

**Family Acaridae** Latreille, 1802

**Subfamily Rhizoglyphinae** Oudemans, 1923

**Tribe Fagacarini** Fain et Norton, 1979, *stat. n.*

Fagacarinae Fain et Norton, 1979: 5 (Acaridae subfam.).

Type genus *Fagacarus* Fain et Norton, 1979, by original designation.

*aa* lacking.

**Adults.** Grandjean's organ reduced. Setae *f*<sub>2</sub>, *ve*, and *c*<sub>3</sub> absent, other idiosomal setae developed; *ba* I–II spiniform, placed near  $\omega_1$ ; copulatory opening of female separated from the anus by a distance that is greater than half of the anus length; male genital apparatus located posteriorly, with widened posterior part; cuticle dorsally and in part ventrally with numerous raised protuberances forming a net; anal suckers vestigial, retain two alveoli of *ad*<sub>1</sub> and *ad*<sub>2</sub> in male; tarsus IV with a dorsal crista in male; chelicera with two short setae, seta *chb* placed slightly posteriad to *cha*; dorsal setae rounded in section, heavily barbate in homeomorphic stages; *ps*<sub>3</sub> placed anteriad to the fore edge of anal suckers in male.

**Hypopi.** *ve* absent; saucer of *e* I very large, triangle, sharpened on tip; *e* II needle-like, shorter than claw;  $\omega_3$  placed in common field with  $\omega_1$ ; *p*, *q*, and *e* III–IV spiniform, with attenuate tip; gnathosoma with one pair of basal setae; *nG* III and  $\phi$  III being absent.

The tribe comprises 1 genus with 1 named and 2 unnamed species distributed in the Holarctic (see material).

### NOTES ON BIOLOGY

Large colonies of *F. verrucosus* and *F. sp.* 1 were found in association with the fungal mycelium in decaying wood. It was noted that the mites preferred the edges of the mycelium mass. I hypothesize that this specific substrate and the microhabitat itself are the ancestral ones for mites of the genus *Fagacarus*. Long and barbed setae, as

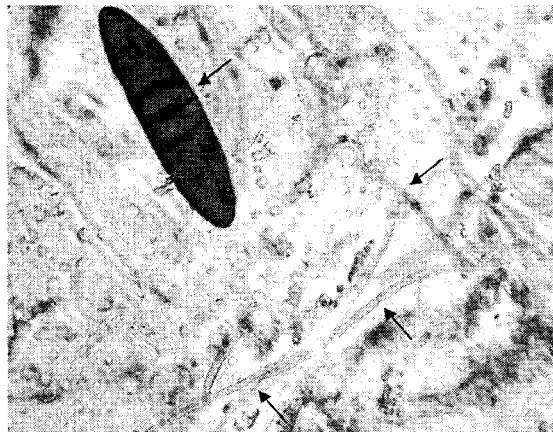


Fig. 4. Fungal hyphae and spores (pointed by arrows) transferred by mite *Fagacarus verrucosus* Fain et Norton.

Рис. 4. Гифы и споры грибов (показаны стрелкой), переносимые клещом *Fagacarus verrucosus* Fain et Norton.

well as the idiosomal sculpture (Fig. 4) may promote the transferring microorganisms of any kind, especially those taking part in the destruction of wood. By the same reason a male cannot use its anal suckers for the attachment and holding a female during copulation. Thus, the anal suckers have become vestigial. This loss is compensated by the development of a crista, the place of the muscle attachment on tarsi IV where functional tarsal suckers are located.

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### REFERENCES

- Akimov I. A. 1985. Biologicheskiye Osnovy Vredonosnosti Akaroidnykh Kleshchey. "Naukova Dumka", Kiev. 160 pp. [in Russian]
- Cunliffe F. 1964. *Tropacarus*, a new genus of Acaridae // Proceedings of Entomological Society of Washington. Vol. 66. No 3. P. 181–183.
- Bongers M. G. H., O'Connor B. M., Lukoschus F. S. 1985. Morphology and ontogeny of histiostomatid mites (Acari: Astigmata) associated with cattle dung in the Netherlands // Zoologische Verhandlungen. Leiden. No 223. S. 1–56.
- Fain A. 1982a. Cinq espèces du genre *Schwiebea* Oudemans, 1916 (Acari, Astigmata) don't trois nouv-



- elles découvertes ans des sources du sous-sol de la ville de Vienne (Autriche) au cours des travaux du métré // *Acarologia*. T.23. Fasc.4. P. 359–371.
- Fain A. 1982b. Revision des genres *Thyreophagus* Rondani, 1874 et *Michaelopus* Fain & Johnston, 1974 (Acari, Acaridae) avec description de neuf especes nouvelles // *Bulletin Institut royal des sciences naturelles de Belgique*. Entomologie. Vol.54. No7. P.1–47.
- Fain A., Chmielewski W. 1987. The phoretic hypopi of two acarid mites described from ants nest: *Tyrophagus formicetorum* Volgin, 1948 and *Lasioacarus nidicolus* Kadzhaja and Sevastianov, 1967 // *Acarologia*. T.28. Fasc. 1. P. 53–61.
- Fain A., Norton R. A. 1979. *Fagacarus verrucosus* n. g., n. sp. (Acari, Astigmata) from decaying beech wood in the U.S.A. // *International Journal of Acarology*. Vol.5. No1. P.5–8.
- Fashing N. J. 1974. A new subfamily of Acaridae, the Naiadacarinae, from water-filled treeholes (Acarina: Acaridae) // *Acarologia*. T.16. Fasc.1. P.166–181.
- Grandjean F. 1939. Quelques genres d'acariens appartenant du groupe des Endeostigmata // *Annales des Sciences Naturelles*. Zool. Ser.11. T.2. P.1–122.
- Grandjean F. 1947. L'origine pileuse des mors et la chaetotaxie de la mandibule chez les Acariens actinochitineux // *Comptes rendus des séances de l'Académie des Sciences*. T. 224. P. 1251–1254.
- Griffiths D. A. 1970. A further systematic study of the genus *Acarus* L., 1758 (Acaridae, Acarina), with a key to species // *Bulletin of the British Museum (Natural History)*. Zoology series. Vol. 19. No 2. P. 85–118.
- Griffiths D. A., Atyeo W. T., Norton R. A., Lynch C. A. 1990. The idiosomal chaetotaxy of astigmatid mites // *Journal of Zoology*. London. Vol. 220. Pt.1. P.1–32.
- Ho Chyi-Chen. 1993. Two new species and a new record of *Schwiebea* Oudemans from Taiwan (Acari: Acaridae) // *International Journal of Acarology*. Vol. 19. No 1. P. 45–50.
- Klimov P. B. 1998a. A new tribe of acarid mites of the subfamily Rhizoglyphinae (Acariformes, Acaridae) // *Far Eastern Entomologist*. No 59. P. 1–19.
- Klimov P. B. 1998b. To the knowledge of acarid mites of the genus *Schwiebea* (Acariformes, Acaridae) from the Far East, with notes on the genus // *Vestnik Zoologii*. Kiev. Vol. 32. No 3. P. 13–30.
- Klimov P. B. 1999. Akaroidnye kleshchi Dal'nego Vostoka Rossii (Acariformes, Acaroidea). Abstract of the Cand. Biol. Sc. dissertation thesis. Vladivostok: Dal'nauka Publ. 18 pp.
- Lombert H. A., Lukoschus F. S., OConnor B. M. 1982. The life-cycle of *Cosmoglyphus inaequalis* Fain & Caceres, 1973, with comments on the systematic position of the genus. Results of the Namaqualand — Namibia Expedition of the King Leopold III Foundation for the Exploration and Protection of Nature (1980) // *Bulletin Institut royal des sciences naturelles de Belgique*. Vol. 54. No 10. P. 1–17.
- Lorenzen S. 1993. The role of parsimony, outgroup analysis, and theory of evolution in phylogenetic systematics // *Zeitschrift für Zoologische Systematik und Evolutionsforschung*. Bd.31. S.1–20.
- Lorenzen S. 1996. The metamorphosis of traditional into advanced phylogenetic systematics and its impact on nematode systematics // *Russian Journal of Nematology*. Vol. 4. No 2. P. 61–70.
- Manson D. C. M. 1972. A contribution to the study of the genus *Rhizoglyphus* Claparede, 1869 (Acarina: Acaridae) // *Acarologia*. T.13. Fasc.4. P. 621–650.
- Nesbitt H. H. J. 1944. Three new mites of the subfamily Rhizoglyphinae // *Canadian Entomologist*. Vol. 76. No 2. P. 21–27.
- OConnor B. M. 1982. Astigmata // In: S. B. Parker (ed.). *Synopsis and Classification of Living Organisms*. Mc Graw-Hill, New York. P. 146–169.
- OConnor B. M. 1989. Systematics, ecology and host associations of *Naiadacarus* (Acari, Acaridae) in the Great Lakes region // *The Great Lakes Entomologist*. Vol.22. No 2. P.79–94.
- OConnor B. M. 1992. Ontogeny and systematics of the genus *Cerophagus* (Acari: Gaudiellidae), mites associated with bumblebees // *The Great Lakes Entomologist*. Vol. 25. No 3. P. 173–189.
- OConnor B. M. 1996. Two new mites (Acari: Acaridae) associated with long-tongued bees (Hymenoptera: Apidae) in North America // *Journal of the Kansas Entomological Society*. Vol. 69. No 4, suppl. P. 15–43.
- OConnor B. M. Historical ecology of the family Acaridae: phylogenetic evidence for host and habitat shifts // *Proceedings of X International Congress of Acarology*. Melbourne (in litt.).
- Shaldybina S. 1975. [External morphology of oribatid mites] // In: M. S. Ghilarov, D. A. Krivolutskii (eds) *Opredelitel' Obitayushchikh v Pochve Kleshchey*. Sarcopiformes. "Nauka", Moscow. P. 21–31. [in Russian]
- Swofford D. L. 1999. PAUP\*. Phylogenetic Analysis Using Parsimony (\*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Woodring J. P. 1966. North American Tyroglyphidae (Acari): III. The Genus *Histiogaster* with description of four new species // *Proceedings of Louisiana Academy of Sciences*. Vol. 29. P. 113–136.
- Wurst E. & Frank B. 1998. Contribution to a revision of the genus *Schwiebea* (Acari: Acaridae). I. Redescription of *Schwiebea talpa* and *Schwiebea nesbitti* // *Stutgarter Beiträge zur Naturkunde. Serie A (Biologie)*. No 579. S.1–52.
- Zachvatkin A. A. 1941. [Tyroglyphoid Mites (Tyroglyphoidea)] // *Fauna SSSR. Paukoobrazniye*. T. 6 (1). "Nauka", Moscow-Leningrad. 475 pp. [in Russian]
- Zachvatkin A.A. 1953. [Investigations on morphology and postembryonic development of tyroglyphid mites (Sarcopiformes, Tyroglyphoidea)] // In: A. A. Zachvatkin. *Sbornik Nauchnykh Rabot*. Moscow Lomonosov State University Publ., Moscow. P. 19–118. [in Russian]

## APPENDIX 1

40 characters, which were used for reconstruction of the phylogenetic relationships of *Fagacarus* are listed below. The characters 1–31 are related to adults, whereas the characters 32–40 are hypopal. All characters are unweighted. For each character the character consistency (ci) on the most parsimonious cladogram is provided (Fig. 3); if a character has more than 2 states, then I indicated whether or not the states were ordered.

## Adults

## Gnathosoma

1. Chelicera with: (0) two setae, *cha* and *chb*; (1) one seta, *cha*. ci=0.333.
2. "Additional" cheliceral seta *chb* placed: (0) proximally; (1) distally. ci=1.000.

## Idiosoma

1. Cuticle dorsally and partly ventrolaterally: (0) without protuberances; (1) with raised protuberances (Fig. 1, A). ci=1.000.
2. Supracoxal organ (*scx*): (0) barbed; (1) smooth. ci=1.000.
3. Grandjean's organ: (0) 4(2)-lobed, with more or less equal lobes; (1) round lobe; (2) stick-like with small fan-like lobe; (3) stick like with membranous lobe which fused with surface of body; (4) simple; (5) very reduced, or absent. Following character-state tree used to describe of this pattern: (1,(((5)4)3)2)0, unordered, ci=1.000.
4. Grandjean's organ: (0) barbed; (1) smooth with rare barbs on apex; (2) smooth. Ordered, ci=1.000.
5. Dorsal setae: (0) serrate (Fig. 1, A); (1) smooth. ci=0.500.
6. Ventral setae (*1a*, *3a*, *3b*, *4a*, *g*): (0) long, at least several setae longer or slightly shorter than femur I; (1) short, much shorter than femur I. ci=0.500.
7. Setae *ve*: (0) long; short, shorter than 10 mm; (1) absent. ci=1.000.
8. Setae *ve* placed on propodosomal shield: (0) anteriorly; (1) medially, reduced or absent. ci=1.000.
9. Setae *scx*: (0) thin, setiform, flattened, or represented by very short spine; (1) massive spine. ci=1.000.
10. Setae *si*: (0) present, long; (1) microsetae; (2) absent. Unordered, ci=0.714.
11. Setae *c<sub>1</sub>*: (0) present; (1) absent. ci=0.750.
12. Setae *c<sub>3</sub>*: (0) present; (1) absent. ci=1.000.
13. Setae *f<sub>2</sub>*: (0) present; (1) absent (Fig. 1, B). ci=1.000.
14. Pseudoanal setae (*ps*) of female: (0) present, setae or alveoli; (1) absent. ci=0.800.
15. Addanal setae (*ad*) of female: (0) present, setae or alveoli; (1) absent. ci=0.750.

16. Copulatory opening of female: (0) placed directly posterior to anus; separated from anus by distance greater than half of anus length (1). ci = 0.333.
17. Male genital apparatus placed: (0) in front of anterior level of trochanters IV, far from anus; (1) behind coxae IV and close to anus. ci=1.000.
18. Male anal suckers: (0) without chitinized ring; (1) with chitinized ring. ci = 0.333.

## Legs

1. Legs: (0) long and slender; (1) short and thick. ci = 0.333.
2. Setae *wa*, *la*, *ra* III–IV, *gTI*–IV, and *hT*, *mG*, *cGI*–II: (0) setiform; (1) spiniform. ci=1.000.
3. Setae *aa*: (0) present; (1) absent. ci=0.500.
4. Solenidion  $\omega_1$ : (0) of equal length and width in males and females; (1) in males longer and thicker than in females; (2) in males shorter than in females. Ordered, ci=0.750.
5. Placement of *ra* I–II: (0) medial; (1) subterminal. ci=1.000.
6. Placement of *la* I–II: (0) medial; (1) subterminal. ci=1.000.
7. Setae *ba* I–II: (0) setiform, placed on middle of tarsus; (1) spiniform, placed at base of tarsus adjacent; (2) absent. Unordered, ci=0.667.
8. Setae *e* I–IV: (0) setiform or needle-like, small; (1) spiniform, massive (Fig. 1, C–H); (2) absent. Unordered, ci=1.000.
9. Legs I of male: (0) not enlarged, without apophysis on femur; (1) enlarged, with apophysis on femur. ci=1.000.
10. Tarsus IV of male: (0) without dorsal crista; (1) with dorsal crista (Fig. 1, H). ci=1.000.
11. Solenidion  $\phi$  IV of male: (0) setiform; (1) spiniform. ci=1.000.

## Hypopus

## Idiosoma

1. Supracoxal organ (*scx*): (0) simple; (1) with bifurcate tip (Fig. 2, A). ci=1.000.
2. Setae *ve*: (0) present; (1) absent. ci=1.000.
3. Retinae: (0) absent; (1) present. ci=0.667.

## Legs

1. Saucer of *e* I: (0) simple; (1) very large, triangle, sharpened on tip (Fig. 2, B). ci=1.000.
2. Setae *aa*: (0) present; (1) absent (Fig. 2, B). ci=0.500.
3. Solenidion  $\omega_2$ : (0) present; (1) absent. ci=0.500.
4. Solenidion  $\omega_3$  positioned: (0) apically, far from  $\omega_1$ ; (1) On middle of tarsus, far from  $\omega_1$ ; (2) adjacent to  $\omega_1$  on tarsus (Fig. 2, B). Ordered, ci=0.750.
5. Ventroapical tarsal setae *p* and *q* III–IV and dorsoapical *e* III–IV: (0) setiform; (1) spiniform, with attenuate tips (Fig. 2, D–E). ci=1.000.

6. Solenidion  $\sigma$  III: (0) present; (1) absent.  
ci=0.667.

## APPENDIX 2. Data matrix

	1234567890	1234567890	1234567890	1234567890
Ancestor	0000000000	0000000000	0000000000	0000000000
<i>Tyrophagus</i>	1?00200000	0000000000	0000000000	0000000100
<i>Acarus</i>	1?00000000	0000000101	0000000010	0000001101
<i>Medeus</i>	1?00101000	0100001000	1010000200	000001100A
<i>Viedebanttia</i>	0100301111	0000000000	1100001100	0000000101
<i>Sancassania</i>	1?0141A111	0100000100	0100100100	0000000101
<i>Rhizoglyphus</i>	1?01421111	0B0001A000	1A10111100	1000010100
<i>Boletoglyphus</i>	1?01420121	0BAA000011	1111111100	1000010101
<i>Fagacarus</i>	0011520121	1001111110	1111111101	1A10110211
<i>Schwiebea</i>	1?01521121	0BA11A1011	111A111100	101A010BA1
<i>Histiogaster</i>	1?01421121	02101AA010	0110111100	1011010101
<i>Thyreophagus</i>	1?01521021	02111A1011	1112112100	1011010201

A= (01)  
B=(12)

## APPENDIX 3

An apomorphy list is given below for the most parsimonious tree (Fig. 3). Node numbers are identical to those in Fig. 3. Single-width arrows (->) indicate anambiguous change and double-width arrows (=>) indicate a change that is unambiguous.

Node 22->Ancestor: 1, 1=>0; 38, 1=>0.

Node 22->*Tyrophagus*: 5, 0=>2.

Node 22->node 21: 37, 0->1; 40, 0=>1.

Node 21->*Acarus*: 18, 0=>1; 20, 0=>1; 29, 0=>1.

Node 21->node 20: 5, 0->1; 7, 0=>1; 12, 0->1; 21, 0=>1; 28, 0->1.

Node 20->*Medeus*: 17, 0=>1; 23, 0=>1; 28, 1->2; 36, 0=>1; 38, 1=>0.

Node 20->node 19: 5, 1->3; 8, 0=>1; 9, 0=>1; 10, 0=>1; 22, 0=>1; 27, 0->1; 37, 1->0.

Node 19->*Viedebanttia*: 1, 1=>0; 2, 0=>1; 12, 1->0.

Node 19->node 18: 4, 0=>1; 5, 3->4; 6, 0=>1; 25, 0=>1.

Node 18->*Sancassania*: 18, 0=>1; 21, 1=>0; 27, 1->0.

Node 18->node 17: 6, 1=>2; 12, 1->2; 16, 0->1; 23, 0=>1; 26, 0=>1; 31, 0=>1; 36, 0=>1.

Node 17->*Rhizoglyphus*: 40, 1=>0.

Node 17->node 16: 9, 1=>2; 13, 0->1; 19, 0=>1; 24, 0->1.

Node 16->*Boletoglyphus*: 7, 1=>0; 16, 1->0; 20, 0=>1.

Node 16->node 15: 15, 0=>1; 17, 0->1; 33, 0=>1; 34, 0->1.

Node 15->node 14: 5, 4=>5; 14, 0=>1; 38, 1=>2.

Node 14->*Fagacarus*: 1, 1=>0; 3, 0=>1; 7, 1=>0; 11, 0=>1; 12, 2=>0; 13, 1->0; 18, 0=>1; 30, 0=>1; 34, 1->0; 35, 0=>1; 39, 0=>1.

Node 14->node 13: 20, 0=>1.

Node 13->*Thyreophagus*: 8, 1=>0; 24, 1=>2; 27, 1=>2.

Node 15->*Histiogaster*: 21, 1=>0; 24, 1->0.