REVIEW OF MITES (ACARI) ASSOCIATED WITH THE EUROPEAN SPRUCE BARK BEETLE, *IPS TYPOGRAPHUS* (COLEOPTERA: CURCULIONIDAE: SCOLYTINAE) IN ASIAN RUSSIA

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ABSTRACT: A total of 68 mite species were collected on *Ips typographus* and in their galleries in Siberia and in the Far East of Russia: *Cercoleipus kuznetsovi* (Cercomegistidae), *Pleuronectocelaeno barbara*, *P. japonica* (Celaenopsidae), *Uroobovella ipidis* (Urodynychidae), *Trichouropoda polytricha*, *T. karawaiewi*, *T. structura* (Trematuridae), *Schizosthetus* sp. (Parasitidae), *Dendrolaelaps* (*Ipidodendrolaelaps*) *quadrisetus*, *Dendrolaelaps* (*Insectolaelaps*) *pini*, *Dendrolaelaps* (*Apophyseodendrolaelaps*) *disetosimilis* (Digamasellidae), *Macrocheles* (s. str.) *ivanovi* (Macrochelidae), *Gamasellodes tatricus* (Ascidae), *Proctolaelaps fiseri*, *P. hystricoides*, *P. juradeus* (Melicharidae), *Ereynetes* (*Huntereynetes*) sp. (Ereynetidae), *Mexechesle virginiensis* (Cheyletidae), *Dolichocybe sibiricus* (Dolichocybidae), *Pyemotes* sp. (Pyemotidae), *Aethiophenax ipidarius* (Acarophenacidae), *Microdispidides moseri*, *Elattoma crossi* (Pygmephoridae), *Coleopygmephorus bogenschutzi*, *C. hylophilus*, *C. typographus* (Neopygmephoridae), *Scutacarus pseudoplurisetus*, *S. scolyti*, *S. muscicola*, *S. palustris* (Scutacaridae), *Iponemus gaebleri gaebleri*, *Tarsonemus striatus*, *T. (Schaarschmidtia) bistridentati*, *T. typographi*, *Heterotarsonemus lindquisti* (Tarsonemidae), *Siculobata* (*Paraleius*) *leontonycha* (Scheloribatidae), *Acarus* sp., *Boletoglyphus boletophagi*, *Forcellinia wasmanni*, *Ipsoglyphus bochkovi*, *Kuzinia laevis*, *Naiadacarus* sp., *Schwiebea* sp. *eurynympha*-group [punctate dorsum], *Sch.* sp. *eurynympha*-group [small, unsclerotized, 1a, 3a filiform], *Sch. nesbitti*, *Sch. nova*, *Sch.* sp.1 *nova*-group [two tibial setae, regular attachment organ], *Sch.* sp. *nova*-group [two tibial setae, wide attachment organ], *Sch.* sp. *nova*-group [granulate dorsum, short legs III–IV], *Sch. scheucherae*, *Thyreophagus corticalis*, *Th. entomophagus*, *Th. aff. odyneri*, *Tyrophagus putrescentiae* (Acaridae), *Divilia* aff. *occidentalis*, *D. sp.*, *Hemisarcoptes* sp., *Nanacarus* sp.1, *N. sp.2*, *Superioropus huronmontanus* (Hemisarcoptesidae), *Parawinterschmidtia kneissli*, *Saproglyphus* aff. *hagensis*, *S. waldorfae* (Winterschmidtidae), *Histiostoma ovalis*, *H. piceae*, *H. pini*, *Probonomoia pini*, *P. sibirica* (Histiostomatidae).

The following taxa are recorded for the first time: for the Palaearctic—*Superioropus huronmontanus* (genus and species); for Russia—*Pleuronectocelaeno japonica*, *Trichouropoda karawaiewi*, *Dendrolaelaps pini*, *Gamasellodes tatricus*, *Scutacarus palustris*, *Tarsonemus typographi*, *Heterotarsonemus lindquisti*, *Hemisarcoptes*, *Saproglyphus waldorfae*, *Naiadacarus*, *Schwiebea nesbitti*, *Histiostoma pini*, and *H. ovalis*. Of them, 60 species were collected by catching beetles with pheromone traps and examining them for phoretic mites.

We provide information on the current distribution, host association, and biology of these mites. In this article, we also discuss the following information, which we have documented: our biological observations of mites in the beetles' galleries, abundance of phoretic mites on hosts, as well as specific sites where they occur. To facilitate morphological diagnostics, common mite species were illustrated using a Scanning Electron Microscope (SEM), as well as light microscopy.

KEY WORDS: Acarina, phoresy, bark beetle, SEM photographs.

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INTRODUCTION

Many mites (Acari) are known to be associated with various bark beetles (Coleoptera: Curculionidae, Scolytinae) (Lindquist 1970a). They include predators, preying on bark beetle eggs and larvae, nematodes, and other mites, which inhabit bark beetle galleries. This group of mites also includes myco- and saprophagous mites, as well as parasitoids of bark beetle eggs and other beetle instars (Hofstetter *et al.* 2015). Most mites that inhabit bark beetle galleries use adult beetles for phoresy (Lindquist 1970a). The association of mite communities to particular bark beetle species is studied only in the cases of several economically important pests. They include: *Dendroctonus fron-*

talis in North and Central America (Kinn and Swanson 1976; Moser and Roton 1971; Stephen and Kinn 1980); *Ips typographus*, *I. sexdentatus*, *Pytyocteines* spp, *Scolytus multistriatus*, *S. pygmaeus* in Europe (Čejka and Holuša 2014; Gwiazdowicz *et al.* 2011, 2012, 2015; Lieutier 1978; Moraza *et al.* 2013; Moser and Bogenschütz 1984; Moser *et al.* 1989; Penttinen *et al.* 2013; Pernek *et al.* 2008, 2012; Takov *et al.* 2009; Vrabec *et al.* 2012); and *Ips typographus japonicus* in Japan (Moser *et al.* 1997).

The widely distributed European spruce bark beetle, *Ips typographus* Linnaeus, 1758 (Coleoptera: Curculionidae: Scolytinae), is one of the most

economically significant pests in the Palaearctic. Although it infests mainly spruce (*Picea* spp.), this beetle also occurs on other conifers, such as *Pinus* spp. and *Abies* spp. (Maslov 2010). Phoretic mites occurring on *I. typographus* have been the subjects of many studies using different sampling techniques. Kielczewski *et al.* (1983) reported about 25 mite species collected manually in Poland. Moser and Bogenschütz (1984) recorded and provided a key to 32 species collected by pheromone traps in Germany. Moser *et al.* (1989) listed 24 mite species collected by pheromone traps in Sweden. Penttinen *et al.* (2013) recorded 33 mite species from pheromone traps in Finland and published their SEM micrographs. Moser *et al.* (1997) recorded 12 species of phoretic mites occurring on *I. typographus japonicus*, collected by Borregaard drain-pipe traps in Japan. Gwiazdowicz *et al.* (2011, 2012, 2015) studied mesostigmatic mites associated with *I. typographus* in Poland using Borregaard pipe traps. Vrabec *et al.* (2012) and Čejka and Holuša (2014) also studied mesostigmatic mites in Slovakia (collected manually) and the Czech Republic (collected with pheromone traps), respectively. Wirth *et al.* (2016) compared mite communities associated with *I. typographus* and *I. cembrae* in Croatia (manual sampling in beetles' galleries). Mites associated with *Ips typographus* in Russia are poorly studied. Redikortzev (1947) described *Pediculoides ipidarius* in northwestern Russia. Maslov and Matusевич (2008) reported about eight mite species from European Russia. They also provided information about mortality of bark beetle eggs destroyed by *Dendrolaelaps quadrisetus*. Khaustov (2017a, 2017b, 2017c) and Trach and Khaustov (2017a, b) described several new species and provided new records of heterostigmatic and mesostigmatic mites in Western Siberia, which were collected by pheromone traps as well as in beetle galleries.

During our study of mites, associated with bark beetles in Asian Russia, we recovered 68 species of mites that were phoretic on or inhabited the galleries of the bark beetle *Ips typographus*. The aim of this paper is to document mite-beetle associations and provide diagnostic illustrations of the most common species.

MATERIAL AND METHODS

A total of 13,451 specimens of the European spruce bark beetle, *Ips typographus* were collected in the vicinity of settlement Uspenka, Tyumen Re-

gion, Tyumen District, Russia, 57° 04' N, 65° 04' E. The beetles were collected in May–June 2017 using five flight intercept pheromone traps “Barrier-500” (Pheromone ltd, Moscow, Russia). The collected bark beetles were placed into vials containing 96% ethanol. Then, the beetle specimens and alcohol sediments from the vials were inspected for phoretic mites using a dissecting microscope Discovery V8 (Carl Zeiss, Germany). Galleries of *Ips typographus* from various localities were also examined. For SEM microscopy, live beetles were frozen at –25 °C. Images of beetles with phoretic mites were obtained using a JEOL–JSM-6510LV SEM microscope. The beetles were not dusted. Mites were mounted in Hoyer's medium (Walter and Krantz 2009). The morphology of mites was studied using a Carl Zeiss Axio Imager A2 microscope with DIC and phase-contrast objectives. Photomicrographs were taken with AxioCam 506 color and Hitachi KP-HD20A digital cameras. The studied material was subsequently deposited to the mite collection of the Tyumen State University Museum of Zoology, Tyumen, Russia.

RESULTS

Order Mesostigmata

Infraorder Cercomegistina

Family Cercomegistidae

Cercoleipus kuznetsovi Khaustov, 1997

(Figs. 1A, B, 42A)

Cercoleipus kuznetsovi was described based on adult mites recovered from the galleries of *Ips sexdentatus*, located under the bark of a Crimean pine (*Pinus nigra pallasiana*), in Crimea (Khaustov 1997). Later, *C. kuznetsovi* has been recorded in the galleries of *Ips mannsfeldi* and *Orthotomicus erosus*, located under the bark of an Eldar pine (*Pinus brutia eldarica*), in Iran (Ahadiyat *et al.* 2011; Ostovan *et al.* 2010). Trach and Khaustov (2017a) gave a complete redescription of all instars of this species based on the material from the galleries of *Ips sexdentatus* and *Orthotomicus* sp., associated with Crimean pine in Crimea. The redescription mentioned above was also based on material from the galleries of *Ips typographus* located on a Siberian spruce (*Picea obovata*), in Western Siberia.

Only adult stages of this mite species are phoretic (Fig. 42A). The development of juvenile stages occurs in bark beetle galleries. During phoresy, males and females of *C. kuznetsovi* freely

Fig. 1. A, B—*Cercoleipus kuznetsovi*, female, dorsal and ventral views, respectively, C, D—*Pleuronectocelaeno barbara*, male, ventral and dorsal views, respectively.

move around the host beetle body without attaching to specific sites (Trach and Khaustov 2017a). All our records of this species originated from either beetle hosts or their galleries; no specimens were collected by pheromone traps.

Material examined. Two females, 2 males, 2 deutonymphs, 7 protonymphs, 1 larva, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uспенка, 57° 04'N, 65° 04'E, on *Ips typographus* and in its galleries under the bark of *Picea obovata*, 5 July 2016, coll. A.A. Khaustov.

Infraorder **Antennophorina**

Family **Celaenopsidae**

Pleuronectocelaeno barbara

Athias-Henriot, 1959

(Figs. 1C, D)

This predatory species is distributed in Algeria (Athias-Henriot 1959), North America (Kinn 1968; Moser and Roton 1971), Sweden (Kinn 1991; Moser *et al.* 1989; Sellnick 1951), Denmark, Norway (Kinn 1991), Crimea (Khaustov 1997), Croatia (Pernek *et al.* 2008, 2012), Italy (Plumari 2008), Iran (Ahadiyat *et al.* 2012) and Western Siberia (Khaustov *et al.* 2016). It is associated with many bark beetle species: *Ips acuminatus* (Sellnick 1951), *Pityogenes* sp. (Kinn 1991), *Tomicus minor*, *Hylurgops palliatus*, *Pityogenes bistridentatus*, *Taphrotychus bicolor* (Khaustov 1997), *Pityocheines curvidens* (Pernek *et al.* 2008, 2012), *Crypturgus cinereus* (Plumari 2008), *Orthotomicus erosus* (Ahadiyat *et al.* 2011), *Dendroctonus frontalis*, *Ips avulsus*, *I. calligraphus*, *I. confusus*, *I. grandicollis*, *I. crebricollis*, *I. typographus*, *Orthotomicus sabinianae* (Hofstetter *et al.* 2015), and *Pityogenes chalcographus* (Khaustov *et al.* 2016).

Only adults are phoretic, while juvenile stages develop in the galleries of bark beetles. We did not observe phoresy of *P. barbara* on *I. typographus*. Probably, this species got into the galleries of *I. typographus* from the galleries of other co-occurring bark beetle species, e.g., *Pityogenes chalcographus*.

Material examined. One female, 2 males, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, 3 August 2016, in the galleries of *Ips typographus* under bark of Siberian spruce (*Picea obovata*), coll. A.A. Khaustov.

***Pleuronectocelaeno japonica* Kinn, 1991**

(Figs. 2A, B)

Pleuronectocelaeno japonica was described from *Ips typographus japonicus*, recovered from pheromone traps in Japan (Kinn 1991; Moser *et al.* 1997). This mite also occurs on bark beetles *Pityocheines curvidens* that live on Silver firs (*Abies alba*) in Croatia (Pernek *et al.* 2008).

Ours is the first record of *P. japonica* in Russia. Previously, *P. japonica* has never been reported in association with *Ips typographus typographus*.

Material examined. One male, Russia, Primorsky Krai, Lazo, 43° 30' 04.6" N, 133° 34' 47.1" E,

28 August 2016, in the galleries of *Ips typographus* under the bark of a Korean spruce *Picea koraiensis*, coll. A.A. Khaustov.

Infraorder **Uropodina**

Family **Urodinychidae**

***Uroobovella ipidis* (Vitzthum, 1923)**

(Figs. 2C, D, 37F, 38A–D, 39A)

This species is known from Austria, Germany, Poland, Croatia, Russia, Lebanon, Slovakia (Mašán 2001), Sweden (Moser *et al.* 1989), Czech Republic (Čejka and Holuša 2014), Bulgaria (Takov *et al.* 2009) and Spain (Fernández *et al.* 2013). Deutonymphs of this species are phoretic on various bark beetles: *Ips typographus* (Čejka and Holuša 2014; Feketeová 2011; Gwiazdowicz *et al.* 2012; Moser and Bogenschütz 1984; Moser *et al.* 1989; Takov *et al.* 2009; Vrabec *et al.* 2012), *Ips sexdentatus* (Fernández *et al.* 2013), *Hylastes cunicularius* (Kršlak *et al.* 2010), *Pityocheines curvidens*, *P. spinidens*, *P. worontzowi* (Pernek *et al.* 2008, 2012), and *Pityogenes chalcographus* (Khaustov *et al.* 2016; Zach *et al.* 2016).

In our study, this was one of the most abundant species. It is usually phoretic on elytral declivities and the ventral thoraxes of coleopteran hosts (Figs. 38A–D, 39A).

Material examined: 893 deutonymphs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 1,009 deutonymphs, same locality, 28 May 2017; 656 deutonymphs, same locality, 5 June 2017; 117 deutonymphs, same locality, 14 June 2017; 54 deutonymphs, same locality, 16 June 2017.

Family **Trematuridae**

***Trichouropoda polytricha*
(Vitzthum, 1923)**

(Fig. 3A, B, 38A)

This species is known from Germany, the Czech Republic, Slovakia, Turkmenistan (Mašán 2001), Sweden (Moser *et al.* 1989), Austria (Kofler and Schmölzer 2000); Poland (Gwiazdowicz and Gutowski 2012), Slovenia (Moraza *et al.* 2013), Finland (Penttinen *et al.* 2013), Spain (Fernández *et al.* 2013), Switzerland, Turkey,

Fig. 2. A, B—*Pleuronectocelaeno japonica*, male, dorsal and ventral views, respectively, C, D—*Uroobovella ipidis*, deutonymph, dorsal and ventral views, respectively.

Canada, USA (Knee *et al.* 2013), Mexico (Chaires-Grijalva *et al.* 2013), Bulgaria (Takov *et al.* 2009) and Russia (Khaustov *et al.* 2016). Deutonymphs of this species are phoretic on various bark beetles: *Ips typographus* (Čejka and Holuša 2014; Feketeová 2011; Fernández *et al.* 2013; Gwiazdowicz and Gutowski 2012; Gwiazdowicz *et al.* 2011; Knee *et al.* 2013; Moser and Bogenschütz 1984; Moser *et al.* 1989; Penttinen *et al.* 2013; Takov *et al.* 2009; Vrabec *et al.* 2012), *Ips sexdentatus* (Fernández *et al.* 2013), *Hylastes*

cunicularius (Kršlak *et al.* 2010), *Dryocoetes autographus*, *Hylurgors palliatus*, *Ips amitinus*, *I. cembrae*, *I. hauseri*, *I. pilifrons utahensis*, *I. woodi*, *I. montanus*, *I. perturbatus*, *I. hunteri*, *I. borealis*, *Pityogenes chalcographus* (Khaustov *et al.* 2016; Knee *et al.* 2013), and *Dendroctonus rhizophagus* (Chaires-Grijalva *et al.* 2013).

In our study, *T. polytricha* was one of the most abundant species (Table 1). It is usually phoretic on elytral declivities of hosts (Figs. 38A).

Fig. 3. A, B—*Trichouropoda polytricha*, deutonymph, dorsal and ventral views, respectively, C, D—*Trichouropoda karawaiewi*, deutonymph, dorsal and ventral views, respectively.

Material examined: 633 deutonymphs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 22 May 2017, coll.

A.A. Khaustov; 415 deutonymphs, same locality, 28 May 2017; 441 deutonymphs, same locality, 5 June 2017; 56 deutonymphs, same locality, 14 June 2017; 161 deutonymphs, same locality, 16 June 2017.

***Trichouropoda karawaiewi* (Berlese, 1904)**

(Figs. 3C, D, 38E, F)

This species is known from the Eastern and Central Europe (Berlese 1903 (1904); Mašán 2001). It has been recorded from various nests of birds and ants, as well as under the bark of dead trees (Mašán 2001). Vrabec *et al.* (2012) reported this species being phoretic on *I. typographus* in Slovakia.

In our study, deutonymphs of *T. karawaiewi* were found to be phoretic on *Ips typographus*. Adults of *T. karawaiewi* were abundant in the galleries of *I. typographus*. This is the first record of *T. karawaiewi* in Russia.

Material examined. Five females, 2 males, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, 22 April–5 May 2016, in the galleries of *Ips typographus*, coll. A.A. Khaustov; 1 deutonymph, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, on *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 12 deutonymphs, same locality, 28 May 2017; 10 deutonymphs, same locality, 5 June 2017; 5 deutonymphs, same locality, 14 June 2017.

Trichouropoda structura**Hirschmann and Zirngiebl-Nicol, 1961**

(Figs. 4A, B)

This species has been recorded in Germany, Poland, Slovakia, and Russia (Siberia) (Mašán 2001). Deutonymphs of this species have been reported to be phoretic on *Thanasimus* sp. (Cleridae). This species was also found in the galleries of *Pityogenes chalcographus* (Curculionidae: Scolytinae) (Kiełczewski and Wiśniewski 1983).

In our study, *T. structura* was a rare species (Table 1). Apparently, it is not associated with *I. typographus* and probably got into our pheromone traps accidentally, with other beetles.

Material examined. Two deutonymphs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 28 May 2017, coll. A.A. Khaustov.

Infraorder **Gamasina**Family **Parasitidae*****Schizosthetus* sp.**

(Figs. 4C, D)

Three species of the genus *Schizosthetus* Athias-Henriot, 1982 have been described: *Sch. lyriformis*

(McGraw and Farrier 1969) from North and Central Americas; *Sch. vicarius* Athias-Henriot, 1982 from North America; and *Sch. simulatrix* Athias-Henriot, 1982 from the Canary Islands and Portugal (Athias-Henriot 1982). In North and Central America, *Sch. lyriformis* is associated with *Ips avulsus*, *I. calligraphus*, *I. confusus*, *I. grandicollis*, *Dendroctonus brevicornis*, *D. frontalis*, *D. simplex*, *D. valens*, *Onthotomicus latidens*. *Sch. lyriformis* preys on the eggs and larvae of bark beetles (Hofstetter *et al.* 2009). Al-Atawi *et al.* (2002) redescribed this species based on all instars. Kalúz *et al.* (2003) redescribed *Sch. simulatrix* based on material from Slovakia, Germany, Sweden, and France. These authors re-examined specimens of *Vulgarogamasus* sp., which were previously reported as associates of bark beetles *Ips sexdentatus* in France (Lieutier 1978) and of *Ips typographus* in Germany (Moser and Bogenschütz 1984) and Sweden (Moser *et al.* 1989). Kalúz *et al.* (2003) identified them as *Sch. simulatrix*. The authors also suggested that specimens identified as *Parasitus* (*Vulgarogamasus*) *lyriformis* in northern Russia (Arkhangelsk) (Tichomirov 1977) and South Siberia (Altai Republic) (Davydova and Nikolskii 1986) also belonged to *Sch. simulatrix*. Plumari (2008) recorded nymphs and adults of *Sch. simulatrix* in Italy in the galleries of bark beetles *Crypturgus cribellus*, *Crypturgus mediterraneus*, *Xyleborinus saxesenii*, and weevils *Brachytemnus porcatus* and *Dryophthorus corticalis*. This mite species has also been recorded in Croatia on *Pityocheilus curvidens* (Pernek *et al.* 2008, 2012) and in Latvia on *Hylurgops palliatus* (Salmane and Telnov 2009). *Sch. vicarius* Athias-Henriot, 1982 is known only from the type series discovered in the moss and soil on the trunk of a *Pseudotsuga menziesii*. We have previously reported deutonymphs of *Schizosthetus* sp. on *Pityogenes chalcographus* in Western Siberia (Khaustov *et al.* 2016).

In our study, we have documented the phoresy of *Schizosthetus* sp.'s deutonymphs on *Ips typographus*. Only two species of the genus *Schizosthetus* are known from deutonymphs (*Sch. lyriformis* and *Sch. simulatrix*), so the correct determination could only be possible after studying adult mites. Deutonymphs of *Schizosthetus* have no preference for a specific attachment site on the bark beetle host; during phoresy, they move freely across a beetle's body.

Material examined. Three deutonymphs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in

Fig. 4. A, B—*Trichouropoda structura*, deutonymph, dorsal and ventral views, respectively, C, D—*Schizosthetus* sp., deutonymph, dorsal and ventral views, respectively.

alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 8 deutonymphs, same locality, 28 May 2017; 1 deutonymph, same locality, 5 June 2017.

Family Digamasellidae

***Dendrolaelaps (Ipidodendrolaelaps) quadrisetus* (Berlese, 1920)**

(Figs. 5A, B, 41A–C, 43A)

Deutonymphs of *Dendrolaelaps quadrisetus* were described based on specimens obtained from

Fig. 5. A, B—*Dendrolaelaps quadrisetus*, deutonymph, dorsal and ventral views, respectively, C, D—*Dendrolaelaps pini*, deutonymph, dorsal and ventral views, respectively.

the bark of a coniferous tree lying on the ground (Berlese 1920 (1921)). This species has been recorded in the Palaearctic (widely distributed in Europe, known in Algeria, Asian Russia, and Japan), the Nearctic (USA, Canada, Mexico) and the Neotropics (Guatemala) (Chaires-Grijalva *et al.*

2013; Hirschmann and Wiśniewski 1982; Knee *et al.* 2013; Shcherbak 1980). Mites were found in association with *Dendroctonus frontalis*, *D. pseudotsugae*, *D. valens*, *Gnathotrichus materarius*, *Ips avulsus*, *I. calligraphus*, *I. confusus*, *I. emarginatus*, *I. grandicollis*, *I. pini*, *I. ponderosa*, *Orthotomicus*

latidens, *Pachylobius picivorus* in the USA (Hunter and Davis 1963; Hurlbutt 1967; Knee *et al.* 2013; Moser and Roton 1971; Pfammatter *et al.* 2016); *Ips typographus* in Germany (Moser and Bogen-schütz 1984); *Ips typographus japonicus* in Japan (Moser *et al.* 1997); *Crypturgus cinereus*, *Dryocoetes autographus*, *Hylastes opacus*, *Hylestinus varius*, *Hylurgops glabratus*, *H. palliatus*, *Ips acuminatus*, *I. amitinus*, *I. cembrae*, *I. typographus*, *Pityogenes chalcographus*, *Pityokteines curvidens*, *P. vorontzowi*, *Polygraphus poligraphus*, *Scolytus intricatus*, *S. ratzeburgii*, *Tomicus minor*, *T. piniperda*, *Xyleborus cryptographus* in Poland (Gwiazdowicz 2008); *P. curvidens*, *P. spinidens*, *P. vorontzowi*, *I. cembrae*, *I. typographus* in Croatia (Pernek *et al.* 2008, 2012; Wirth *et al.* 2016); *I. typographus* in Bulgaria (Takov *et al.* 2009); *I. typographus* in Slovakia (Vrabec *et al.* 2012); *Ips sexdentatus* in Slovenia (Moraza *et al.* 2013); *I. typographus* in Finland (Penttinen *et al.* 2013); *I. typographus* in the Czech Republic (Čejka and Holuša 2014); *I. typographus* in Romania (Poliță *et al.* 2016). In Russia, this species is known from the Arkhangelsk Region and Primorsky Krai (Shcherbak 1980). The biology of *D. quadrisetus* was studied in detail by Kinn (1967), who has noted that in view of its predaceous habits, this mite may have an important role in controlling bark beetle populations. We have observed *D. quadrisetus* deutonymphs feeding on the eggs of *Ips typographus*. During this process, the mite deutonymphs have significantly increased in size (Fig. 43A). Deutonymphs of *D. quadrisetus* are usually phoretic on the elytral declivities (Figs. 41A, B) or under the elytra of bark beetles.

This is the first record of *D. quadrisetus* in Western Siberia and on the Kuril Islands.

Material examined. One deutonymph, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, 5 May 2017, on *Ips typographus* collected under the bark of Siberian spruce (*Picea obovata*), coll. A.A. Khaustov; 1 deutonymph, same locality, 26 July 2016, in alcohol sediments containing numerous specimens of *I. typographus* collected by pheromone traps, coll. A.A. Khaustov; 4 females, 1 male, same locality, 27 July 2016, in galleries of *I. typographus* under the bark of Siberian spruce, coll. A.A. Khaustov; 5 deutonymphs, Russia, Primorsky Krai, Lazo, 43° 30' 04.6" N, 133° 34' 47.1" E, 28 August 2016, in the galleries of *Ips typographus* under the bark of Korean spruce *Picea koraiensis*, coll. A.A. Khaustov; 1,990 deutonymphs, Russia, Tyumen Region,

Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 628 deutonymphs, same locality, 28 May 2017; 1,274 deutonymphs, same locality, 5 June 2017; 295 deutonymphs, same locality, 14 June 2017; 126 deutonymphs, same locality, 16 June 2017; 5 deutonymphs, Russia, Kunashir Island, on *Ips typographus japonicus*, 5 August 2017, coll. A.A. Khaustov.

***Dendrolaelaps (Insectolaelaps) pini* Hirschmann, 1960**

(Figs. 5C, D)

Dendrolaelaps pini was described based on specimens obtained from bark beetles *Hylurgus ligniperda* and *Hylastes* sp. discovered on pine trees in Germany (Hirschmann 1960). Skorupski and Gwiazdowicz (1996) recorded this species on specimens recovered through alcohol washing of the contents of *Ips typographus* pheromone traps in Poland. Salmane (2005) reported this species in Latvia on multiple species of polypore fungi. The record of *D. pini* from the former USSR by Shcherbak (1980) refers to another species, *D. lato-pini* Hirschmann and Wisniewski, 1982 (Hirschmann and Wiśniewski 1982).

D. pini is new for the fauna of Russia.

Material examined. Three deutonymphs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov.

***Dendrolaelaps (Apophyseodendrolaelaps) disetosimilis* Hirschmann, 1960**

(Figs. 6A, B)

This species was described from Germany as an associate of *Dryocoetes autographus* (Hirschmann 1960). Shcherbak (1980) reported this species in Russia (Novosibirsk Region, Kamchatka Region) and Ukraine. *Dendrolaelaps disetosimilis* has been recovered from the nest of a European sand martin (*Riparia riparia*) in Ukraine (Shcherbak and Balan 1982); under the bark of the Scots pine (*Pinus sylvestris*) infested by *Hylurgops palliatus* in Latvia (Salmane 2006). This species was recorded in association with bark beetles: *Cryphalus piceae*, *Dryocoetes autogra-*

Fig. 6. A, B—*Dendrolaelaps disetosimilis*, female, dorsal and ventral views, respectively, C, D—*Macrocheles ivanovi*, female, dorsal and ventral views, respectively.

phus, *Hylurgops glabratus*, *H. palliatus*, *H. ligniperda*, *Ips amitinus*, *I. cembrae*, *I. typographus*, *Orthotomicus laricis*, *Pityogenes chalcographus*, *Pityokteines curvidens*, *P. spinidens*, *P. vorontzovi*, *Polygraphus poligraphus*, *Tomicus piniperda* in Poland (Gwiazdowicz 2008). It was also

recorded in the soil of Central Yakutia (Russia) (Aleksiev *et al.* 2011).

Material examined. Two females, one male, Russia, Sakhalin Island, in the galleries of *I. typographus* under the bark of Sakhalin spruce *Picea glehnii*, 46° 47' 04.9" N, 142° 23' 13.0" E, coll. A.A. Khaustov.

Family Macrochelidae

***Macrocheles* (s. str.) *ivanovi* Bregetova and Koroleva, 1960**

(Figs. 6C, D, 41D–F)

This species was described based on samples obtained from a rotten spruce tree in western Russia (Leningrad Region), as well as from a striped field mouse (*Apodemus agrarius*) in eastern Russia (Primorsky Krai) (Bregetova and Koroleva 1960). These mites also occur in the galleries of *Dryocoetes* sp. in pine branches in Germany (Bregetova 1977b; Hirschmann 1970).

Previously, *Macrocheles ivanovi* had never been reported as an associate of *Ips typographus*. We did not observe phoresy of this species on *I. typographus*.

Material examined. One female, 2 deutonymphs, Russia, Primorsky Krai, Lazo, 43° 30' 04.6" N, 133° 34' 47.1" E, 28 August 2016, in the galleries of *Ips typographus* under the bark of Korean spruce *Picea koraiensis*, coll. A.A. Khaustov; 2 females, Tomsk Region, vicinity of Tomsk, in the galleries of *Ips typographus* under the bark of Siberian spruce *Picea obovata*, 16 September 2017, 56° 18' 56.7" N, 085° 10' 36.9" E, coll. A.A. Khaustov.

Family Ascidae

***Gamasellodes tatricus* Gwiazdowicz and Walter, 2005**

(Figs. 7A, B)

Gamasellodes tatricus was described based on specimens obtained from forest litter in the Tatra National Park in Poland (Gwiazdowicz and Walter 2005). It has never been recollected since. Other species of the genus *Gamasellodes* have been recovered from soil, litter, humus, sod, debris, plants, ant nests, and bark beetle galleries. *Gamasellodes rectiventris* Lindquist, 1971 was described based on specimens recovered from *Dendroctonus frontalis* 'boring dust, which was discovered under the bark of a Loblolly pine (*Pinus taeda*). *G. rectiventris* specimens were also obtained from the inner bark of *P. taeda*, from which *D. frontalis* emerged. Finally, *G. rectiventris* specimens were obtained from under the bark of *P. taeda*, from which *Ips avulsus* and *I. calligraphus* emerged (De Moraes *et al.* 2016; Lindquist 1971). *Gamasellodes bicolor* (Berlese, 1918) and *G. insignis* (Hirschmann, 1962) were also found in the galleries of bark beetles (Gwiazdowicz 2007; Hurlbutt 1971; Kiełczewski and Wiśniewski 1983; Walter 1987).

Previously, *Gamasellodes* has never been reported as a phoretic mite. This is the first record of *G. tatricus* in Russia.

Material examined. One female, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, 28 May 2017, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, coll. A.A. Khaustov.

Family Melicharidae

***Proctolaelaps fiseri* Samšiňák, 1960**

(Figs. 7C, D)

This species was identified in Slovakia, in association with *Ips typographus* (Samšiňák 1960). This predatory species is widely distributed in the Holarctic, where it is associated with various subcortical beetles, especially bark beetles (Hofstetter *et al.* 2015). Westerboer (1963) recorded *P. fiseri* in Germany as an associate of several species of bark beetles (*I. typographus*, *Hylurgops palliatus*, *Dryocoetes autographus*, *Tomicus piniperda*, *Pityokteines curvidens*, *Ernoporicus fagi*), as well as of a cerambycid beetle *Spondylis buprestoides*. In the USA, Lindquist and Hunter (1965) reported *P. fiseri* in the galleries of *Ips calligraphus*; Moser (1975)—in the galleries of *Dendroctonus frontalis*; Knee *et al.* (2013)—in the galleries of *Hylastes porculus*. *P. fiseri* has also been recorded in Latvia on a dead pine that was inhabited by *Hylurgops palliatus* (Salmane 2007). *P. fiseri* was also recovered in the galleries of *I. typographus* in Finland (Penttinen *et al.* 2013). Gwiazdowicz (2008) also identified this mite in Poland as an associate of 38 species of bark beetles. Furthermore, it has been recorded in European Russia in the galleries of *I. typographus* (Maslov and Matusевич 2008) and in Western Siberia (Davydova and Nikolskii 1986). We have previously reported this species in association with *Polygraphus proximus*, *P. subopacus*, *Ips typographus*, *I. typographus japonicus*, *Hylurgops glabratus*, *Ips acuminatus*, and *Tetropium* sp. (Cerambycidae) in Asian Russia (Trach and Khaustov 2017b). Our erroneous identification of *P. fiseri* on *Pityogenes chalcographus* in Western Siberia is corrected here to *Proctolaelaps hystricoides* Lindquist and Hunter, 1965 (Khaustov *et al.* 2016; Trach and Khaustov 2017b) (see below).

Females of *P. fiseri* have no specific attachment sites for phoresy on bark beetles; they freely move across a beetle's body during phoresy.

Fig. 7. A, B—*Gamasellodes tatricus*, female, dorsal and ventral views, respectively, C, D—*Proctolaelaps fiseri*, female, dorsal and ventral views, respectively.

Material examined. One female, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, 14 July 2016, in galleries of *Ips typographus* under the bark of Siberian spruce (*Picea obovata*), coll. A.A. Khaustov; 5 females, same locality, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, 5 June 2017; 4 females, Russia, Sakhalin Region, Sakhalin Island, on *Ips typographus* and in its galleries under the bark of Sakhalin spruce (*Picea glehnii*), 46° 47' 04.9" N, 142° 23' 13.0" E, 13 August 2017, coll. A.A. Khaustov.

***Proctolaelaps hystricoides*
Lindquist and Hunter, 1965**

(Figs. 8A, B)

The type series of *P. hystricoides* originated from the galleries of *Orthotomicus caelatus*, *Dendroctonus monticolae*, *Trypodendron rufitarsis* and *Ips calligraphus* under the bark of different species of pine trees in Canada and the USA (Lindquist and Hunter 1965). This species has also been recorded in the galleries of *Dendroctonus frontalis* in the USA (Moser 1975; Moser and Roton 1971).

Fig. 8. A, B—*Proctolaelaps hystricoides*, female, dorsal and ventral views, respectively, C, D—*Proctolaelaps juradeus*, female, dorsal and ventral views, respectively.

Later, this species was recorded in soil from Iran (Kazemi and Rajaei 2013). Haddad Irani Nejad *et al.* (2001) reported this species in cotton fields in Iran. These mites also occur on bark beetles *Pityokteines* spp. that inhabit Silver fir (*Abies alba*) in Croatia (Pernek *et al.* 2008). We previously re-

ported this species associated with *Pityogenes chalcographus*, *Polygraphus proximus*, *Hylurgops glabratus*, *Ips subelongatus* and *I. typographus* in Asian Russia (Trach and Khaustov 2017b).

Material examined. One female, Russia, Tyumen Region, Tyumen District, vicinity of settle-

ment Uspenka, 57° 04' N, 65° 04' E, 5 July 2017, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, coll. A.A. Khaustov.

***Proctolaelaps jueradeus* (Schweizer, 1949)**

(Figs. 8C, D)

This species is widely distributed in the Holarctic (including Russia) in association with soil and related substrates (Bregetova 1977a; Chant 1963; Evans 1958; Gwiazdowicz 2007; Karg 1993; Makarova 2012; Marchenko 2002, 2012; Salmane 2001; Schweizer 1949; Westerboer 1963). Once it has been recorded in the galleries of an unknown bark beetle species in Poland (Gwiazdowicz 2007). We collected *P. jueradeus* in the sediments produced in the process of alcohol washing of *Ips typographus* (Trach and Khaustov 2017b).

Phoresy of *P. jueradeus* has never been reported previously.

Material examined. One female, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, 22 May 2017, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, coll. A.A. Khaustov.

Order **Trombidiformes**
Suborder **Prostigmata**
Family **Ereynetidae**

Ereynetes (Huntereynetes) sp.

(Figs. 9A, B)

This species has been reported as *Ereynetes scutulis* Hunter, 1964, *E. near scutulis* and *E. propescutulis* Hunter and Rosario, 1989 in several localities in Europe in associations with various bark beetles (Moser *et al.* 1989; Penttinen *et al.* 2013; Pernek *et al.* 2008). Our specimens differ from *E. scutulis* by distinctly longer (but shorter than those in *E. propescutulis*) dorsal idiosomal setae, and they may represent an undescribed species. This species is abundant in the galleries of *Ips typographus*; however, it is very difficult to collect because it is one of the fastest mites.

This species has no specific attachment sites on hosts; it actively moves around the beetle's body during phoresy.

Material examined. One female, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments

containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 3 females, same locality, 28 May 2017; 7 females, same locality, 5 June 2017; 2 females, same locality, 16 June 2017.

Family **Cheyletidae**

***Mexeches virginiensis* (Baker, 1949)**

(Figs. 9C, D)

This species was described in the USA (Virginia) (Baker 1949). Later, it has been recorded in various other localities in North America: USA (Alabama, Louisiana, Mississippi, Nevada, and Utah), Canada and Honduras (Smiley and Moser 1970; Summers and Price 1970). In the Old World, it has been recently recorded in Finland as an associate of *Ips typographus* (Penttinen *et al.* 2013) and in European Russia (Bochkov and Abramov 2016). This is a new record of this species in the Asian part of Russia.

The attachment site of this species on beetles is unknown. We collected females of *M. virginiensis* only in the alcohol sediments and in galleries.

Material examined. One female, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 5 June 2017, coll. A.A. Khaustov; 1 female, same locality, in the galleries of *I. typographus*, 5 July 2016; 1 male, same locality, in the galleries of *I. typographus*, 3 August 2016.

Family **Dolichocybidae**

***Dolichocybe sibiriensis* Khaustov, 2017**

(Figs. 10A, B)

This species was described in Western Siberia, where it was recovered from alcohol washing of the contents of *Ips typographus* pheromone traps (Khaustov 2017c).

The attachment site of this species on beetles is unknown. We collected females of *D. sibiriensis* only in alcohol sediments.

Material examined. Three females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov.

Fig. 9. A, B—*Ereyntes* sp., female, dorsal and ventral views, respectively, C, D—*Mexecheles virginiensis*, female, dorsal and ventral views, respectively.

Family Pyemotidae

Pyemotes sp.

(Figs. 10C, D)

Only one female of an undetermined species belonging to the *ventricosus* species-group was

collected. In this species group, identification of species is only possible using males (Cross *et al.* 1981). Mites of the *ventricosus* group attack a wide range of prey, e.g., small larvae of Lepidoptera, Hymenoptera and Coleoptera, including juvenile stages of bark beetles (Khaustov 1998). Mites of

Fig. 10. A, B—*Dolichocybe sibiriensis*, female, dorsal and ventral views, respectively, C, D—*Pyemotes* sp., female, dorsal and ventral views, respectively.

the *ventricosus* species-group could be dispersed by wind.

Material examined. One female, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 5 June 2017, coll. A.A. Khaustov.

Family Acarophenacidae

Aethiophenax ipidarius (Redikortzev, 1947)

(Figs. 11A, B, 36A–D, 43B)

This species was described in central Russia, where it was recovered from *Ips typographus* (Redikortzev 1947). It has also been recorded in Finland, Poland, Germany and Sweden as an associate of *Ips typographus* (Kiełczewski and Wiśniewski 1983; Moser and Bogenschütz 1984;

Fig. 11. A, B—*Aethiophenax ipidarius*, female, dorsal and ventral views, respectively, C, D—*Microdispodides moseri*, female, dorsal and ventral views, respectively.

Moser *et al.* 1989; Penttinen *et al.* 2013). Cross and Moser (1971) reported this species in North America (Ontario and California). Khaustov (1999) redescribed this species based on specimens collected in northwestern Russia from bark beetles *Ips typographus*, *I. amitinus*, and *Ortho-*

tomicus laricis. It has recently been recorded in Western Siberia in association with *Ips typographus* and *I. sexdentatus* (Khaustov *et al.* 2017). The biology of *Ae. ipidarius* is unknown, but all members of the family Acarophenacidae are egg parasitoids of various insects (Kaliszewski *et al.*

1995), and this species is probably a parasitoid of bark beetle eggs.

Females of this mite usually attach to the area between the coxae of *I. typographus* (Figs. 36A–D, 9B). One or two females are phoretic on one beetle, but in some cases, up to 15 females can be found on one beetle (Fig. 43B).

Material examined. Ten females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 5 females, same locality, 28 May 2017; 3 females, same locality, 5 June 2017; 3 females, same locality, 14 June 2017; 3 females, Tomsk Region, vicinity of Tomsk, 56° 18' 56.7" N, 085° 10' 36.9" E, on *Ips typographus*, 31 May 1916, coll. A.A. Khaustov.

Family Pygmephoridae

***Microdispodides moseri* Khaustov, 2018**

(Figs. 11C, D)

This species was described in Western Siberia, where it was recovered through alcohol washing of the contents of *Ips typographus* traps (Khaustov 2018).

The attachment site of this species on beetles is unknown. We collected females of *M. moseri* only in the alcohol sediments.

Material examined. Two females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, 16 June 2017, coll. A.A. Khaustov.

***Elattoma crossi* Khaustov, 2000**

(Figs. 12A, B, 35A–C)

This species was described based on specimens collected in European Russia, where they were associated with the *Ips duplicatus* (Sahlberg) bark beetle (Khaustov 2000b). This species has been recently recorded on *Ips typographus*, in Western Siberia (Khaustov 2017b).

During phoresy, females of this species attach between the coxae of a beetle (Figs. 35A, B).

Material examined. 35 females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* col-

lected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 23 females, same locality, 28 May 2017; 5 females, same locality, 5 June 2017.

Family Neopygmephoridae

***Coleopygmephorus bogenschutzi* (Mahunka and Moser, 1982)**

(Figs. 12C, D)

This species was originally described as belonging to the *Pseudopygmephorus* genus Cross, 1965 in Germany, recovered from *Ips typographus* (Mahunka and Moser 1982). It was recently redescribed and placed into the genus *Coleopygmephorus* Khaustov and Mandelshtam, 2016 based on material from *Ips typographus* in Western Siberia (Khaustov 2017b).

The attachment site of this species on the beetle is unknown. We collected females of *C. bogenschutzi* only in the alcohol sediments.

Material examined. Two females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 1 female, same locality, 5 June 2017.

***Coleopygmephorus hylophilus* (Cooreman, 1963)**

(Figs. 13A, B)

This species was originally described based on specimens from Belgium, as an associate of bark beetles *Hylastes ater* and *H. cunicularius* (Cooreman 1963). It had been redescribed based on a specimen phoretic on *Hylastes ater* in Crimea (Khaustov 2017a). *Coleopygmephorus hylophilus* has also been recorded in Germany, where this species was phoretic on *Ips typographus* (Moser and Bogenschütz 1984). Khaustov (2017b) has recently recorded this species in Western Siberia, on *I. typographus*.

The attachment site of this species on the beetle is unknown. We collected females of *C. hylophilus* only in the alcohol sediments.

Material examined. Twenty seven females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 5 females, same locality, 28 May 2017; 2 females, same locality, 14 June 2017.

Fig. 12. A, B—*Elattoma crossi*, female, dorsal and ventral views, respectively, C, D—*Coleopygmephorus bogenschutzi*, female, dorsal and ventral views, respectively.

***Coleopygmephorus typographus*
Khaustov, 2017**

(Figs. 13C, D)

This species was described based on specimens from Western Siberia (Khaustov 2017a),

where it was an associate of bark beetle *Ips typographus*.

The attachment site of this species on the beetle is unknown. We collected females of *C. typographus* only in the alcohol sediments.

Fig. 13. A, B—*Coleopygmephorus hylophilus*, female, dorsal and ventral views, respectively, C, D—*Coleopygmephorus typographus*, female, dorsal and ventral views, respectively.

Material examined. Three females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus*

collected by pheromone traps, 24 June 2016, coll. A.A. Khaustov; 1 female, same locality, 16 June 2017.

Family Scutacaridae

***Scutacarus pseudoplurisetus* Khaustov, 2017**

(Figs. 14A, B)

This species was described based on specimens from Western Siberia (Khaustov 2017b), where it was associated with *Ips typographus*.

The attachment site of this species on the beetle is unknown. We collected females of *S. pseudoplurisetus* only in the alcohol sediments.

Material examined. Two females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov.

***Scutacarus scolyti* Mahunka and Moser, 1980**

(Figs. 14C, D, 35D–F)

This species was described based on specimens from Germany (Mahunka and Moser 1980), where these mites were phoretic on *Ips typographus*. It has also been recorded in European Russia, where the mites were recovered from the galleries of *Pityogenes chalcographus* (Khaustov 2008); and in Western Siberia, where the mites were discovered on *I. typographus* (Khaustov 2017b).

Phoretic females usually attach between the coxae of the host beetle (Figs. 35D, E).

Material examined. Eight females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 28 May 2017, coll. A.A. Khaustov; 5 females, Russia, Tomsk Region, vicinity of settlement Zavarzino, 56° 27' 55.7" N, 085° 06' 55.6" E, on the *Ips typographus* under the bark of *Picea obovata*, 28 April 2017, coll. A.A. Khaustov.

***Scutacarus muscocolica* Sevastianov, 1983**

(Figs. 15A, B)

This species was described based on specimens that came from mosses in Eastern Siberia (Sevastianov 1983). It has also been recorded in Ukraine (Khaustov 2008) and Hungary (Dobrev and Mahunka 1991). We collected it in Western Siberia in

alcohol sediments containing *Ips typographus* (Khaustov 2017b).

The attachment site of this species on the beetle is unknown. We collected females of *S. muscocolica* only in the alcohol sediments.

Material examined. Three females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov.

***Scutacarus palustris* Rack, 1966**

(Figs. 15C, D)

This species is known from Germany, Austria, Hungary, France, Ireland, Lithuania, USA, India, and Ukraine (Khaustov 2008). Usually it inhabits wet soil and forest litter. Previously, it has never been recorded as an associate of any insect. This is the first record of this species in Russia.

The attachment site of this species on the beetle is unknown. We collected females of *S. palustris* only in the alcohol sediments.

Material examined. One female, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, 5 June 2017, coll. A.A. Khaustov; 6 female, same locality, 14 June 2017.

Family Tarsonemidae

***Iponemus gaebleri gaebleri* (Schaarschmidt, 1959)**

(Figs. 16A, B, 36E, F, 39A–D, 42B, 43C, D)

This species was described based on specimens from Germany, as an associate of *Ips typographus* (Schaarschmidt 1959). It has also been recorded in Austria, Poland, Switzerland, Sweden, and Japan, as an associate of *Ips typographus* (Lindquist 1969; Moser and Bogenschütz 1984; Moser *et al.* 1989; Moser *et al.* 1997). In Canada and the USA, this species is known in association with *Ips borealis*, *I. perterbatus*, *I. engelmanni*, *I. oregonis*, *I. swain-ei*, *I. hunter*, *I. pilifrons*, *I. utahensis*, and *Orthotomicus* sp. (Lindquist 1969). It has also been reported in Western Siberia, as an associate of *Ips typographus* and *I. duplicatus* (Khaustov *et al.* 2017). *Iponemus gaebleri* is a parasitoid of bark beetles' eggs, which affects the population of bark beetles (Figs. 42B, 43C, D). According to Balazy

Fig. 14. A, B—*Scutacarus pseudoplurisetus*, female, dorsal and ventral views, respectively, C, D—*Scutacarus scolyti*, female, dorsal and ventral views, respectively.

and Kielczewski (1965), in Poland, the egg mortality due to *I. gaebleri* varies from less than 1% to 10%. Our study of egg mortality of *I. typographus* in the Tyumen Region confirms these data.

We collected numerous females attached to the elytral declivity of *I. typographus* (Figs. 36E, F, 39A–D,). However, some specimens can be phoretic under the elytra of the beetles.

Material examined: 828 females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of *Ips*

typographus collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 766 females, same locality, 28 May 2017; 231 females, same locality, 5 June 2017; 34 females, same locality, 14 June 2017, 12 females, same locality, 16 June 2017.

***Tarsonemus (s. str.) striatus*
Khaustov, 2017**

(Figs. 16C, D)

This species, belonging to a *minimax* species-group, has recently been described in the Far East

Fig. 15. A, B—*Scutacarus muscoticola*, female, dorsal and ventral views, respectively, C, D—*Scutacarus palustris*, female, dorsal and ventral views, respectively.

of Russia, where these mites were collected from the galleries of and phoretic on the four-eyed bark beetle, *Polygraphus proximus* (Khaustov 2017d). This is the first record of *T. striatus* in association with *Ips typographus*.

Females of *T. striatus* usually attach to the areas between the coxae of bark beetles (Khaustov 2017d).

Material examined. 30 females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol

Fig. 16. A, B—*Iponemus gaebleri*, female, dorsal and ventral views, respectively, C, D—*Tarsonemus striatus*, female, dorsal and ventral views, respectively.

sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 7 females, same locality, 14 June 2017, 12 females, same locality, 16 June 2017.

***Tarsonemus* (s. str.) *typographi*
Magowski and Moser, 2003**

(Figs. 17C, D)

This species, belonging to a *minimax* species-group, was described in Germany and Sweden, where it was phoretic on *Ips typographus* (Ma-

gowski and Moser 2003). This is the first record of *T. typographi* in Russia.

The attachment site of this species on the beetle is unknown. We collected females of *S. palustris* only in the alcohol sediments.

Material examined. 13 females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 24 females, same locality, 5 June 2017; 1 female, same locality, 14 June 2017.

Fig. 17. A, B—*Tarsonemus bistridentati*, female, dorsal and ventral views, respectively, C, D—*Tarsonemus typographi*, female, dorsal and ventral views, respectively.

***Tarsonemus* (Schaarschmidtia)
bistridentati Magowski and Khaustov, 2006**

(Figs. 17A, B)

This species was described in Crimea, in the galleries of *Pityogenes bistridentatus* (Magowski

and Khaustov 2006). It has also been recorded in Poland, in the galleries of *Pityogenes chalcographus*, *Polygraphus polygraphus*, *Crypturgus* sp., *Ips typographus*, *Trypodendron lineatum*; and in Spain and Switzerland, where it was phoretic on *Ips acuminatus* (Magowski 2010). Recently, it was

Fig. 18. A, B—*Heterotarsonemus lindquisti*, female, dorsal and ventral views, respectively.

found in Western Siberia, phoretic on *Pityogenes chalcographus* (Khaustov *et al.* 2016).

The phoretic behavior of this species was described by Khaustov *et al.* (2016).

Material examined. Two females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov.

***Heterotarsonemus lindquisti* Smiley, 1969**

(Figs. 18A, B)

This species was described based on specimens from the USA, as an associate of the *Dendroctonus frontalis* bark beetle (Smiley 1969). Lindquist (1970b) redescribed this species and provided new records from the USA and Honduras from *Ips cribricollis*, *I. kmausi*, *I. emarginatus*, *I. confusus*, *Dendroctonus monticolae*, *Trypodendron rufitarsis*, and *Aulonium ferrugineum*. It has also been recorded in Sweden, phoretic on *Ips typographus* (Moser *et al.* 1989; Smiley and Moser 1985). This is the first record of *H. lindquisti* in Russia.

The attachment site of this species on the beetle is unknown. We collected females of *H. lindquisti* only in the alcohol sediments.

Material examined. Two females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol

sediments containing numerous specimens of *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 16 females, 6 males, 6 larvae, same locality, in the galleries of *I. typographus*, 5 July 2016.

Order Sarcoptiformes

Suborder Oribatida

Family Scheloribatidae

***Siculobata (Paraleius) leontonycha*
(Berlese, 1910)**

(Figs. 40A–F, 44A, B)

This species is distributed in the Holarctic region, in association with numerous species of bark beetles (reviewed in Ahadiyat and Akrami, 2015).

In our study, this was the most abundant species, recovered both in the galleries of and phoretic on *I. typographus* (Table 1). Usually, phoretic mites attach to the long hairs of the beetle, mainly on the head and thorax (Figs. 40A–F, 44A, B).

Material examined: 2,774 females, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, in alcohol sediments containing numerous specimens of European spruce bark beetle *Ips typographus* collected by pheromone traps, 22 May 2017, coll. A.A. Khaustov; 4,137 females, same locality, 28 May 2017; 1,802 females, same locality, 5 June 2017; 239 females, same locality, 14 June 2017; 281 females, same locality, 16 June 2017.

Hyporder **Astigmata**Family **Acaridae*****Acarus* sp. [short dorsal setae]**

(Figs. 19A, B)

Many species of the genus *Acarus* are common stored-product pests, known based on both adult and deutonymphal stages (Griffiths 1964, 1970). In natural situations, species of *Acarus* commonly occur in nests of rodents and birds, while deutonymphs are phoretic on their hosts' parasites, e.g. fleas (Fain and Beaucournu 1972; OConnor and Pfaffenberger 1987). Several other non-synantropic species are known from forest litter (*Acarus tyrophagoides* (Zachvatkin, 1941)) and old dung (*Acarus mirabilis* Volgin, 1965). These species are only known based on adults, whereas their deutonymphs still remain undescribed (Griffiths 1970; Volgin 1965; Zachvatkin 1941). During our research, we have found deutonymphs which could potentially belong to these species. They are distinct in having very short scapular setae, which makes them similar to the associates of vertebrate nests, *Acarus nidicolous* Griffiths, 1970 and *Acarus monopsyllus* Fain and Schwan, 1984 (Fain and Schwan 1984; Griffiths 1970). In the latter two species, the scapular setae are relatively short, yet not represented by microsetae. In our species, the scapular setae and all other dorsal setae are microsetae; coxal setae 4b are situated in a posterior position—a character state similar to that of *Acarus nidicolous* Griffiths, 1970.

Material examined. 7 heteromorphic deutonymphs (HDNs), Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57°04'N, 65°04'E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 1 HDN, same data, 5 June 2017.

***Boletoglyphus boletophagi*
(F. Turk and S. Turk, 1952)**

(Figs. 19B, C)

This species is known from specimens collected in the United Kingdom (Scotland) (Turk and Turk 1952), Slovakia (Samšínák 1957), Poland (Haitlinger 2004; Haitlinger and Lupicki 2012), Finland (Penttinen *et al.* 2013), Siberia, and the European part of Russia (Bugrov 1997; Klimov 1998a; Volgin 1953). A similar species, *Boletoglyphus extremiorientalis*, occurs in eastern Russia and Japan (Klimov 1998a).

Feeding stages of *B. boletophagi* are common in the tube layers of old bracket fungi (Aphyllorphales; Polyporaceae; mainly *Fomes fomentarius*, which grows on birch trees) sporocarps. The mites feed on fungal tissues and spores. Phoretic deutonymphs attach to the tenebrionid beetle *Bolitophagus reticulatus* (Coleoptera: Tenebrionidae), which lives in the same fungus. Occasionally, deutonymphs can be found on ciid beetles (Ciidae), whose brood also develops in bracket fungi.

Penttinen *et al.* (2013) reported deutonymphs of *B. boletophagi*, which were collected by *Ips typographus* pheromone traps in Finland. We consider this and our record as an accidental phoretic association.

Material examined. 2 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57°04'N, 65°04'E, alcohol sediments from pheromone traps for *Ips typographus*, 5 June 2017, coll. A.A. Khaustov.

***Forcellinia wasmanni* (Moniez, 1892)**

This is a myrmecophilous species distributed throughout the Palaearctic (Černý and Samšínák 1971; Chmielewski 1977; Fain 1987; Kadjaia 1994; Kielczewski and Wiśniewski 1971; Klimov 1997; Mahunka 1983; Sevastianov 1970; Türk and Türk 1957; Zachvatkin 1941). Feeding stages live in ant nests, consuming dead ants and various organic debris. Phoretic deutonymph live on adult ants (Wasmann 1897; Zachvatkin 1941). There is a single species of *Forcellinia* found in association *Forecellinia insolita*—with bark beetles that live in the USA (Woodring and Moser, 1970). Phoretic deutonymphs of this species were collected from *Dendroctonus frontalis* (Woodring and Moser 1970) and *Ips grandicollis* (Moser and Roton 1971). In addition, mites of this species were sampled from the galleries of *Dendroctonus frontalis* (Moser 1975). It is likely that some ant-associated species are phoretic.

Material examined. 2 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57°04'N, 65°04'E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov.

***Ipsoglyphus bochkovi*
Klimov and Khaustov, 2018**

(Figs. 20A, B)

This species has been described previously as part of our current survey (Klimov and Khaustov, 2018).

Fig. 19. A, B—*Acarus* sp. (short dorsal setae), phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Boletoglyphus boletophagi*, phoretic deutonymph, dorsal and ventral views, respectively.

Material examined. 38 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov.

***Kuzinia laevis* (Dujardin, 1849)**

This species is known from the Palaeractic region. It had been introduced to the Australian region (Australia, Tasmania, and New Zealand) with commercial bumblebee colonies used for crop

Fig. 20. A, B—*Ipsoglyphus bochkovi*, phoretic deutonymph, dorsal and ventral, views, respectively, C, D—*Naiadacarus* sp., phoretic deutonymph, dorsal and ventral views, respectively.

pollination (Halliday 2002; Macfarlane 2005). Published records of *Kuzinia laevis* obtained from native bumblebees from the New World, along with several other co-occurring species of *Kuzinia*, may

be stemmed from the existing taxonomical impediment in species identification in this genus (Klimov *et al.* 2016). Feeding stages of *Kuzinia laevis* live in nests of bumblebees (*Bombus* spp.),

where they feed on various organic debris, bumble bee cocoon material, honey, pollen, nematodes, and fungi (Chmielewski 1969; Grobov 1978). Occasionally, phoretic deutonymphs can be found on other bees, wasps, and other insects, as well as in rodent burrows (which can be nesting sites for bumblebees) (Klimov *et al.* 2016). It is likely that our mites come from a single bumblebee individual that accidentally got into the pheromone trap.

Material examined. 4 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57°04'N, 65°04'E, alcohol sediments from pheromone traps for *Ips typographus*, 5 June 2017, coll. A.A. Khaustov.

***Naiadacarus* sp.**

[granulate dorsum, long legs III–IV]

(Figs. 20C, D)

This species has a heavily punctate dorsum, genual solenidion σ III absent, represented an alveolus only, and long legs III–IV. Morphologically, our deutonymphs are very close to *Naiadacarus fashingi* OConnor, 1989, which are phoretically associated with syrphid flies in the USA. The differences between the two species include: longer setae *scx*; and solenidion ω_2 grouped with solenidia ω_1 and ω_3 in the same cluster (ω_2 situated at base of tarsus, proximally from $\omega_1 + \omega_3$ cluster in *N. fashingi*). The most common hosts of *N. fashingi*, syrphid flies *Brachypalpus oarus* and *Chalcosyrphus* sp., live in subcortical spaces and in decaying wood as larvae. Mite deutonymphs presumably attach to female flies during oviposition, as evidenced by the predominant presence of mites on females in most host species (OConnor 1989). We expect that our species lives in subcortical habitats as well. This is the first record of the genus *Naiadacarus* in Russia (see below).

Remark. In North America, *Naiadacarus arboricola* live in water-filled treeholes, feeding on submerged, skeletonizing, decaying leaves (Fashing 1975). Deutonymphs of *N. arboricola* are phoretic on syrphid flies (mostly the *Mallota* genus), whose larvae develop in the same habitat. Other North American mite species, *N. fashingi* and *N. mydophilus*, are known based only on deutonymphs' description. Based on the biology of phoretic hosts, these mites may inhabit wet decaying wood and/or moist (rather than water-filled) treeholes (OConnor 1989). Furthermore, an undescribed species was reported from a bromeliad in Guatemala (Okabe and OConnor 2001). In the Old World, *Naiadacarus*

nepenthicola was described based on adults and deutonymphs collected in Brunei from fluid-filled pitcher-plants *Nepenthes bicalcarata*. This mite probably feeds on decomposing leaves that fall into pitchers as well as on decomposing insects trapped by pitchers. Deutonymphs of this species are phoretic on the *Campanotus schmitzi* ant, which inhabits exclusively the hollow tendrils of *N. bicalcarata* pitchers (Fashing and Chua 2002). Finally, feeding stages of an undescribed species of *Naiadacarus* have been reported based on specimens recovered from a water-filled hole in a tree stump in Austria (Wurst 2006).

Material examined. 31 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57°04'N, 65°04'E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 1 HDN, same data, 28 May 2017; 11 HDNs, same data, 5 June 2017.

***Schwiebea* sp. *eurynympha*-group**
[punctate dorsum]

(Figs. 21A, B)

This morphospecies belongs to the *eurynympha*-group. It is distinct from all species in the *eurynympha*-group by the punctate dorsal idiosoma. It is different from *Schwiebea eurynympha* (Oudemans, 1911) in: 1) ovoid coxal setae *4a* (transversely elongated in *S. eurynympha*); and 2) setae *si* being situated posteriorly to setae *se* (vs. being situated on the same transverse level in *S. eurynympha*). By the shape of coxal setae *4a* and the position of the scapular setae, this species is similar to *Schwiebea tshernyshevi* Zachvatkin, 1941 and *Schwiebea stammeri* Wurst, 2002 (the deutonymph of *S. stammeri* was described in Türk and Türk (1957) as *S. "eurynymphae"*). *Schwiebea tshernyshevi* has been synonymized with *Uropoda parallela* Müller, 1860 by Samšiňák (1958). However, as evidenced by the morphology of legs I–II, Müller's Figures 3 a–d (Müller 1859 (1860)) actually show a histiostomatid. We, therefore, do not accept this synonymy.

Schwiebea stammeri was cited to differ from *S. tshernyshevi* by subequal setae e_2 and h_2 in males (Wurst 2002). However, these setae are also subequal in males of *S. tshernyshevi* (Zachvatkin 1941: Figs. 344, 345). Zachvatkin's text indeed compares setae *sae* ($=f_2$) and *lp* ($=e_2$) (*lp* 2 times shorter than *sae*, p. 201), despite the absence of *sae* was cited as diagnostic to *Schwiebea* (p. 197). The short setae on Fig. 344 are attributable to " f_2 " of general-

Fig. 21. A, B—*Schwiebea* sp. *eurynympha*-group (punctate dorsum), phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Schwiebea* sp. *eurynympha*-group (small, unsclerotized, 1a and 3a filiform), phoretic deutonymph, dorsal and ventral views, respectively.

ized acarid (but not *Schwiebea*), while the typical setae e_2 was also present on this figure. This sug-

gests that the short setae on Fig. 344 are probably non-existent and represent an artifact. Designation

of a neotype for *S. tshernyshevi* is needed to solve the status of *Schwiebea stammeri*.

Material examined. 1 HDN, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov.

***Schwiebea* sp. *eurynympha*-group
[small, unsclerotized, 1a, 3a filiform]**

(Figs. 21C, D)

This species has broadly parallel posterior borders of coxal fields II and IV (as in the *eurynympha*-group) and filiform coxal setae 1a and 3a. This is a small and weakly sclerotized species.

Material examined. 1 HDN, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 5 June 2017, coll. A.A. Khaustov.

***Schwiebea nesbitti*
F. Türk and E. Türk, 1957**

(Figs. 22A, B)

This species is known from females and phoretic deutonymphs collected in Germany, Austria, Belgium, and Poland (Haitlinger 1988; Türk and Türk 1957; Wurst 2002; Wurst and Frank 1998). We record it for the first time for Russia. It is probably parthenogenetic, since males have not been found (Wurst 2002; Wurst and Frank 1998). Feeding stages live in deeper layers of rotten wood, especially in rotten tree stumps (Wurst and Frank 1998). Heteromorphic deutonymphs are phoretic on the following arthropods: *Dorcus parallelipipedus* (Lucanidae), *Melanotus rufipes* (larvae) (Elaterridae), *Pterostichus anthracinus* (Carabidae), *Carabus glabratus* (Carabidae), *Serviformica fusca* (Formicidae), *Unciger foetidus* (Julidae) (Haitlinger 1988; Türk and Türk 1957; Wurst 2002; Wurst and Frank 1998), and *Ips typographus* (our data).

Remark. *Schwiebea nesbitti* is likely to be a junior synonym of *Schwiebea pachyderma* Zachvatkin, 1941 known from females collected in Ukraine and Russia (Zachvatkin 1941). Females of *S. pachyderma* have a strongly sclerotized, brown-colored idiosoma and indistinguishable boundaries of the propodosomal shield. These character states are diagnostic for *S. nesbitti* and distinguish both *S. pachyderma* and *S. nesbitti* from *Schwiebea talpa* Oudemans, 1916 (idiosoma not sclerotized, propodosomal shield with distinct boundaries). However,

in *S. pachyderma*, seta *mG* on genu I was originally figured elongated and not thorn-shaped (setae *mG* I–II are thorn-shaped in *S. nesbitti* and elongated in *S. talpa*). The former two character states (idiosomal sclerotization, prodorsal shield) are easily observable and were mentioned in the original description of *S. pachyderma*, while the latter character state (the shape of *mG* I–II) is a relatively difficult to observe with precision. Additional research is needed to verify the status of *S. pachyderma*.

Our specimens differ from the most recent re-description of *Schwiebea nesbitti* (Wurst and Frank 1998) by the absence of fine pectinations of *kT* III and *r* IV (present in *S. nesbitti*) and the prodorsum covered with small and faint dimples in contrast to the hysteronotum (both propodorsum and hysteronotum lack dimples in *S. nesbitti*).

Material examined. 2 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 28 May 2017, coll. A.A. Khaustov.

***Schwiebea nova* (Oudemans, 1906)**

(Figs. 22C, D)

This species has been originally described from specimens obtained in Germany (Oudemans 1906) and then was reported in various localities in the Holarctic region. Feeding stages are subcortical, living under the bark of dead trees and feeding on decaying plant material and fungal hyphae. Deutonymphs are commonly found on various arthropods that visit rotten wood, predominantly beetles (reviewed Hutcheson *et al.* 2015). Among bark beetles, it has been recorded from *Tomicus piniperda* in Poland (Michalski and Ratajczak 1989) and *Scolytus ratzeburgi* in Russia (Ermilov *et al.* 2007). This species may be difficult to identify accurately (see below).

Remark. *Schwiebea nova* was briefly described as *Tyroglyphus novus* based on a deutonymph collected in Bremen, Germany (Oudemans 1906). Later, a more detailed and illustrated description appeared (Oudemans 1907). *Tyroglyphus novus* was designated as the type species of a new deutonymphal genus *Troupeauia* Zachvatkin, 1941 (Zachvatkin 1941). However, when adults have been discovered, this genus was placed into synonymy of *Schwiebea* Oudemans, 1916 (Türk and Türk 1957). Unfortunately, the sample of Türk and Türk (1957) contained two similar species, with and without tibial setae *hT* I–II. *Schwiebea nova* (no setae *hT* I–II)

was redescribed from deutonymphs and adults from Russia (Klimov 1998b). A similar species has been reported from adults and deutonymphs from Germany as “nG-Art3” (Wurst 2002).

In the genus *Schwiebea*, Wurst (2002) proposed the *nova* species group having filiform tarsal setae *la* I–II. Because he dismissed the conventional subdivision of *Schwiebea* into groups with one (*Schwiebea* s.str.) or two genual solenidia (σ' and σ'') (*Megnini-etta*, *Jakotietta*) in feeding stages, his *nova*-group included a mix of species presenting both of these character states: *S. nova* (Oudemans, 1906) (2 σ , *hT* I–II absent), *S. ulmi* (Jacot, 1936) (2 σ , ?*hT* I–II absent), *S. rossica* Zachvatkin, 1941 (2 σ , *hT* I–II absent), *S. falticis* Woodring, 1966 (2 σ , *hT* I–II absent), *S. longibursata* Fain and Wauthy, 1979 (2 σ , *hT* I–II absent), *S. subterranea* Fain, 1982 (2 σ , *hT* I–II present), *S. cepa* Karg, 1987 (2 σ , ?), *S. montana* Bugrov, 1995 (1 σ , *hT* I–II absent); plus *S. jiangxiensis* Jiang 1995 (2 σ , *hT* I–II present), which should also be placed here. In addition, Wurst (2002) identified nine undescribed morphospecies from Central Europe and reported intermediate populations between some of them. Based on this evidence, he suggested that breeding experiments and DNA sequence data are needed to resolve the species boundaries in the *nova*-group. No key to species of the *nova* group was, therefore, provided in Wurst (2002). Here, we use an old species concept, and call the species with a single setae *gT* I–II on tibia I–II (*hT* I–II are absent) in all stages *S. nova*. A similar species, having two setae on tibia I–II (*gT* I–II and *hT* I–II) in all stages is called here *Schwiebea* sp.1 (= *S. longibursata* sensu Klimov (1998b)). Types of *Schwiebea longibursata* have a single tibial setae (Wurst 2002). We recognize that careful morphological examination, as well as a correlation of feeding and deutonymphal stages, along with molecular data are needed. Therefore, we consider our species assignments putative.

Material examined. 154 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57°04'N, 65°04'E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 49 HDNs, same data, 28 May 2017; 31 HDNs, same data, 5 June 2017; 5 HDNs, same data, 15 June 2017; 1 HDN (slide 71), same data, 16 June 2017; 1 HDN, same data, June 2017.

***Schwiebea* sp.1 *nova*-group [two tibial setae, regular attachment organ]**

(Figs. 23A, B)

Remark. This morphospecies has two setae on tibia I–II (*gT* I–II and *hT* I–II) and corresponds to

our earlier interpretation of *S. longibursata* sensu Klimov (1998b). Types of *Schwiebea longibursata*, however, have a single tibial setae (Wurst 2002). Similarly to *S. nova*, this species may be difficult to identify accurately (see above for *S. nova*).

Material examined. 18 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57°04'N, 65°04'E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 3 HDNs, same data, 28 May 2017; 12 HDNs, same data, 5 June 2017.

***Schwiebea* sp. *nova*-group [two tibial setae, wide attachment organ]**

(Figs. 23C, D)

This morphospecies belongs to the *nova*-group. It has two setae on tibia I–II (*gT* I–II and *hT* I–II). The attachment organ is distinctly wider than in the previous species.

Material examined. 3 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57°04'N, 65°04'E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 1 HDN, same data, 15 June 2017; 1 HDN, same data, 16 June 2017.

***Schwiebea* sp *nova*-group [granulate dorsum, short legs III–IV]**

(Figs. 24A, B)

This morphospecies belongs to the *nova*-group. It is distinct by a well-punctate dorsum and a wider attachment organ.

Material examined. 3 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57°04'N, 65°04'E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 1 HDN, same data, 28 May 2017.

***Schwiebea scheucherae*
F. Türk and E. Türk, 1957**

(Figs. 24C, D)

This species is known from adults and deutonymphs collected in Germany, Austria, France, Belgium, Poland, Romania, Slovakia, Hungary, Ukraine, and Russia (Bugrov 1995; Fain 1977; Haitlinger 1988; Mahunka 1961; Sevastianov 1970; Türk and Türk 1957; Wurst 2002). Feeding stages are frequently found under moist, decomposing bark and in rotten wood. Deutonymphs are phoretic on *Craspedosoma rawlinsii alemannicum* (*Craspedo-*

Fig. 22. A, B—*Schwiebea nesbitti*, phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Schwiebea nova*, phoretic deutonymph, dorsal and ventral views, respectively.

somatidae), *Julus scandinavicus* (Julidae), *Carabus hortensis* (Carabidae), *Camponotus ligniperdus*, *Lasius niger*, *Lasius fuliginosus*, *Formica rufa* (For-

micidae) (Haitlinger, 1988; Kiełczewski and Wiśniewski, 1971; Sevastianov, 1970; Türk and Türk, 1957) and *Ips typographus* (our data).

Fig. 23. A, B—*Schwiebea* sp. *nova*-group (two tibial setae, regular attachment organ), phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Schwiebea* sp. *nova*-group (two tibial setae, wide attachment organ), phoretic deutonymph, dorsal and ventral views, respectively.

Fig. 24. A, B—*Schwiebea* sp. nova-group (granulate dorsum, short legs III–IV), phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Schwiebea scheucherae*, phoretic deutonymph, dorsal and ventral views, respectively.

Our specimens differ from the most recent re-description of *Schwiebea scheucherae* (Wurst 2002) by the gnathosoma being longer and wider at the base than at the tip. It is possible that the perceived differences result from the orientation of the gnathosoma in the illustration of this specimen by Wurst (2002).

Material examined. 1 HDN, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 16 June 2017, coll. A.A. Khaustov (vial 20); 2 HDNs, same data, 15 June 2017; 1 HDN, same data, 5 June 2017.

***Thyreophagus corticalis* (Michael, 1885)**

(Figs. 25A, B)

This is a widely distributed species known from the Palearctic and Australian regions: England (Michael 1885), Italy (Castagnoli *et al.* 1994; Simoni *et al.* 2014), France (Fain and Beaucournu 1993), Belgium (Fain 1982), Germany (Moser and Bogenschütz 1984), Netherlands (Oudemans 1924), Poland (Chmielewski 1977; Haitlinger 1988), Hungary (Ripka *et al.* 1999; Ripka and Szabo 2010), Slovakia (Mašán 1999), Sweden (Moser *et al.* 1989), Ukraine (Sevastianov 1970), Russia (Bugrov 1997; Klimov and Tolstikov 2011), and Australia (Domrow 1992).

Feeding stages have been found under the epidermis of dead stems of *Phragmites communis* (Michael 1903) and under the bark of numerous (31) tree species (Ripka *et al.* 1999), including a dead apple tree (Fain 1982). The feeding stages have also been recovered from inside the nuts of Asian hazel *Corylus heterophylla* (our data); beech forest soil (Fain 1982); as well as nests of the following birds: *Columba palumbus*, *Apus apus*, “aquatic bird” (Fain 1982), *Puffinus tenuirostris* (Domrow 1992). They have also been identified in association with *Chionaspis salicis* (Diaspididae) and *Phylloxera populi* (Phylloxeridae) (Ripka and Szabo 2010); on various materials in beehives of *Apis mellifera*, including debris, bee bread, pollen, combs/wax, fungi (mold) (Chmielewski 1977, 1991). Feeding stages have also been recorded on the edible dormouse *Clis glis* (phoretic mite female) (Fain 1982). Deutonymphs are phoretic on various arthropods, such as springtail *Allacma fusca* (Sminthuridae), *Oiceoptoma thoracicum* beetles (Mašán 1999), *Carabus arcensis* (Haitlinger 1988), *C. granulatus* (Haitlinger 1988), *C. coriaceus* (Haitlinger 1988), *Helops lanipes* (Türk and Türk 1957). They

are also phoretic on red wood ants *Formica rufa* (Kiełczewski and Wiśniewski 1971; Sevastianov 1970; Türk and Türk 1957); on *Lasius fuliginosus*, *Myrmica ruginodis* (Kiełczewski and Wiśniewski 1971); on parent bugs *Elasmucha grisea* (Pentatomidae) (Fain and Baugnee 1996); on the flea *Ceratophyllus columbae*, which is in turn parasitic on rock doves *Columba livia* (Fain and Beaucournu 1993). Bark beetle hosts include *Hylurgops palliatus* and *Pityogenes chalcographus* in Poland (Kiełczewski and Wiśniewski 1980); as well as *Ips typographus* in Germany and Sweden (Moser and Bogenschütz 1984; Moser *et al.* 1989).

Thyreophagus corticalis may play a role in spontaneous recovery of chestnuts (*Castanea sativa*) from a fungal disease known as chestnut blight. This disease is caused by the virulent strains of a pathogenic fungus *Cryphonectria parasitica*. Hypovirulent fungal strains contain a hypovirus and lose their pathogenicity. Viral double-stranded RNA from the hypovirulent mycelia can be ingested by the mites or carried on their cuticles. The RNA can subsequently be transmitted to the mycelia of virulent strains. This process causes their conversion to a hypovirulent strain, resulting in the recovery of the host tree from chestnut canker (Simoni *et al.* 2014).

This mite can also be a vector of several spruce pathogens, such as *Ophiostoma bicolor* and *Ophiostoma europaoides*. Ascospores of these fungi have been found to be hyperphoretic on deutonymphs of *Thyreophagus corticalis* (Moser, Perry *et al.* 1989). Although these fungal species can kill considerable portions of the phloem, they do not cause discoloration of the sapwood (Kirisits 1998).

Material examined. 1 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 15 June 2017, coll. A.A. Khaustov.

***Thyreophagus entomophagus* (Laboulbène and Robin, 1862)**

(Figs. 25C, D)

This is probably a cosmopolitan species. It has been reported from the following countries (a non-inclusive list): France (type locality) (Laboulbène and Robin 1862); Spain (Iglesias-Souto *et al.* 2009); Italy (Goracci *et al.* 1985), including Sicily (Fumouze and Robin 1867); England (Fain 1982; Michael 1903; Newstead and Morris 1920); Germany (Fain 1982); Belgium (Fain 1982) the Czech

Fig. 25. A, B—*Thyreophagus corticalis*, phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Thyreophagus entomophagus*, phoretic deutonymph, dorsal and ventral views, respectively.

Republic (Ždárková 1967); Poland (Chmielewski 1975, 1977); former Yugoslavia (Chmielewski 1975); Bulgaria (Nachev and Trenchev 1987); Russia (Zachvatkin 1941); Georgia (Reck 1976); Iran (Kamali *et al.* 2001); Egypt (Elkawas 2011); Republic of Côte d'Ivoire (Fain 1974); Cuba (de la Torre Morin *et al.* 2006); Canada (Sinha 1964), USA (Hughes 1976; Philips 2009); Brazil (Mazzuco *et al.* 2000); the Philippines (Olsen 1983); China (C. Li *et al.* 2014), including Hong Kong (Olsen 1983) and Taiwan (Tseng 1989); New Zealand (Cotter *et al.* 2011); and Australia (Womersley 1941).

Thyreophagus entomophagus is a pest of various commodities, such as: flour (Cotter *et al.* 2011; Mazzuco *et al.* 2000; Newstead and Morris 1920; Zachvatkin 1941; Ždárková 1967); dry Spanish fly *Lytta vesicatoria* harvested for medicinal use (Fumouze and Robin 1867); vanilla pods and saffron for medicinal use (Moniez 1892); dried medicinal plants, including ergot and cardamom; stimulants; spices; food products and fodders (rye and wheat bran) (Chmielewski 1975); poultry meal (Newstead and Morris 1920). Ingesting infested food may produce occupational respiratory disorders and anaphylaxis (Iglesias-Souto *et al.* 2009; Mazzuco *et al.* 2000; Musken *et al.* 2000). This species has also been recorded as a pest in entomological collections, preferentially developing on large insects; being especially abundant on *Locusta migratoria* (Orthoptera) and *Sesia* (Lepidoptera) (Laboulbène and Robin 1862). It is common pest in southern France (Laboulbène and Robin 1862), whereas only a few specimens infesting insect collections have been found in Belgium and England (Fain 1982; Michael 1903). It has also been found in association with scale insects (Elkawas 2011; Nachev and Trenchev 1987). It can feed on larval skins and live coccids (Nachev and Trenchev 1987); on trogid beetles (Philips 2009); ergot of rye (Michael 1903); bird nests (Wasylik 1959; Woodroffe 1953); bracket fungi *Fomitopsis betulina* (Pielou and Verma 1968); and various materials in beehives of *Apis mellifera*, such as debris, bee bread, pollen, dead bee brood, and mold (Chmielewski 1977, 1991).

Remark. This mite has been reported as a pest infesting dry insect collections in France and named (without a formal description) *Acarus entomophagus* (Laboulbène 1852). Later, this taxon was properly described based on adults and nymphs (Laboulbène and Robin 1862). Although in the latter work, the authorship of "*Acarus entomophagus*" (nomen nudum) is attributed to Laboulbène, the use of the phrase "*Tyroglyphus entomophagus*

nobis" (*Tyroglyphus entomophagus* new), without explicitly attributing it to Laboulbène (p. 321), indicates that this species should have a joint authorship of Laboulbène and Robin. Therefore, the author and year of this species should be reported as *Thyreophagus entomophagus* (Laboulbène and Robin, 1862), not "(Laboulbène, 1852)", as often cited in the literature (De Camargo Barbosa *et al.* 2016; Fain 1982; Fain *et al.* 2000).

Material examined. 1 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 1 HDN, same data, 28 May 2017.

Thyreophagus aff. *odyneri*

(Figs. 26A, B)

Our specimen is similar to *Thyreophagus odyneri* Fain, 1982 but differs by: robust apical, ventral, tarsal setae III (*s*, *u'*, *u''*, *v'*, *v''*), being approximately 1/3 of the condylophore length (shorter than 1/3 of the condylophores in *Th. odyneri*); absence of tibial setae *hT* I–II (present as a minute spine in *Th. odyneri*); presence of tarsal setae *w* III alveolus (absent in *Th. odyneri*). The latter two character states are also similar to those of *Thyreophagus cooremani* Fain, 1982 but *T. cooremani* is much smaller and the anterior part of the spermatheca is not vase-shaped as in *Th. aff. odyneri* and *Th. odyneri*.

Material examined. 1 female, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 5 June 2017, coll. A.A. Khaustov.

Tyrophagus putrescentiae (Schrank, 1781)

This species is cosmopolitan; its range includes Antarctica. It occurs on a wide variety of commodities and hosts, and is common in stored food, house dust, as well as peridomestic and agricultural habitats. Feeds on various organic materials, fungi, and nematodes. It is a pest of stored food, agricultural produce, as well as microbiological, plant, and insect cultures (Klimov *et al.* 2016). It causes allergies in humans and domestic animals (Arlian *et al.* 1984; Erban *et al.* 2016). Phoretic deutonymphs are not formed, and dispersal is accomplished by the feeding stages' active movement, air currents, or host movement (Klimov *et al.* 2016). Mites can spread dangerous

Fig. 26. A, B—*Thyreophagus* aff. *odyneri*, female, dorsal and ventral views, respectively.

fungi (e.g., those that develop on grain) by carrying fungal spores on their bodies, in the digestive system, or in feces (Griffiths *et al.* 1959). Experiments have shown that *Tyrophagus putrescentiae* is able to spread genetic variants of the fungus *Ophiostoma ulmi*, one of the causative agents of the Dutch elm disease. Crosses of pathogenic and non-pathogenic strains of this fungus resulted in partial reproductive incompatibility (Brasier 1978).

Mite associations with bark beetles include the following species: *Dendroctonus frontalis*, *Gnathotrichus materiarius*, *Ips avulsus*, *Ips calligraphus*, *Ips grandicollis*, *Ips pini*, *Trypodendron scabricollis* in the USA (Moser 1975; Moser and Roton 1971; Pfammatter *et al.* 2013). *T. putrescentiae* can be found in beetles' galleries as well as on adult beetles.

Material examined. 3 females, 3 males, Russia, Tomsk Region, nr. Tomsk, galleries of *Polygraphus proximus*, lab culture 6 May 2017; 1 male, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 15 June 2017, coll. A.A. Khaustov.

Family Hemisarcoptidae

Divilia aff. *occidentalis*

(Figs. 27 A, B)

Mites of the genus *Divilia* are primarily associated with subcortical and wood-visiting Coleoptera and Hymenoptera, but this genus is also known from tabanid (Mullen *et al.* 1989), syrphid (O'Connor 1989), and asilid flies (O'Connor 1991). The genus is distributed in the Holarctic, with three described Palearctic species (see below) and at

Fig. 27. *Divilia* aff. *occidentalis*, phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Divilia* sp. (smooth dorsum, 5 setae on tarsus IV, no sigma II), phoretic deutonymph, dorsal and ventral views, respectively.

least five undescribed species in North America (Mullen *et al.* 1989; OConnor 1991):

Divilia oculata Sevastianov, 1969. Known from phoretic deutonymphs, on *Lasius fuliginosus* in Ukraine and *Formica rufa* and *Formica polyctena* (Formicidae) in Russia (Sevastianov 1969).

Divilia occidentalis Fain, Hurst, Tweddle, Lachlan, Majerus and Britt, 1995. Known from phoretic deutonymphs on ladybugs *Chilocorus renipustulatus* in England (Fain *et al.* 1995).

Divilia exigua Fain, Hurst, Fassotte, Webberley, Sloggett, Majerus, 1997. Known from phoretic deutonymphs found on ladybugs *Vibidia duodecimguttata* in Poland (Fain *et al.* 1997).

Our specimens differ from other described species by the following character states: dorsal striation is present, at least on the posterior hysterosoma (absent in *D. exigua*, present in *D. oculata* and *D. occidentalis*); palps are elongated (same in *D. occidentalis* and *D. oculata*, short in *D. exigua*); anterior coxal apodemes III extend at an angle to meet the median sclerite (same in *D. occidentalis* and *D. exigua*, almost transverse in *D. oculata*); alveoli *1a* and *3a* are not visible (same in *D. oculata* and *D. occidentalis*, visible in *D. exigua*); solenidion σ II is absent (same in *D. oculata* and *D. occidentalis*; present in *D. exigua*); setae *cG* II are situated at the base of genu II (same in *D. occidentalis*; nearly at the middle of the segment in *D. exigua*; unknown in *D. oculata*); tarsus IV with 5 setae—3 short and 2 long (*D. occidentalis* and *D. exigua* have 4 setae: 2 short and 2 long—although, it is possible that the other short seta has not been observed; *D. oculata* was depicted with a single short seta).

Remark. Our specimens show variable striation pattern of the dorsum, ranging from both prodorsum and hysterosoma being completely striated to only the posterior hysterosoma being striated. Thus, given that the number of short setae in tarsus IV may not have been accurately detected in the original description of *D. occidentalis* (coupled with the fact that the pattern of dorsal striation is variable), our species can be identified as *D. occidentalis*. However, before our specimens can be confidently assigned to *D. occidentalis*, the type material of *D. occidentalis* needs to be re-examined and an extensive study of the natural variation in the striation pattern needs to be done.

Material examined. 1 HDN, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May

2017, coll. A.A. Khaustov; 3 HDNs, same data, 5 June 2017.

***Divilia* sp. [smooth dorsum,
5 setae on tarsus IV, no sigma II]**

(Figs. 27C, D)

Our specimens have a completely smooth dorsal idiosoma (no striation pattern) and short palps, which is similar to *D. exigua*. Our specimens, however, differ by: the presence of 5 setae on tarsus IV (vs. 4 setae in *D. exigua*); alveoli *1a* and *3a* either not being visible or only alveolus *3a* being visible (*1a* and *3a* are distinct in *D. exigua*); solenidion σ II being absent (present in *D. exigua*); setae *cG* II being situated at the base of genu II (in *D. exigua* they are nearly in the middle of the segment).

Material examined. 2 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 5 June 2017, coll. A.A. Khaustov.

***Hemisarcoptes* sp.**

(Figs. 28A, B)

Species of *Hemisarcoptes* are predators of armored scale insects (Diaspididae): they feed on the insects themselves or on their eggs. All non-deutonymphal stages occur under the scale cap, with their chelicerae imbedded into the host tissues. Mites display no preference for a particular host species. Mite attacks result either in a decreased or no egg production of the insect host (1–10 mites attacking together), or death (if more than 10 mites attack) (Gerson and Schneider 1981). Deutonymphs disperse on coccinellid beetles of genus *Chilocorus*, which are also predators of scale insects. The mites attach to the beetle elytron, in the subelytral surface during transport (Houck 1999). Attached mites can extract coleopteran host haemolymph by perforating the hypodermis of the elytron with the help of negative pressure exerted by their powerful caudoventral suckers (Houck and Cohen 1995). The beetle hemolymph contains toxic alkaloids, which appear not to affect the mites (Houck 1994). The genus *Hemisarcoptes* is distributed worldwide (Houck 1999), but it has not been recorded in Russia previously. While the genus can be identified by the elongated ambulacra in non-deutonymphal stages, the identification to species in our case is not possible because we had only discovered a single larva. Here, we list known

European species along with their type hosts and localities (Dzibladze 1969; Fain and Ripka 1998; Lignières 1893):

Hemisarcoptes coccisugus Lignières, 1893. On the apple mussel scale *Lepidosaphes ulmi* (Diaspididae) on apple branches in France; André (1942) considered it as a junior synonym of *Hemisarcoptes malus* (Shimer, 1868) from *Lepidosaphes conchiformis* (Diaspididae) on apple trees in Ohio, USA, but see Fain and Ripka (1998)

Hemisarcoptes budensis Fain and Ripka, 1989. On *Unaspis euonymi* (Diaspididae) on the Oriental bittersweet *Celastrus orbiculatus*, holotype phoretic deutonymph was collected from *Chilocorus renipustulatus* (Coccinellidae) in the same locality in Hungary; other five host species of armored scale insects, attacking 12 species of ornamental trees were listed.

Hemisarcoptes dzhashii Dzibladze, 1969. On *Lepidosaphes beckii* (type host), *Lepidosaphes gloverii*, *Aonidiliella citrina*, *Chrysomphalus dictyospermi* (Diaspididae) on *Citrus reticulata* in Georgia (Dzibladze 1969).

Material examined. 1 larva, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 28 May 2017, coll. A.A. Khaustov.

***Nanacar* sp.1 (prodorsum striated, c₁ widely separated)**

(Figs. 29A, B)

Species of the genus *Nanacar* inhabit bark, subcortical spaces, woody bracket fungi, and the burrows of wood-boring insects. These species show little or no specificity in phoretic hosts (O'Connor 1982). One species, *Nanacar minutus*, is known to occur in bird, soil, stored food products, and house dust (see below). The genus *Nanacar* inhabits the Old World and North America (Halliday 2000; Oudemans 1901; Pielou and Verma 1968). Several species were described (see below) but a careful revision is necessary to identify them. Numerous undescribed species have also been reported (Halliday 2000; Hofstetter 2011; Hofstetter *et al.* 2013; Kurosa 2000; Matthewman and Pielou 1971; Mercado *et al.* 2014; O'Connor 1991; Penttinen *et al.* 2013; Pielou and Verma 1968). Among them, multiple, apparently sympatric morphospecies are known: three in Japan (Kurosa 2000) and five in Michigan, USA (O'Connor 1991).

Bark beetle hosts include (all mite species are undescribed/unidentified): *Ips typographus* in Finland (Penttinen *et al.* 2013) and Germany (Moser and Bogenschütz 1984); *Pityokteines curvidens* in Switzerland (Pernek *et al.* 2012); *Dendroctonus frontalis* in Arizona, USA (Hofstetter 2011; Hofstetter *et al.* 2013); *Dendroctonus ponderosae* in North America (Mercado *et al.* 2014).

Species of *Nanacar*

Nanacar astoma (E. Türk and F. Türk, 1957) [= *Calvolia astoma* E. Türk and F. Türk, 1957]. Only phoretic deutonymphs are known from *Formica rufa* and *Lasius fuliginosus* (Formicidae) in Germany (Türk and Türk 1957), *Formica polyctena*, *Myrmica laevinodis*, *Myrmica ruginodis*, *Lasius fuliginosus* in Poland (Kielczewski and Wiśniewski 1971).

Nanacar collembolicola (Fain and Johnston, 1974) [= *Congovidiella collembolicola* Fain and Johnston, 1974]. Known from phoretic deutonymphs, on the springtail *Allacma fusca* (Sminthuridae) in England (Fain and Johnston 1974). SEM images of *Nanacar* sp. from *Ips typographus* in Finland (Penttinen *et al.* 2013) resemble this species.

Nanacar hieroglyph (Fain and Elsen, 1971). Known from phoretic deutonymphs from tsetse flies *Glossina fuscipes fuscipes* and *Glossina fuscipes quanzensis* from the Democratic Republic of the Congo.

Nanacar hungaricus Halmai and Mahunka, 1980. Adults, HDNs. *Oryctolagus cuniculus* cage in Hungary. Fain (1988) stated that HDNs are similar to *Nanacar minutus*.

Nanacar minutus (Oudemans, 1901). Non-deutonymphal stages were collected from mammals *Eptesicus serotinus* (type host), *Pipistrellus pipistrellus*, *Sorex araneus* from Germany, bird *Megapodius reinwardt buruensis* (Megapodiidae) from Buru Island, Indonesia (Oudemans 1928), bee *Xylocopa (Koptorthosoma) tenuiscapa* from Java, Indonesia (Oudemans 1901, 1903), wheat in Belgium (Fain 1988), nest of a wild pigeon (with phoretic deutonymphs) in Belgium (Fain 1988), in the former Czechoslovakia (Černý and Samšíňák 1971), flour in Russia (Zachvatkin 1941), house dust in Japan (Oshima 1977), stored food in China (L.-S. Li *et al.* 1992) and from soil in Saudi Arabia (Bayoumi and Al-Khalifa 1983). Phoretic deutonymphs HDNs are known but undescribed: on the longhorn beetle *Leipopus nebulosus*, unidentified insects (Fain 1988), a coccinellid *Adalia*

Fig. 28. A, B—*Hemisarcoptes* sp., larva, dorsal and ventral views, respectively.

sp. in Belgium (Fain *et al.* 1997), *Vibidia duodecimguttata* and *Exochomus quadripustulatus* (Coccinellidae) in Poland (Fain *et al.* 1997). Oudemans (1939) synonymized this species with

Acarus caudatus Canestrini and Fanzago, 1877 from Italy (nom. preocc. De Geer, 1778), but we do not support this synonymy because “*Acarus caudatus*” has claws and long legs.

Fig. 29. A, B—*Nanacarus* sp.1 (prodorsum striated, c_1 widely separated), phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Nanacarus* sp.2 (prodorsum smooth or nearly smooth, c_1 closely separated), phoretic deutonymph, dorsal and ventral views, respectively.

Nanacarus pragensis (Samšínák, 1983). Czech Republic. Known from a single phoretic deutonymph, collected from soil under trees, where people feed pigeons (Samšínák and Vobrázková 1983).

Note: '*Nanacarus*' *nominis* Woodring, 1966 belongs to Suidasiidae: Sapracarinae.

Our specimen has striated prodorsum, intercalary sclerites between anterior apodemes III and

the ventrum; setae c_1 widely separated; and a short, almost conical, tarsus III. These character states, except for the widely separated c_1 , are similar to those of *Nanacarus collembolicola* (c_1 not widely separated). In the descriptions of *Nanacarus praagensis* and *N. hungaricus*, tarsi III are shown somewhat elongated and not conical, and intercalary sclerites are lacking.

Material examined. 2 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 1 HDN, same data, June 2017.

***Nanacarus* sp.2 [prodorsum smooth or nearly smooth, c_1 closely separated]**

(Figs. 29C, D)

The prodorsum is nearly smooth; setae c_1 are closely separated; intercalary sclerites between apodemes III and ventrum are absent, tarsus III is short, almost conical.

Material examined. 2 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 28 May 2017, coll. A.A. Khaustov; 2 HDNs, same data, 5 June 2017; 1 HDN, 15 June 2017; 1 HDN, June 2017.

***Superioropus huronmontanus*
OConnor and Houck, 1989**

(Figs. 30A, B)

This species is known from phoretic deutonymphs collected from *Exeristes comstockii* (Ichneumonidae) in Michigan, USA (OConnor 1991; OConnor and Houck 1989). Comparison of our specimens did not reveal any substantial differences with the original description. This is the first record of this genus and species for the Palearctic region.

Material examined. 5 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 5 June 2017, coll. A.A. Khaustov; 4 HDNs, same data, 15 June 2017; 3 HDNs, same data, June 2017.

Family **Winterschmidtidae** Oudemans, 1923

***Parawinterschmidtia kneissli*
(Krausse, 1919)**

(Figs. 30C, D)

This is a European species known based on descriptions of both phoretic deutonymphs and

adults (Khaustov 2000a; Türk and Türk 1957). Feeding stages are mycophagous in bark beetle galleries. Phoretic hosts include a broad array of subcortical and wood-visiting arthropods, such as bark beetles and their predators (e.g., the ant beetle *Thanasimus formicarius*). Bark beetle hosts are: *Orthotomicus laricis* (Krause 1917 (1919)) (type host); *Tomicus piniperda* (Khaustov 2000a), *Hylastes attenuatus* (Ermilov et al. 2007). Non-bark beetle hosts: *Brachyderes incanus* (Türk and Türk 1957), *Hylobius abietis* (Ermilov et al. 2008; Türk and Türk 1957), *Pissodes pini* (Ermilov et al. 2008), *Pissodes piniphilus* (Türk and Türk 1957) (Curculionidae); *Acanthocinus aedilis* (Türk and Türk 1957); *Mesosa nebulosa* (Samšínák 1957); *Plagionotus detritus*, *Monochamus galloprovincialis*, *Spondylis buprestoides*, *Rhagium sycophanta* (Ermilov and Mokrousov 2008); *Rhagium inquisitor* (Khaustov 2000a) (Cerambycidae); *Sericus brunneus* (Elatridae) (Ermilov et al. 2006); *Thanasimus formicarius* (Cleridae) (Khaustov 2000a; Türk and Türk 1957); *Crypticus quisquilius* (Tenebrionidae) (Türk and Türk 1957); *Myzia oblongoguttata* (Coccinellidae) (Türk and Türk 1957); *Raphidia* sp. (larva) (Raphidioptera: Raphidiidae); *Crossocerus vagabundus* (common), *Crossocerus leucostoma*, *Ectemnius cavifrons*, *Ectemnius cephalotes* (Crabronidae), *Sceliphron deforme* (Sphecidae), *Astata kashmirensis* (Astatinae) (Ermilov and Mokrousov 2010); and a centipede *Lithobius forficatus* (Lithobiomorpha: Lithobiidae) (Türk and Türk 1957). This species has been recorded from the following countries: Germany (Krause 1917 (1919); Türk and Türk 1957), Belgium (Cooreman 1963), former Czechoslovakia (Černý and Samšínák 1971), Poland (Kielczewski and Wiśniewski 1980), and Russia (Ermilov et al. 2007; Khaustov 2000a).

Material examined. 4 HDNs, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 2 HDNs, 5 June 2017, same data; 1 HDN, June 2017, same data.

***Saproglyphus* aff. *hagensis* [striate]**

(Figs. 31A, B)

Here, we treat the genus *Calvolia* Oudemans, 1911 (part.) as a junior synonym of *Saproglyphus* Berlese, 1890 (Fain and Rack 1987; Klimov et al. 2016). *Saproglyphus hagensis* Oudemans, 1911 is

Fig. 30. A, B—*Superioropus huronmontanus*, phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Parawinterschmidtia kneissli*, phoretic deutonymph, dorsal and ventral views, respectively.

known from phoretic deutonymphs in the Netherlands (Oudemans 1919), Belgium (Fain and Rack 1987), Switzerland (Kuhlmann 1998), and Russia

(Bugrov 1997). The *Hylaeus nivalis* (Colletidae) bee was reported as a phoretic host (Kuhlmann 1998). Our specimen is very similar to *S. hagensis*,

Fig. 31. A, B—*Saproglyphus* aff. *hagensis*, phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Saproglyphus waldorfae*, phoretic deutonymph, dorsal and ventral views, respectively.

which has been redescribed from the holotype that came from the Netherlands (Fain 1972), as well as

based on specimens collected in Belgium (Fain and Rack 1987). It differs by the much stronger and

Fig. 32. A, B—*Histiotoma ovalis*, phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Histiotoma piceae*, phoretic deutonymph, dorsal and ventral views, respectively.

longer tibial seta *kT* IV, which clearly extends beyond tarsus IV (in *S. hagensis*, it does not extend-

ing or nearly reaches the tip of tarsus IV); setae *wF* IV are also long and extend tarsus IV (clearly not

Fig. 33. A, B—*Histiostoma pini*, phoretic deutonymph, dorsal and ventral views, respectively.

extending in *S. hagensis*); tarsus III is distinctly longer than 3 times its width at the base (nearly 3 times as long as its base in *S. hagensis*).

Material examined. 1 HDN, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov.

***Saproglyphus waldorfae*
(Fain and Johnston, 1974)**

(Figs. 31C, D)

Our specimen resembles very closely *Saproglyphus waldorfae*, collected from *Allacma fusca* (Sminthuridae) [springtail] in England (Fain and Johnston 1974). There is a minor difference: tarsus IV is longer, as long as the short tarsal seta IV. While in the paratype of *S. waldorfae*, tarsus IV was depicted shorter than the short tarsal seta IV, in the holotype, this seta is longer than the tarsus. These discrepancies may be explained if tarsi IV of the specimens from England were oriented at an angle to the vertical plane of the slide. Other differences include: posterior sternal shield is well-separated from the anterior coxal apodemes III (vs. close to each other in *S. waldorfae*); setae

vi are separated from the eye lenses; pigmented eye spots extend posteriorly to form longitudinal sclerites (in *S. waldorfae*, setae *vi* are adjacent to the eye lenses and longitudinal sclerites are absent/not visible). We consider these differences as artifacts of preservation because our specimen was somewhat compressed as compared to the specimen from England. This is the first record of *Saproglyphus waldorfae* in Russia and continental Europe.

Material examined. 1 HDN, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 5 June 2017, coll. A.A. Khaustov.

Family **Histiostomatidae** Berlese, 1897

***Histiostoma ovalis* (J. Müller, 1860)**

(Figs. 32A, B)

This species is primarily associated with *Ips sexdentatus* in the Western Palaearctic. It is considered an important vector of plant-pathogenic fungi (Fernández *et al.* 2013; Mahunka 1970; Moraza *et al.* 2013; Samšínák 1958; Vissa and Hofstetter 2017). Phoretic deutonymphs of this mite species are very abundant on their bark beetle

Fig. 34. A, B—*Probonomoia pini*, phoretic deutonymph, dorsal and ventral views, respectively, C, D—*Probonomoia sibirica*, phoretic deutonymph, dorsal and ventral views, respectively.

hosts and they can carry a large number of hyperphoretic fungi (Moraza *et al.* 2013). Multiple hyperphoretic fungal ascospores and conidia have been detected in a survey of *H. ovalis*, phoretic on *Ips sexdentatus* in France. Ascospores of *Pichia* (Saccharomycetaceae), *Ophiostoma brunneociliatum*, *Ophiostoma minus*, *Ophiostoma picea*, *Ophiostoma* section *Ceratocystis*, *Ceratocystiopsis minuta* (Ophiostomataceae); conidia of *Lepptographium*, *Sporothrix* (Ophiostomataceae), *Fu-*

sarium sp. (Nectriaceae), *Ceratocystis* (Ceratocystidaceae), *Cladosporium* sp. (Davidiellaceae), *Altenaria* sp. (Pleosporaceae); as well as unidentified yeast have been detected (Levieux *et al.* 1989). Of them, *Ophiostoma minus* is a pathogenic bluestain fungus of economic importance (Gorton and Webber 2000).

The mite host range is (Müller's historical records are also listed for informational purposes): *Ips sexdentatus* (Fernández *et al.* 2013; Levieux

Fig. 35. SEM photographs of mites phoretic on *Ips typographus*. A–C—*Elattoma crossi*, females: A—general view, B, C—detailed view; D–F—*Scutacarus scolyti*, D—general view, E, F—detailed view.

et al. 1989; Mahunka 1968, 1970; Müller 1859 (1860); Samšiňák 1958; Wirth and Garonna 2015), *Ips cembrae* (Mahunka 1968, 1970; Scheucher 1957), *Tomicus minor* (Kielczewski and Wiśniewski 1980), *Orthotomicus laricis* (Müller 1859 (1860)), *Pityokteines curvidens* (Müller 1859 (1860)) (Curculionidae: Scolytinae), *Cerylon histeroides* (Cerylonidae) (Müller 1859 (1860)), *Margarinotus bipustulatus* (Histeridae) (Müller 1859 (1860)), *Platysoma compressum* (Histeridae)

(Mahunka 1976b), and *Dendrolaelaps quadrisetus* (Digamasellidae) (phoretic on *Ips sexdentatus*) (Wirth and Garonna 2015). *Histiostoma ovalis* is known from the following countries: Bulgaria, Austria, Ukraine (Samšiňák 1958), France (Levieux *et al.* 1989; Samšiňák 1958), Belgium (Cooreman 1963), Croatia (Wirth and Garonna 2015), the Czech Republic (Müller 1859 (1860)), Germany (Scheucher 1957; Wirth and Garonna 2015), Hungary (Mahunka 1968, 1970), Italy

Fig. 36. SEM photographs of mites phoretic on *Ips typographus*. A–D—*Aethiophenax ipidarius*, females: A, C—general view, B, D—detailed view; *Iponemus gaebleri*, females: E—general view of elytral declivity with mites, F—detailed view of mites.

(Fernández *et al.* 2013; Wirth and Garonna 2015), Poland (Kielczewski and Wiśniewski 1980), Romania (Mahunka 1970), Slovakia (type locality) (Wirth and Garonna 2015), and Russia (first record).

Remarks. This species was originally described based on a phoretic deutonymph from *Ips sexdentatus* and several other beetle species collected near Brno, the Czech Republic (Mülller 1859 (1860)). The type material is deemed to be lost and a neotype

was designated based on a deutonymph from *Ips sexdentatus* from Slovakia (Wirth and Garonna 2015). It is possible that Scheucher (1957) has identified the same species collected from *Ips sexdentatus* and *Ips cembrae* in Germany under the name *Histiostoma gladiger* (Vitzthum, 1926). The latter species was originally described from *Ips subelongatus* from eastern Russia (Khabarovskiy Krai) (Vitzthum 1926). The main difference be-

Fig. 37. SEM photographs of mites phoretic on *Ips typographus*. A–C—deutonymphs of *Histiostoma piceae* on ventral abdomen of the beetle; D, E—deutonymph of *Histiostoma piceae* (large mites) and females of *Iponemus gaebleri* (small mites) on elytral declivity of the beetle: D—general view, E—detailed view; F—deutonymph of *Uroobovella ipidis* with hyperphoretic deutonymphs of *Histiostoma piceae*.

tween *Histiostoma gladiger* and *Histiostoma ovalis*—the absence of long scapular setae in the former species—was dismissed by several authors (Cooreman 1963; Scheucher 1957) on the ground that these setae could be broken off on Vitzthum's specimen. Samšínák (1958) treated both *H. ovalis* (= *H. gladiger* sensu Scheucher (1957)) and *H. gladiger* s.str. as two valid species. However, Cooreman

(1963) used the name *H. gladiger* for both of these putative species, while Mahunka (1970) used the name *H. ovalis*, which has priority over *H. gladiger*.

Here we provisionally treat *H. ovalis* and specimens from the Western Palaearctic identified as “*H. gladiger*” as the same species, whereas we provisionally consider *H. gladiger* s.str. from the Eastern Palaearctic as a separate species.

Fig. 38. SEM photographs. A—elytral declivity of the beetle with phoretic females of *Iponemus gaebleri* (small mites) and deutonymphs of *Trichouropoda polytricha* (large mite on the left) and *Uroobovella ipidis* (large mite on the right); B, C—deutonymphs of *Uroobovella ipidis* with hyperphoretic deutonymphs of *Histiostoma piceae* between legs II of the beetle, D—deutonymph of *Uroobovella ipidis* with hyperphoretic deutonymphs of *Histiostoma piceae* on elytral declivity of the beetle; E, F—*Trichouropoda karawaiiewi*, female: E—dorsal view, F—ventral view with phoretic deutonymph of *Histiostoma piceae*.

Material examined. 1 HDN, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 1 HDN, 28 May 2017; 3 HDNs, 5 June 2017, same data.

***Histiostoma piceae* Scheucher, 1957**

(Figs. 32C, D, 37A–F, 38C, D)

Histiostoma piceae is a bark beetles specialist, preferring microhabitats where fungal mycelium and spores are abundant (Hofstetter *et al.*

Fig. 39. SEM photographs of mites phoretic on *Ips typographus*. A—females of *Iponeus gaebleri* (small mites), deutonymphs of *Uroobovella ipidis* (large mites) with hyperphoretic deutonymphs of *Histiostoma piceae* on elytral declivity of the beetle, B–D—numerous females of *Iponeus gaebleri* on elytral declivity of the beetle: B—general view, C, D—detailed view.

2013). Mites are commonly associated with *Ips typographus*, who attack the Norway spruce *Picea abies*, but other bark beetle species can be involved (see below). While carried by its coleopteran hosts, phoretic deutonymphs of this mite can transport a large number of hyperphoretic ascospores of fungi that are pathogenic to the following spruce trees: *Ophiostoma bicolor*, *Ophiostoma euophioides*, *Ophiostoma penicillatum*, *Ophiostoma polonicum*, *Ceratocystiopsis minuta* (Moser, Perry *et al.* 1989). Of these fungi, *Ophiostoma polonicum* is the most pathogenic species, which causes obvious discoloration of the sapwood and is able to kill the host tree. Some other fungi (*O. bicolor*, *O. euophioides*) can kill considerable portions of the phloem without killing the host or causing discoloration of the sapwood (Kirisits 1998). In addition, ascospores of the fungal genus *Pichia* (which is commonly associated with decaying plants) were also found (Moser, Perry *et al.* 1989).

Feeding stages of the mite are common in bark beetle galleries when fresh boring dust is available. Deutonymphs, on the other hand, appear when the boring dust disappears (Scheucher 1957). Lab rearing without the presence of host beetles failed to produce a sustainable colony (Scheucher 1957).

Phoretic deutonymphs commonly disperse on *Ips typographus* (Lieutier 1978; Moser *et al.* 1989; Scheucher 1957; Takov *et al.* 2009; Wirth *et al.* 2016), preferring subelytral spaces (Moser and Bogenschütz 1984). Other bark beetle species can also serve as phoretic hosts: *Dryocoetes hectographus* (Kielczewski and Wiśniewski 1980), *Ips typographus japonicus* (Moser *et al.* 1997), *Ips cembrae* (Wirth *et al.* 2016), *Pityogenes chalcographus* (Khaustov *et al.* 2016), *Pityokteines curvidens* (Pernek *et al.* 2008; Pernek *et al.* 2012), *Pityokteines spinidens*, *Pityokteines vorontzowi* (Pernek *et al.* 2008). Notice that the taxonomic identification of the mites from *Pityokteines* in Croatia (Pernek *et al.* 2008; Pernek *et al.* 2012)

Fig. 40. SEM photographs of adults of *Siculobata (Paraleius) leontonycha* phoretic on *Ips typographus*: A, C—general view, B, D–F—detailed view.

has been questioned (Wirth and Pernek 2012). Other phoretic hosts include various beetles and mites occurring in the galleries of the following bark beetles: Staphylinidae (Scheucher 1957), *Siculobata (Paraleius) leontonycha* (Khaustov *et al.* 2016), *Trichouropoda* sp. and *Uroobovella ipidis*. Furthermore, *H. piceae* is known to be hyperphoretic on the *Uroobovella ipidis* mite carried by the *Pityogenes chalcographus* beetle (Khaustov *et al.* 2016).

Histiostoma piceae is distributed in various countries of the Palaearctic region: Bulgaria (Takov *et al.* 2009), Croatia (Pernek *et al.* 2008; Pernek *et al.* 2012; Wirth *et al.* 2016), France (Lieutier 1978), Germany (Burjanadze *et al.* 2008; Moser and Bogenschütz 1984; Scheucher 1957), Japan (Moser *et al.* 1997), Poland (Kielczewski and Wiśniewski 1980), Slovakia (Zamec 2013), Sweden (Moser *et al.* 1989; Moser, Perry *et al.* 1989), and Russia (Khaustov *et al.* 2016). There

Fig. 41. SEM photographs. A–C—phoresy of deutonymphs of *Dendrolaelaps* (*Ipidodendrolaelaps*) *quadrisetus* on elytral declivity of *Ips typographus*: A—general view, B—elytral declivity with mites, C—dorsal view of mite; D–F—female of *Macrocheles ivanovi*: D—dorsal view, E—dorsal view of anterior part of the body, F—ventral view.

is a single record from Canada (Walter and Latonas 2012).

Material examined. 500+ HDNs Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov same data, 28 May 2017; same data, 5 June 2017; 15 June 2017, same data; June 2017, same data.

***Histiostoma pini* Scheucher, 1957**

(Figs. 33A, B)

This species is a bark beetle specialist. The host range includes *Hylastes ater* (Mahunka 1968, 1970; Scheucher 1957), *Hylastes brunneus* (Kiełczewski and Wiśniewski 1980), *Hylastes cunicularius* (Coreman 1963), *Tomicus piniperda* (Kiełczewski and Wiśniewski 1980). *H. pini* is known from

Fig. 42. A—adult of *Cercoleipus kuznetsovi* on *Ips typographus*, B—eggs and larvae of *Iponemus gaebleri* in the galleries of *Ips typographus*.

Germany (Scheucher 1957), Belgium (Cooreman 1963), Poland (Kielczewski and Wiśniewski 1980), Hungary (Mahunka 1968, 1970), and Russia (new record).

Material examined. 100+ HDNs: Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 05 June 2017, same data; June 2017, same data.

***Probonomoia pini* (Scheucher, 1957)**

(Figs. 34 A, B)

This Palaearctic species typically inhabits galleries of bark beetles (Scheucher 1957), while dispersal occurs on a range of wood-visiting arthropods, including the following bark beetles: *Hylastes ater* (Mahunka 1970; Scheucher 1957), *Ips acuminatus* (Michalski and Ratajczak 1989), *Ips cembrae* (Wirth *et al.* 2016), *Ips typographus* (Penttinen *et al.* 2013;

Fig. 43. A—deutonymph of *Dendrolaelaps quadrisetus* in the galleries of *Ips typographus*, B—females of *Aethiophenax ipidarius* phoretic on *Ips typographus*, C–D—feeding of female of *Iponemus gaebleri* on egg of *Ips typographus*: C—physogastric female of *I. gaebleri* on the egg of the beetle, D—physogastric female of *I. gaebleri* with eggs.

Wirth *et al.* 2016), *Tomicus minor* (Michalski and Ratajczak 1989), and *Tomicus piniperda* (Scheucher 1957). The non-bark beetle hosts are: *Hylobius abietis*, *Pissodes pini* (Ermilov *et al.* 2008) (Curculionidae), *Acanthocinus aedilis* (Ermilov and Mokrousov 2008; Samšiňák 1962; Scheucher 1957), *Monochamus galloprovincialis*, *Rhagium inquisitor* (Ermilov and Mokrousov 2008), *Rosalia alpina* (Haitlinger 2004), cerambycid larvae (Scheucher 1957) (Cerambycidae), *Dorcus parallelipedus* (Scheucher 1957) (Lucanidae), *Epuraea* sp., *Glischrochilus quadripunctatus* (Scheucher 1957) (Nitidulidae), *Myzia oblongoguttata* (Scheucher 1957) (Coccinellidae), *Selatosomus aeneus* (Elateridae) (Ermilov *et al.* 2006), *Thanasimus formicarius* (Cleridae) (Scheucher 1957), “*Helops quisquilius* Sturm” (Scheucher 1957) (Tenebrionidae), *Ammophila sabulosa* (Ermilov and Mokrousov 2010) (Sphecidae), *Crossocerus barbipes*, *Ectemnius gut-*

tatus, *Ectemnius spinipes*, *Mellinus arvensis*, *Passaloecus borealis*, *Passaloecus eremita*, *Passaloecus monilicornis*, *Pemphredon lugens*, *Trypoxylon figulus*, *Trypoxylon medium* (Ermilov and Mokrousov 2010) (Crabronidae), *Myrmica laevinodis* (Kielczewski and Wiśniewski 1971), *Formica rufa* (Sevastianov 1970) (Formicidae), *Medetera ambigua* (Fain and Greenwood 1991) (Dolichopodidae), *Lithobius* sp. (Scheucher 1957) (Lithobiidae).

Probonomoia pini has been recorded from the following countries: Croatia (Wirth *et al.* 2016), the Czech Republic (Samšiňák 1962), England (Fain and Greenwood 1991), Finland (Penttinen *et al.* 2013), Germany (Scheucher 1957), Hungary (Mahunka 1970, 1976a), Japan (Kurosa 2000), Poland (Haitlinger 2004; Michalski and Ratajczak 1989), and Russia (Bugrov 1997; Ermilov and Mokrousov 2008, 2010; Ermilov *et al.* 2008; Ermilov *et al.* 2006; Sevastianov 1970).

Fig. 44. A, B—adults of *Siculobata leontonycha* on *Ips typographus*.

Material examined. 1 HDN, Russia, Tyumen Region, Tyumen District, vicinity of settlement Uspenka, 57° 04' N, 65° 04' E, alcohol sediments from pheromone traps for *Ips typographus*, 22 May 2017, coll. A.A. Khaustov; 2 HDNs, 5 June 2017, same data.

***Probonomoia sibirica* (Wirth, 2016)**

(Figs. 34 C, D)

Phoretic deutonymphs of this species are known based on a single record from the great spruce bark

beetle, *Dendroctonus micans*, collected in its galleries in *Pinus silvestris* in Russia. Feeding stages were reared in the lab (Wirth 2016). We collected this mite from *Ips typographus*. The deutonymph of *P. sibirica* is very similar to *Probonomoia humprehti* (Samšínák, 1956) collected from the robber fly *Laphria flava* in the Czech Republic (Samšínák 1956). In particular, they are similar in that the shape of the gnathosoma is trapezoidal.

Material examined. 1 HDN, Russia, Tyumen Region, Tyumen District, vicinity of settlement

Uspenka, 57°04'N, 65°04'E, alcohol sediments from pheromone traps for *Ips typographus*, 15 June 2017, coll. A.A. Khaustov.

PHORESY OF MITES ON *IPS TYPOGRAPHUS*

Using pheromone traps, we collected a total of 13,451 individuals of *Ips typographus* and a broad range of associated mites belonging to 60 species (Table 1). Six of them, *Siculobata leontonycha* (35.44%), *Uroobovella ipidis* (13.01%), *Trichouropoda polytricha* (8.13%), *Dendrolaelaps quadrisetus* (20.57%), *Histiostoma piceae* (10.04%), and *Iponemus gaebleri* (8.92%) were dominant and together represented 96% of all collected mites. *Trichouropoda karawaiewi*, *Schwiebea nova*, *Histiostoma pini*, *Aethiophenax ipidarius*, *Elattoma crossi*, *Coleopygmephorus hylophilus*, *Tarsonemus striatus*, *Tarsonemus typographi*, *Ipsoglyphus bochkovi*, *Naiadacarus* sp., and *Schwiebea* sp.1 nova-group were subdominants, representing together nearly 3% of all collected mites. Other mite species were collected in low numbers.

Some species had specific phoretic attachment sites on bark beetle bodies. Deutonymphs of *Trichouropoda polytricha* and *Uroobovella ipidis* mainly attached to the ventral thorax and elytral declivity of the beetle. More rarely, they attached to the legs and head. Females of *Elattoma crossi* and *Aethiophenax ipidarius* always attached between coxae I and II of the beetle. Females of *Iponemus gaebleri* usually attached to the elytral declivity of the beetle. In cases when large phoretic deutonymphs of uropodid mites also attached to the elytral declivity, tiny tarsonemids hid under large mites. Deutonymphs of *Histiostoma picea* preferred to attach to the elytral declivity and abdomen of the beetle, but if the number of phoretic mite was large, they could attach to any part of the body, as well as to other phoretic mites (hyperphoresy). Deutonymphs of *Dendrolaelaps quadrisetus* were usually phoretic under the elytra of the beetles, but sometimes also on the elytral declivity. Adults of *Siculobata leontonycha* attached to the long hairs of the beetle on the head, thorax or legs. Females of *Ereynetes* sp. and deutonymphs of *Schizosthetus* sp. were observed actively moving around the beetle body.

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Table 1

Abundance of mites phoretic on *Ips typographus* collected by pheromone traps in Western Siberia

№	Mite species and phoretic stage	Location on beetle	Total number of phoretic mites	Percent of total mites found (n=20,966)
1	<i>Trichouropoda polytricha</i> Deutonymph	Mainly on abdomen, between legs	1,706	8.13
2	<i>Trichouropoda karawaiewi</i> Deutonymph	Elytral declivity, thorax	28	0.13
3	<i>Trichouropoda structura</i> Deutonymph	Elytral declivity, thorax	2	<0.01
4	<i>Uroobovella ipidis</i> Deutonymph	Elytral declivity, thorax	2,729	13.01
5	<i>Schizosthetus</i> sp. Deutonymph	All body	12	0.57
6	<i>Dendrolaelaps quadrisetus</i> Deutonymph	Elytral declivity, under elytra	4,313	20.57
7	<i>Dendrolaelaps pini</i> Deutonymph	Unknown	3	0.01
8	<i>Proctolaelaps fiseri</i> Female	All body	5	0.02
9	<i>Gamasellodes tatricus</i> Female	Unknown	1	<0.01
10	<i>Ereynetes</i> sp. Female	All body	13	0.06
11	<i>Mexacheles virginensis</i> Female	Unknown	1	<0.01
12	<i>Dolichocybe sibiriensis</i> Female	Unknown	3	0.01
13	<i>Pyemotes</i> sp. Female	Unknown	1	<0.01
14	<i>Aethiophenax ipidarius</i> Female	Between coxae of legs I and II	21	0.10
15	<i>Microdispodides moseri</i> Female	Unknown	2	<0.01
16	<i>Elattoma crossi</i> Female	Between coxae of legs I and II	63	0.30

17	<i>Coleopygmephorus bogenschutzi</i> Female	Unknown	3	0.01
18	<i>Coleopygmephorus hylophilus</i> Female	Unknown	34	0.16
19	<i>Coleopygmephorus typographus</i> Female	Unknown	1	<0.01
20	<i>Scutacarus pseudoplurisetus</i> Female	Unknown	2	<0.01
21	<i>Scutacarus scolysi</i> Female	Between coxae of legs I and II	8	0.03
22	<i>Scutacarus muscocicola</i> Female	Unknown	3	0.01
23	<i>Scutacarus palustris</i> Female	Unknown	7	0.03
24	<i>Iponemus gaebleri</i> Female	Elytral declivity, under elytra	1,871	8.92
25	<i>Tarsonemus striatus</i> Female	Unknown	49	0.23
26	<i>Tarsonemus bistridentati</i> Female	Unknown	2	<0.01
27	<i>Tarsonemus typographi</i> Female	Unknown	38	0.18
28	<i>Heterotarsonemus lindquisti</i> Female	Unknown	2	<0.01
29	<i>Siculobata leontonycha</i> Adults	Mainly on the head and thorax	7,431	35.44
30	<i>Acarus</i> sp. Deutonymph	Unknown	8	0.03
31	<i>Boletoglyphus boletophagi</i> Deutonymph	Unknown	2	<0.01
32	<i>Forcellinia wasmanni</i> Deutonymph	Unknown	2	<0.01
33	<i>Ipsoglyphus bochkovi</i> Deutonymph	Unknown	38	0.18
34	<i>Kuzinia laevis</i> Deutonymph	Unknown	4	0.01
35	<i>Naiadacarus</i> sp. Deutonymph	Unknown	43	0.20
36	<i>Schwiebea</i> sp. <i>eurynympha</i> -group [punctate dorsum] Deutonymph	Unknown	1	<0.01
37	<i>Schwiebea</i> sp. [small, unsclerotized, <i>1a</i> , <i>3a</i> filiiform] Deutonymph	Unknown	1	<0.01
38	<i>Schwiebea nesbitti</i> Deutonymph	Unknown	2	<0.01

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39	<i>Schwiebea nova</i> Deutonymph	Unknown	210	1.00
40	<i>Schwiebea</i> sp.1 <i>nova</i> -group [two tibial setae, regular attachment organ] Deutonymph	Unknown	33	0.15
41	<i>Schwiebea</i> sp. <i>nova</i> -group [two tibial setae, wide attachment organ] Deutonymph	Unknown	5	0.02
42	<i>Schwiebea</i> sp. <i>nova</i> -group [granulate dorsum, short legs III–IV] Deutonymph	Unknown	4	0.01
43	<i>Schwiebea scheucherae</i> Deutonymph	Unknown	4	0.01
44	<i>Thyreophagus corticalis</i> Deutonymph	Unknown	1	<0.01
45	<i>Thyreophagus entomophagus</i> Deutonymph	Unknown	2	<0.01
46	<i>Thyreophagus</i> aff. <i>odyneri</i> Female	Unknown	1	<0.01
47	<i>Tyrophagus putrescentiae</i> Adults	Unknown	1	<0.01
48	<i>Divilia</i> aff. <i>occidentalis</i> Deutonymph	Unknown	4	0.01
49	<i>Divilia</i> sp. Deutonymph	Unknown	2	<0.01
50	<i>Nanacarus</i> sp.1 Deutonymph	Unknown	3	0.01
51	<i>Nanacarus</i> sp.2 Deutonymph	Unknown	6	0.02
52	<i>Superioropus huronmontanus</i> Deutonymph	Unknown	12	0.05
53	<i>Parawinterschmidtia kneissli</i> Deutonymph	Unknown	7	0.03
54	<i>Saproglyphus</i> aff. <i>hagensis</i> Deutonymph	Unknown	1	<0.01
55	<i>Saproglyphus waldorfae</i> Deutonymph	Unknown	1	<0.01
56	<i>Histiostoma ovalis</i> Deutonymph	Unknown	5	0.02
57	<i>Histiostoma piceae</i> Deutonymph	All body	2,105	10.04
58	<i>Histiostoma pini</i> Deutonymph	Unknown	100	0.47
59	<i>Probonomoia pini</i> Deutonymph	Unknown	3	0.01
60	<i>Probonomoia sibirica</i> Deutonymph	Unknown	1	<0.01