

To the memory of Jan Koteja

Extinct four-winged precoccids and the ancestry of scale insects and aphids (Hemiptera)

Вымершие четырёхкрылые прекокциды и происхождение червецов и тлей (Hemiptera)

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KEY WORDS: scale insects, coccids, aphids, Coccoomorpha, Aphidomorpha, Sternorrhyncha, Hemiptera, Boreoscytidae, Pincombeidae, Simulaphididae, Naibiidae, Ortheziidae, fossils, Sakhalin amber, phylogeny, Permian, Triassic, Jurassic, Paleocene.

КЛЮЧЕВЫЕ СЛОВА: червецы, тли, Coccoomorpha, Aphidomorpha, Sternorrhyncha, Hemiptera, Boreoscytidae, Pincombeidae, Simulaphididae, Naibiidae, Ortheziidae, ископаемые, сахалинский янтарь, филогения, пермь, триас, юра, палеоцен.

ABSTRACT. The Naibiidae **fam.n.** (Triassic–Paleocene) is described, comprising *Cocavus supercubitus* **gen. et sp.n.** (Cocavinae **subfam.n.**), *Panirena sukatshevae* **gen. et sp.n.**, *P. tenella* **sp.n.** and *Naibia zherichini* **gen. et sp.n.** This family, demonstrating several coccid apomorphies combined with still aphid-like habitus, is placed in the infraorder Coccoomorpha s.l. (as a separate superfamily) and considered to be ancestral to the true scale insects. Close relationship of Aphidomorpha and Coccoomorpha is confirmed by fossils, and both groups are derivable from the same stem lineage represented by Boreoscytidae (Permian), Pincombeidae (Permian–Triassic) and Simulaphididae **fam.n.** (Permian *Simulaphis shaposhnikovii* **gen. et sp.n.**, possibly also Triassic). These three families are included in the suborder Aphidinea s.l. (as infraorder Pincombeomorpha) along with aphids and coccids. New synonymies are established and *Dinoscyta microcephala* **gen. et sp.n.** is described in Boreoscytidae. All the taxa dealt with are keyed, and a phylogram of Aphidinea is proposed. Evolution of coccid forewing is discussed.

РЕЗЮМЕ. Описано семейство Naibiidae **fam.n.** (триас–палеоцен), включающее *Cocavus supercubitus* **gen. et sp.n.** (Cocavinae **subfam.n.**), *Panirena sukatshevae* **gen. et sp.n.**, *P. tenella* **sp.n.** и *Naibia zherichini* **gen. et sp.n.** Это семейство, демонстрирующее ряд кокцидных апоморфий в сочетании с ещё афидным габитусом, отнесено к инфраотряду Coccoomorpha s.l. (в качестве отдельного надсемейства) и рассматривается как предковое для настоящих червецов. Близкое родство Aphidomorpha и Coccoomorpha подтверждено ископаемыми: обе группы произошли от предкового ствола, представленного семей-

ствами Boreoscytidae (пермь), Pincombeidae (пермь–триас) и Simulaphididae **fam.n.** (пермь: *Simulaphis shaposhnikovii* **gen. et sp.n.**, возможно также триас). Эти три семейства включены в подотряд Aphidinea s.l. (как инфраотряд Pincombeomorpha) наряду с тлями и червецами. Установлены новые синонимы и описан *Dinoscyta microcephala* **gen. et sp.n.** в семействе Boreoscytidae. Для всех рассматриваемых таксонов даны определительные таблицы. Приведена филогенетическая диаграмма Aphidinea. Обсуждается эволюция переднего крыла червецов.

Introduction

Coccids (or scale insects) and aphids are believed to be more closely related to one another than to the remaining two subdivisions of Hemiptera Sternorrhyncha (psyllids and whiteflies), as first pointed out by Börner [1904] and later confirmed by Theron [1958] and Schlee [1969a, b]. Aphids and coccids always appear as sister groups in the molecular phylogenetic analyses [von Dohlen & Moran, 1995; Campbell et al., 1995; Aleshin et al., 1995]. The fossil record of aphids is traced back to the Triassic [Heie, 1987; Shcherbakov & Wegierek, 1991]. Permian Archescytinidae (Fig. 1) once regarded as ancestral to aphids [Mordvilko, 1934] (in fact to all the other Hemiptera [Popov, 1980]) are separated from them by a distinct gap which could be filled with the families Boreoscytidae (Permian), Pincombeidae (Permian–Triassic), and Simulaphididae **fam.n.** (Permian and possibly Triassic).

The earliest undoubted scale insects known from the Late Jurassic (undescribed, see below) and earliest Cretaceous [Koteja, 1988, 1989, 1999] are much younger than

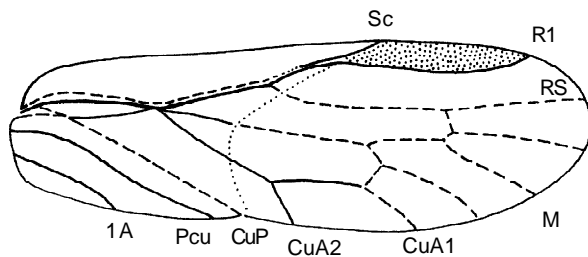


Fig. 1. *Archescytina permiana* Tillyard, 1926, holotype, Lower Permian of Kansas: forewing venation. Here and later in venation diagrams, concave veins, grooves and folds in broken line, nodal line in dotted line, pterostigma stippled.

Рис. 1. *Archescytina permiana* Tillyard, 1926, голотип, нижняя пермь Канзаса: жилкование переднего крыла. Здесь и далее в схемах жилкования вогнутые жилки, бороздки и складки показаны прерывистой линией, нодальная линия пунктиром; птеростигма заполнена точками.

aphids; *Mesococcus* Becker-Migdisova, 1959 from the Early Jurassic of Kyrgyzstan (formerly considered to be the Triassic) is not a coccid [Koteja, 1990]. "All the available [scale insect] fossils are generally similar to the recent forms, and none shows any 'intermediate' condition between the coccids and the suggested aphid sister group; but it must be kept in mind that coccid male at some time had functional mouthparts and well-developed metathoracic wings, the female was alate, the tarsus was provided with two claws, etc. The problem is whether we will be clever enough to recognize ancestors of scale insects in such forms as and when they have been discovered" [Koteja, 1990: 158]. Now, fortunately having such fossils at hand we should only attempt to be 'clever enough'. Compression fossils and amber inclusions described below in Naibiidae **fam.n.** (Triassic–Paleocene) confirm the supposition that coccids evolved from aphid-like ancestors. First preliminary account on this family was given at the VI International Symposium of Scale Insect Studies, Cracow, 1990 [Shcherbakov, 1990].

Type specimens of the new taxa described below are deposited in the Paleontological Institute, Russian Academy of Sciences, Moscow (PIN) and the Natural History Museum, London (NHM).

Taxonomy

Suborder Aphidinea Handlirsch, 1903, *sensu lato*

REVISED DIAGNOSIS. Small Hemiptera (except for some Permian forms) with membranous wings. Hindwing much shorter than forewing and coupled with it in flight or lost. Complete concave Sc adjoining nearly straight convex R–R1 (in forewing, Sc apex is free and termed dSc). In forewing, C ecarinate and claval veins (Pcu and 1A) fused at least distally. Forewing CuA2 supporting coupling fold (and usually continuing CuA stem), nodal line running distad of CuA2, clavus narrow (CuP separating it usually reduced to claval fold and could be lost altogether); if not so, hindwing minute or absent. Metanotum smaller and less convex than mesonotum. Coxae widely separated (distant from midventral line). Hind legs not jumping (the only known exception: Early Cretaceous aphid, *Bajsaphtis* Shaposhnikov, 1985 [Wegierek 1990]).

KEY TO SUBGROUPS OF APHIDINEA S.L. (FOREWING)

1. Basal cell (between R+M and CuA base) and crossvein *m-cu* present. RS branched. Clavus with Y-vein Boreoscytidae
- Basal cell, free CuA base and *m-cu* absent. RS simple or reduced. Clavus with one simple vein 2
2. *r-m* present. M strong and convex up to nodal line. RS originating well before small pterostigma. Claval vein remote from posterior margin Pincombeidae
- *r-m* absent. M fold-like before nodal line, or originating beyond it, or reduced 3
3. RS originating well before enlarged pterostigma. CuA1 much shorter than CuA stem. Claval vein remote from posterior margin Simulaphididae **fam.n.**
- RS originating near base of pterostigma or beyond it, or reduced. CuA1 not shorter than CuA stem, or CuA simple or reduced. Claval vein (sub)marginal 4
4. Coupling fold reaching at least CuA2. M three-branched to simple 5
- Coupling fold restricted to wing base (hindwing reduced to hamulohaltere). Both M and CuA simple or reduced Cocomorpha s.str.
5. Sc extending (as a filiform convex structure) into pterostigma. Claval margin slightly angulate. Long CuA stem margined with a groove posteriorly. RS long, M simple Naibiidae **fam.n.**
- Sc entering costal margin at base of pterostigma. Claval margin not angulate. CuA stem without groove, often undeveloped, if long then RS reduced or M branched ... Aphidomorpha

Infraorder Pincombeomorpha Shcherbakov, 1990

Superfamily Pincombeoidea Tillyard, 1922

DIAGNOSIS. Forewing: RS originating well before pterostigma, convex up to nodal line and concave beyond it; nodal line crossing RS (near base); M and CuA forming a short common stalk; claval vein(s) remote from posterior margin, Pcu+1A entering margin before claval apex.

COMPOSITION. Boreoscytidae, Pincombeidae and Simulaphididae **fam.n.**

REMARKS. Boreoscytids and pincombeids were variously placed within Sternorrhyncha. Becker-Migdisova [1962] included Pincombeidae in Aphidomorpha, but later [1985b] erected the superfamily Pincombeoidea within Psylomorpha. Szelegiewicz [1971] and then Klimaszewski & Wojciechowski [1992] assigned both these families to Psylomorpha on account of misinterpreted or homoplastic forewing characters: C 'thickened' in Pincombeidae (in fact not); M and CuA forming a common stalk (acquired independently as well as in some Auchenorrhyncha and Psocoptera).

Family Boreoscytidae Becker-Migdisova, 1949

REVISED DIAGNOSIS. Largest Aphidinea with rich venation. Forewing (5–23 mm long): Sc+R+M elbowed near base; basal cell subtriangular, subcostal groove distad of it with a convex vein-like posterior margin; RS with 2–5(6), M with 3–10 branches, both normally pectinate towards margin; both *r-m* and *m-cu* present; clavus with Y-vein occupying its posterior half, 1A and Pcu+1A connected to margin by oblique veinlets. Hindwing with coupling lobe at anterior margin before Sc apex, 1.3–1.4 times shorter than forewing and differing from it in: basal cell widening towards apex, broader pterostigmal cell, less branched RS and M (both concave throughout as well as CuA), and free Pcu and 1A.

Tarsi of 3 segments (third longest), with well-developed pretarsal lobes. Ovipositor of cutting type, short, not reaching apex of abdomen (structure of the tarsi and ovipositor is known only in *Dinoscyta* **gen.n.**).

REMARKS. The Lower Cretaceous *Megaleurodes* tentatively assigned to the Boreoscytidae [Hamilton 1990] has nothing in common with this family and probably belongs to Fulgoroidea on account of the tegulae and hind leg pectens; Sorensen et al. [1995] tentatively related the genus to Fulgoridiidae on account of non-aristoid antenna, but the antennal structure seems to be misinterpreted in the fossil.

KEY TO GENERA AND SPECIES OF BOREOSCYTIDAE (FOREWING)

1. Costal space basally wide with anterior margin arcuate. M with 4–10 branches. CuA–CuA2 at ca. 50° to R stem and CuA1 base. Forewing elongate (ca. 3:1), 12–23 mm long *Dinoscyta* **gen.n.**
 — *D. microcephala* **sp.n.**, Lower Permian of Urals
- Costal space narrow throughout with anterior margin nearly straight. M with 3–5 branches. CuA–CuA2 at ca. 80° to R stem and CuA1 base. Forewing subtriangular (ca. 2.2:1), 5.6–9.0 mm long *Boreoscyta* Becker-Migdisova, 1949, Middle Permian of Northern Russia ... 2
2. RS and M with (6)7–11 branches altogether, RS usually forking before midlength. Both CuA base and CuA stem nearly straight (or latter slightly sigmoidal), M+CuA distinct. Forewing (6.8) 7.5–9.0 mm long
 *B. nefasta* Becker-Migdisova, 1949
- RS and M with 6(7) branches altogether, RS forking beyond midlength. Both CuA base and CuA stem slightly arched backwards, M+CuA extremely short (or undeveloped). Forewing 5.6–6.4 mm long
 *B. latipennis* (Martynov, 1933), **comb.n.**

Genus *Dinoscyta* Shcherbakov, **gen.n.**

TYPE SPECIES. *D. microcephala* **sp.n.**

DIAGNOSIS. Largest boreoscytids. Forewing: elongate (ca. 3:1); costal space widening towards base; subcostal groove deep; R1 reaching far beyond first RS fork and subparallel to RS1; second RS fork short or absent; RS base (up to nodal line) very short and oblique; M with 4–10 branches; CuA–CuA2 at ca. 50° to R stem and CuA1 base. Hindwing: 1.4 times shorter than forewing; Sc+R+M elbowed near base; pterostigmal cell triangular; RS with long fork; M with up to 7 branches; CuA2 subparallel to CuA1; claval area somewhat enlarged. Head small, clypeus swollen (with muscle impressions), rostrum longer than height of head capsule. Pronotum not enlarged. Coxae elongate and probably widely separated, femora wider than tibiae. Abdomen long and massive.

COMPOSITION. Monobasic.

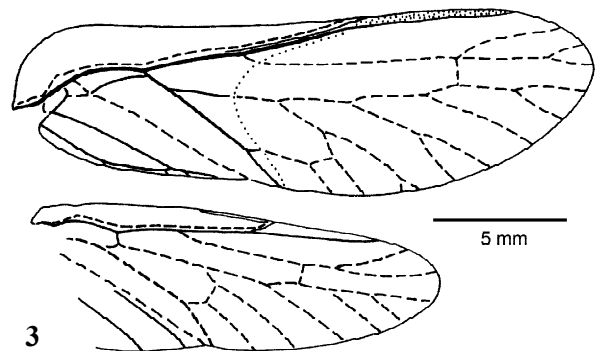
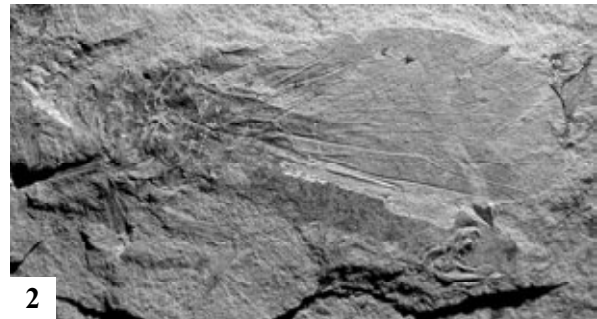
REMARKS. The increase of hindwing claval area in this genus (not characteristic of other Aphidinea) is probably connected with large body size and massive abdomen.

ETYMOLOGY. Greek *deinos*, terrible, and genus *Boreoscyta*.

Dinoscyta microcephala Shcherbakov, **sp.n.**

Figs 2–3

MATERIAL. Holotype: female, PIN 1700/4282 (part & counterpart), paratypes: left forewing PIN 1700/4284 and left hindwing PIN 1700/4283 (parts & counterparts), and incomplete insect (sex unknown) PIN 1700/4914 (on the same rock slab as the holotype of *Mycteroptila dina* Rasnitsyn) — Chekarda 25 km southeast of Suksun, Sylva River, Perm Region, Russia; Lower Permian, Kungurian, Koshelevka Formation.



Figs 2–3. *Dinoscyta microcephala* **gen. et sp.n.**, Lower Permian of Urals: 2 — holotype PIN 1700/4282, female; 3 — fore- and hindwing venation (based on paratypes PIN 1700/4284 and 4283, CuA fork in forewing after holotype).

Рис. 2–3. *Dinoscyta microcephala* **gen. et sp.n.**, нижняя пермь Урала: 2 — голотип ПИН 1700/4282, самка; 3 — жилкование переднего и заднего крыла (по паратипам ПИН 1700/4284 и 4283, развилки CuA в переднем крыле по голотипу).

DESCRIPTION. Forewing: 21.5–22.6 mm long, 6.7–7.1 mm wide; costal margin strongly arched near base and then feebly concave up to almost linear (more than 10:1) pterostigma; basal cell narrow; both R+M and CuA base slightly arched forwards; RS straight from nodal line to fork, with 3 branches; M with 7–10, CuA with 2–4, both with 11–12 branches altogether; CuA1 crossed by nodal line and feebly bent at ca. 1/3 of the way to *m-cu*; claval angle extremely obtuse. Hindwing: 15.3–16.2 mm long; costal margin feebly concave before a long coupling lobe; *r-m* close to RS bifurcation; M with 5–7 branches and (nearly) pectinate towards margin. Head capsule ca. 2.7 mm high, rostrum no less than 3.0 mm long. Legs clinging; coxae deflected cephalad in lateral aspect. Femora slightly widened to apices, especially hind one (which is nearly twice as wide apically as tibia), claws strong; hind femur 4.0, tibia 5.5, and tarsus 2.3 mm long. Abdomen showing no visible segmentation, ca. 17 mm long (total body length ca. 26 mm), apex with an indistinct outgrowth directed ventrally (?anal tube). Ovipositor well-developed, with arcuate valvulae and robust valvifers.

REMARKS. A further specimen from the same locality (PIN 1700/4913) is a much smaller male (body 15 mm, forewing 12 mm long) with less elongate wings (forewing 2.9:1) and pterostigma (8:1) and poorer venation (in forewing, RS once forked and M with 4 branches). It may belong to the same species, the more so that striking sexual dimorphism is highly probable in *Boreoscyta* and *Naibia* **gen.n.** as well.

ETYMOLOGY. Greek *mikros*, small, and *kephale*, head.

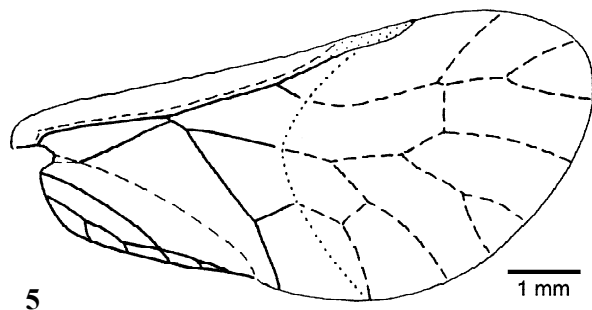
Genus *Boreoscyta* Becker-Migdisova, 1949*Boreoscyta* Becker-Migdisova, 1949: 172*Archescytinopsis* Becker-Migdisova, 1949: 174, **syn.n.**TYPE SPECIES. *B. nefasta* Becker-Migdisova, 1949.

DISTRIBUTION. Soyana River, Arkhangelsk Region; Middle Permian (Upper Permian according to stratigraphic scale used in Russia before 2005), Lower Kazanian, Iva-Gora Beds.

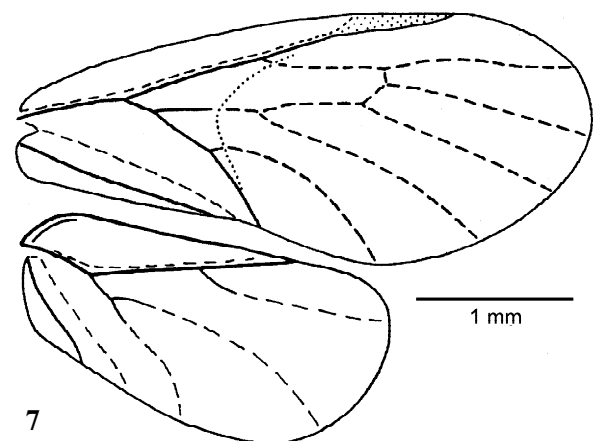
REMARKS. Re-examination of the type material and seven additional forewings from the type locality of all known Middle–Upper Permian boreoscytids allows reducing two genera and seven species formerly described to two variable and poorly separated species of a single genus (possibly just females and males of a single species).

Boreoscyta nefasta Becker-Migdisova, 1949

Figs 4–5

Boreoscyta nefasta Becker-Migdisova, 1949: 173*Boreoscyta mirabilis* Becker-Migdisova, 1949: 172, **syn.n.***Boreoscyta imperfecta* Becker-Migdisova, 1949: 174, **syn.n.***Archescytinopsis flexuosa* Becker-Migdisova, 1949: 175, **syn.n.***Coleoscyta ramosa* Becker-Migdisova, 1960: 43, **syn.n.**REMARKS. The holotype of *B. mirabilis* deposited in PIN bears the collection no. PIN 94/587 (not given in the original description). One of two *A. flexuosa* syntypes (PIN 94/1017) is designated here as a lectotype in accordance with Becker-Migdisova's note on its collection label, the other belongs rather to *B. latipennis*.*Boreoscyta latipennis* (Martynov, 1933), **comb.n.***Sojanoscytina*(?) *latipennis* Martynov, 1933: 887*Archescytinopsis latipennis* (Martynov); Becker-Migdisova, 1949: 175*Archescytinopsis vitrea* Becker-Migdisova, 1949: 176, **syn.n.**Figs 4–5. *Boreoscyta nefasta* Becker-Migdisova, 1949. PIN 3353/716, Middle Permian of North European Russia; 4 — forewing; 5 — venation of forewing.Рис. 4–5. *Boreoscyta nefasta* Becker-Migdisova, 1949. ПИН 3353/716, средняя пермь севера Европейской России: 4 — переднее крыло; 5 — жилкование переднего крыла.

Family Pincombeidae Tillyard, 1922

REVISED DIAGNOSIS. Forewing: 3.0–5.5 mm long; basal cell and free CuA base absent; pterostigma short; RS simple; M with three long branches; *m-cu* (rarely also *r-m*) absent; RS, M and CuA1 concave beyond nodal line; coupling fold at CuA2; clavus with a simple vein near midline. Hindwing: much shorter than forewing (at most 1.5 times shorter, not twice as stated by Becker-Migdisova [1985b]); RS, M and CuA simple, distally concave, two latter usually forming a short common stalk; narrow claval area with a short simple vein; free CuA base and crossveins absent. Body compact. Legs short; tarsi of three short segments. Abdomen short, ovoid (body structure is known in the type genus only; Figs 6–7).REMARKS. *Psocopsyllidium* Davis, 1942, *Psyllidiana* Evans, 1943 and *Protopsylllops* Evans, 1943 were synonymized with *Pincombea* Tillyard, 1922; hindwing described as *Eupincombea* Davis, 1942 (holotype reexamined) probably belongs to this genus as well [Becker-Migdisova, 1985b]. *Protopincombea* Evans, 1943 was transferred to Archescytinidae [Becker-Migdisova, 1985a]. Body characters and relative size of the hindwing of *Pincombea* were studied from undescribed NHM specimens.Figs 6–7. *Pincombea* sp., Upper Permian of Australia: 6 — NHM In. 45314; 7 — fore- and hindwing venation, forewing based on *P. media* (Davis, 1942) and *P. davisia* (Evans, 1943), hindwing NHM In. 45221.Рис. 6–7. *Pincombea* sp., верхняя пермь Австралии: 6 — NHM In. 45314; 7 — жилкование переднего и заднего крыла, переднее по *P. media* (Davis, 1942) и *P. davisia* (Evans, 1943), заднее NHM In. 45221.

KEY TO GENERA OF PINCOMBEIDAE (FOREWING)

1. R stem converging with C. Straight R1 bordering narrow pterostigma. Long *r-m* connecting straight RS to M1 base. CuA2 at ca. 60° to R stem, longer than width of CuA fork. Clavus narrow triangular *Pincombea* Tillyard, 1922.
5 spp., Upper Permian of Australia
(see Becker-Migdisova [1985b])
- R stem subparallel to C. R1 bent at base of (and arched below) small lanceolate pterostigma. Very short *r-m* connecting RS and M1+2 bases bent towards each other. CuA2 at ca. 90° to R stem, not longer than width of CuA fork. Clavus linear *Madygenopsyllidium* Becker-Migdisova, 1985
M. djailautshoense Becker-Migdisova, 1985,
Middle or Upper Triassic of Kyrgyzstan.

Family Simulaphididae Shcherbakov, **fam.n.**TYPE GENUS. *Simulaphis* **gen.n.**

DIAGNOSIS. Forewing: ca. 3.5 mm long; basal cell and free CuA base absent; R1 sharply bent at base of enlarged lanceolate pterostigma; RS simple, convex before nodal line; M fold-like before nodal line, with three long branches; crossveins absent; CuA fork very small; coupling fold reaching near CuA1 apex; claval fold distinct (CuP not developed as a vein); clavus with a simple vein near midline.

COMPOSITION. Monobasic (but see REMARKS under the genus).

Genus *Simulaphis* Shcherbakov, **gen.n.**TYPE SPECIES. *S. shaposhnikovi* **sp.n.**

DIAGNOSIS. Costal margin arched basally and then nearly straight up to lanceolate pterostigma (ca. 4:1) occupying nearly 0.3 of wing length. R1 converging with C. CuA1 twice shorter than CuA stem. CuA2 at ca. 90° to R stem, not longer than width of CuA fork. Clavus narrow triangular.

COMPOSITION. Monobasic.

REMARKS. A basal half of the wing (PIN 3320/32; estimated length 4.5 mm) resembling *Simulaphis* (M seems to be fold-like proximally; CuA1 1.4 times shorter than CuA stem), but with the costal space narrow like in *Madygenopsyllidium*, was found in the Upper Triassic (Protopyvka Formation) of East Ukraine (Garazhivka near Izyum; Kharkov Region) and may represent another genus of the family.

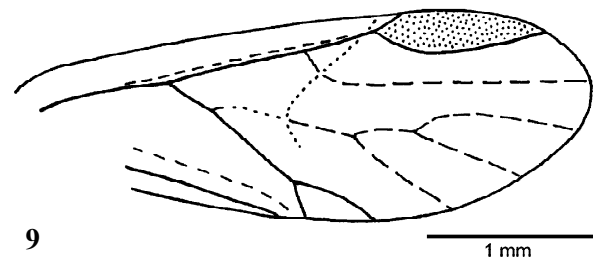
ETYMOLOGY. Latin *simulo*, imitate, and genus *Aphis*; gender feminine.

Simulaphis shaposhnikovi Shcherbakov, **sp.n.**

Figs 8–9

MATERIAL. Holotype: right forewing NHM In. 45240 & 45309 (part & counterpart) — Warner's Bay, nr. Belmont, New South Wales, Australia, Uppermost Permian.

DESCRIPTION. Forewing (somewhat distorted distally and incomplete near base) 3.5 mm long, 1.35 mm wide, elongate (2.6:1). R(+M) nearly straight at CuA origin. Sc as faint groove. Proximal R1 continued by dSc. RS leaving about 2/3 of distance from CuA origin to pterostigma and consisting of short, subtransverse, feebly convex base and longitudinal, slightly sinuous (perhaps originally more straight), distinctly concave remaining part. M originating from CuA stem not close to its base, indistinct and fold-like before nodal line and concave beyond it; M1+2 thrice shorter than M1. CuA–CuA1 sharply convex, CuA2 less so; CuA fork small, adjacent to wing margin; CuA stem not continued by CuA2. Nodal line passing before dSc (C depigmented there) and probably distad of CuA1 apex. Membrane smooth. Veins dark; pterostigma dark, slightly raised.



Figs 8–9. *Simulaphis shaposhnikovi* **gen. et sp.n.**, holotype NHM In. 45240 & 45309, Upper Permian of Australia, forewing: 8 — NHM In. 45309; 9 — venation (natural wing shape and vein course restored).

Рис. 8–9. *Simulaphis shaposhnikovi* **gen. et sp.n.**, голотип NHM In. 45240 & 45309, верхняя пермь Австралии, переднее крыло: 8 — NHM In. 45309; 9 — жилкование (восстановлены первоначальная форма крыла и положение жилок).

REMARKS. The holotype wing is preserved with the upper and lower membranes separated (the case not uncommon in alcohol preserved modern aphids) and displaced (e.g. along M1 and M2), with some fragments of the lower membrane separated and overturned (e.g. CuA fork, and most probably also some 'extra veinlets' visible on the photo but not figured in the venation diagram); displacement of M relative to RS and CuA confirms that both *r-m* and *m-cu* crossveins are really absent.

ETYMOLOGY. To the memory of Georgy Ch. Shaposhnikov, eminent aphidologist.

Infraorder Cocomorpha Fallen, 1814, sensu lato

REVISED DIAGNOSIS (winged forms). Forewing: Sc tracheate, extending distally along R–R1; RS concave or lost; M simple, concave and (at least proximally) fold-like, CuA margined with a groove posteriorly (one or both veins may be lost); crossveins absent; claval margin angulate with simple marginal Pcu+1A; membrane tuberculate to corrugate. Hindwing, if not lost or reduced to hamulohaltere, with 2 convex oblique veins. Head with persistent larval eyes. Pronotum and metanotum more or less reduced. Mesepisternum with lateropleurite (if the latter desclerotized then its ridged borders retained). Tarsi of 1–2 segments with 1–2 claws, pretarsal lobes lacking. Anal tube never transformed into cauda.

COMPOSITION. Naibioidea **superfam.n.**, Orthezioidea (=Archaeococcoidea) and Coccoidea s.str. (=Neococcoidea).

Superfamily Naibioidea Shcherbakov, **superfam.n.**

DIAGNOSIS. Coccid sexual dimorphism not developed (both sexes presumably flying and feeding). Forewing with coupling fold reaching CuA2. Hindwing well-developed. Antennae with rhinaria and processus terminalis.

COMPOSITION. Naibiidae **fam.n.**

Family Naibiidae Shcherbakov, **fam.n.**TYPE GENUS. *Naibia* **gen.n.**

DIAGNOSIS. Small aphid-like Aphidinea. Forewing: 1–5 mm long; costal space narrow; Sc extending distally (as a filiform convex structure in groove along R) beyond proximal limit of pterostigmal thickening; R1 curved along margin and nearly reaching wing apex; RS long; M originating from base of CuA stem (rarely from base of R stem); long CuA stem (as well as R+M+CuA) margined with a groove posteriorly; claval margin slightly angulate; membrane tuberculate (sometimes also partly corrugate). Hindwing: much smaller than forewing; main vein nearly straight; two convex oblique veins. Head flattened dorsoventrally. Antennae 5–6-segmented with rounded subapical rhinaria and a short processus terminalis. Compound eye with comparatively few ommatidia, larval eye forming ocular tubercle. Thorax compressed laterally, pronotum short, mesonotum humped with prescutum subtriangular, metanotum membranized. Mesothorax with a transverse ventral suture. Tarsi of 2 segments (first one short and triangular) with 2 claws. Abdomen with small two-segmented anal tube (structure of the hindwing, antennae, legs and abdomen is known only in the type genus).

KEY TO GENERA AND SPECIES OF NAIBIIDAE (FOREWING)

- Sc entering C basad of RS origin. CuA stem continued rather by convex CuA1. CuA2 usually doubled (replaced by a pair of parallel branches). Forewing 4.5 mm or longer *Coccavinae* **subfam.n.**
Coccavus **gen.n.**: *C. supercubitus* **sp.n.**, Middle or Upper Triassic of Kyrgyzstan
 — Sc extended along R1 beyond RS origin. CuA stem continued rather by a single CuA2. Forewing 4.3 mm or shorter *Naibiinae* **subfam.n.** ... 2
- CuA1 convex, about as thick as CuA2, the latter arched forwards. Forewing ca. 1–2 mm long with membrane sparsely tuberculate *Naibia* **gen.n.**
N. zherichini **sp.n.**, Paleocene of Sakhalin
 — CuA1 concave (sometimes except for the very base) and feeble as well as M and RS. CuA2 arched backwards. Forewing ca. 3–4 mm long with membrane densely tuberculate *Panirena* **gen.n.** ... 3
- RS leaving about midlength of R–R1. CuA1 convex at base. Membrane corrugate near posterior wing margin *P. sukatshevae* **sp.n.**
 Upper Jurassic or Lower Cretaceous of eastern Siberia
 — RS leaving about 2/3 of R–R1 length. CuA1 concave throughout, very feeble as well as M *P. tenella* **sp.n.**
 Middle Jurassic of southern Siberia

Subfamily Coccavinae Shcherbakov, **subfam.n.**TYPE GENUS. *Coccavus* **gen.n.**

DIAGNOSIS. Larger naibiids. Forewing: Sc entering C basad of RS origin; CuA stem continued by a convex CuA1 (CuA–CuA1 usually straight); CuA2 usually doubled (represented with two branches, CuA2 and CuA3).

COMPOSITION. Monobasic.

Genus *Coccavus* Shcherbakov, **gen.n.**TYPE SPECIES. *C. supercubitus* **sp.n.**

DIAGNOSIS. As for subfamily.

COMPOSITION. Monobasic.

ETYMOLOGY. Genus *Coccus*, and Latin *avus*, grandfather; gender masculine.

Coccavus supercubitus Shcherbakov, **sp.n.**

Figs 10–11

MATERIAL. Holotype: left forewing PIN 2555/2312 (part & counterpart); paratypes: right forewings PIN 2555/2392, 2785/3544 and left forewing 2555/2936 (wings distorted due to linear deformation of clay matrix) — Dzhauloucho, Madygen 30 km west of Isfara, southern Fergana, Kyrgyzstan; Middle or Upper Triassic, Ladinian–Carnian, Madygen Formation.

DESCRIPTION. Forewing 4.5–6.3 mm long, 1.9–1.3 mm wide (variation of linear measurements is exaggerated by rock deformation, wing area being less variable: wing length multiplied by width 7.3–8.6 mm²). Costal space rather wide, C and R+M subparallel before CuA origin. R(+M) distinctly bent near CuA origin. Pterostigmal thickening very narrow, without groove along R–R1. RS leaving about midlength of R–R1. CuA2 normally (except for PIN 2555/2936) doubled, CuA2 and CuA3 brought together or widely separated, CuA–CuA1 straight or slightly bent at their origins, and groove behind CuA sometimes traceable up to CuA2. Claval fold visible, coupling fold reaching distad of CuA2. Posterior claval angle about halfway to posterior-most CuA branch. Membrane indistinctly densely tuberculate.

ETYMOLOGY. Latin *super*, over, and cubital vein.

Subfamily Naibiinae Shcherbakov, **subfam.n.**TYPE GENUS. *Naibia* **gen.n.**

DIAGNOSIS. Smaller naibiids. Forewing: Sc extended along R1 beyond RS origin; CuA stem continued by a single CuA2.

COMPOSITION. Type genus and *Panirena* **gen.n.**

Genus *Panirena* Shcherbakov, **gen.n.**TYPE SPECIES. *P. sukatshevae* **sp.n.**

DIAGNOSIS. Medium-sized naibiids. Forewing: Sc extending along R1 beyond RS origin; CuA1 concave and feeble; CuA2 arched backwards and nearly continuing CuA stem; membrane covered with dense tubercles (more than 10 per distance from RS to M).

COMPOSITION. Type species and *P. tenella* **sp.n.**

ETYMOLOGY. The genus and its type species are named after Pani Irena Sukatsheva, palaeoentomologist, head of the expedition which collected the species.

Panirena sukatshevae Shcherbakov, **sp.n.**

Figs 12–13

MATERIAL. Holotype: PIN 923/5, both forewings with fragments of head and thorax; paratype forewings PIN 923/6, 7, 8, 9, 10 (parts & counterparts) — middle part of Kempendyai River (right tributary of Vilyui River) ca. 40 km upstream of Kempendyai, Suntar District, Yakutia-Sakha; Upper Jurassic or Lower Cretaceous, clay lens in fluvial sands.

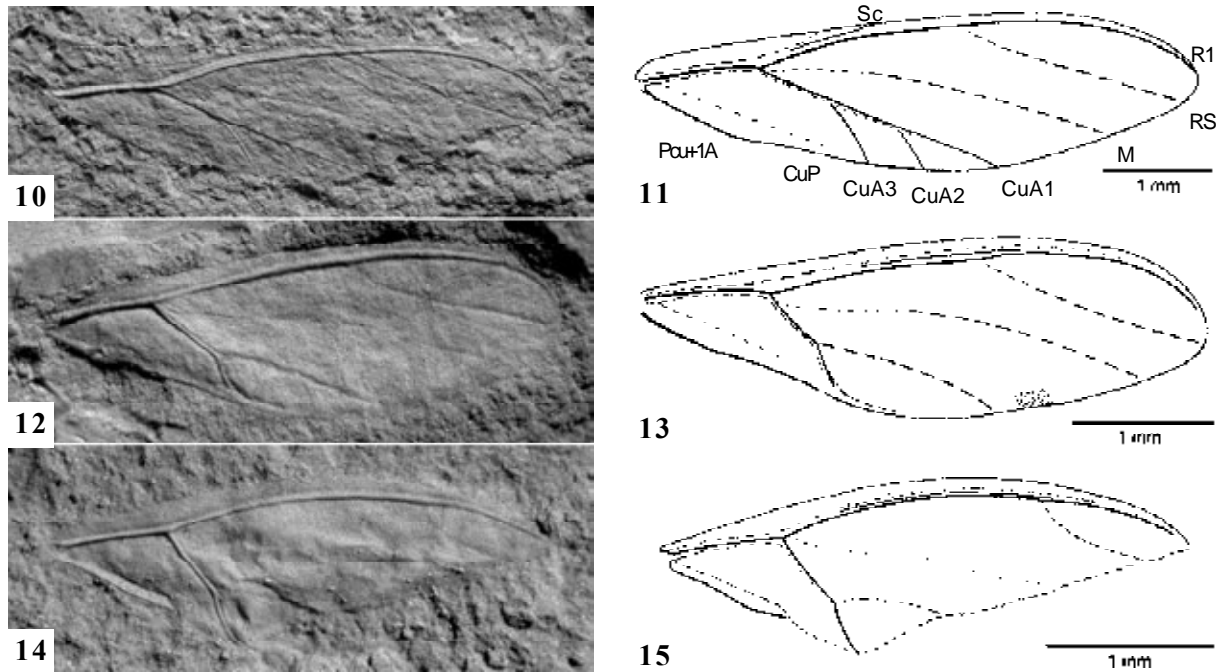
DESCRIPTION. Forewing 3.2–4.3 mm long, 1.1–1.4 mm wide, elongate (2.9–3.2:1). R(+M) only slightly bent at CuA origin. RS leaving about midlength of R–R1, usually straight basally, diverging from R1 except in distal third. CuA1 with a more or less developed convex base. CuA2 continued by a groove curved along wing margin and reaching about halfway to CuA1. Claval fold traceable; coupling fold just a little not reaching CuA2 apex. Posterior claval angle before halfway to CuA2. Membrane corrugated near posterior wing margin.

Panirena tenella Shcherbakov, **sp.n.**

Figs 14–15

MATERIAL. Holotype: left forewing PIN 1255/992 (part & counterpart) — Kubekovo near Krasnoyarsk, Yenisei River, southern Siberia, Middle Jurassic, Aalenian–Bathonian, Itat Formation.

DESCRIPTION. Forewing (incompletely preserved) estimated to be about 3.2 mm long and 1.2 mm wide. R(+M)



Figs 10–15. Naibiidae, forewings: 10–11 — *Coccavus supercubitus* gen. et sp.n., paratype PIN 2555/2392, Middle or Upper Triassic of Kyrgyzstan; 12–13 — *Panirena sukatsbevae* gen. et sp.n., paratypes PIN 923/6 (photo) and 923/7 (venation diagram; membrane corrugation shown), Upper Jurassic or Lower Cretaceous of eastern Siberia; 14–15 — *P. tenella* sp.n., holotype PIN 1255/992, Middle Jurassic of southern Siberia.

Рис. 10–15. Набииды, передние крылья: 10–11 — *Coccavus supercubitus* gen. et sp.n., паратип ПИН 2555/2392, средний или верхний триас Киргизии; 12–13 — *Panirena sukatsbevae* gen. et sp.n., паратипы ПИН 923/6 (фото) и 923/7 (жилкование; показана гофрировка мембраны), верхняя юра или нижний мел Восточной Сибири; 14–15 — *P. tenella* sp.n., голотип ПИН 1255/992, средняя юра Южной Сибири.

distinctly bent at CuA origin. RS leaving about 2/3 of R–R1 length, curved basally and further subparallel to R1. M hardly traceable. CuA1 without convex base. Claval fold distinct. Posterior claval angle about halfway to CuA2.

ETYMOLOGY. Latin *tenellus*, diminutive of *tener*, delicate.

Genus *Naibia* Shcherbakov, gen.n.

TYPE SPECIES. *N. zherichini* sp.n.

DIAGNOSIS. Small naibiids. Forewing: Sc entering C beyond level of RS base; CuA1 convex and rather thick; CuA2 arched forwards and nearly continuing CuA stem; posterior claval angle about 1/3 of the way to CuA2; membrane covered with sparse tubercles (about 5 per distance from RS to M). Hindwing with 2 hamuli, oblique veins originating not far from each other. Antennae with 3rd segment longest. Rostrum with two last segments short. Tibiae with small apical spurs. 2nd tarsomere with a pair of dorsoapical setae. Anal tube constricted at base.

COMPOSITION. Monobasic.

ETYMOLOGY. From Naiba River where the source deposit of Sakhalin amber is situated; gender feminine.

Naibia zherichini Shcherbakov, sp.n.

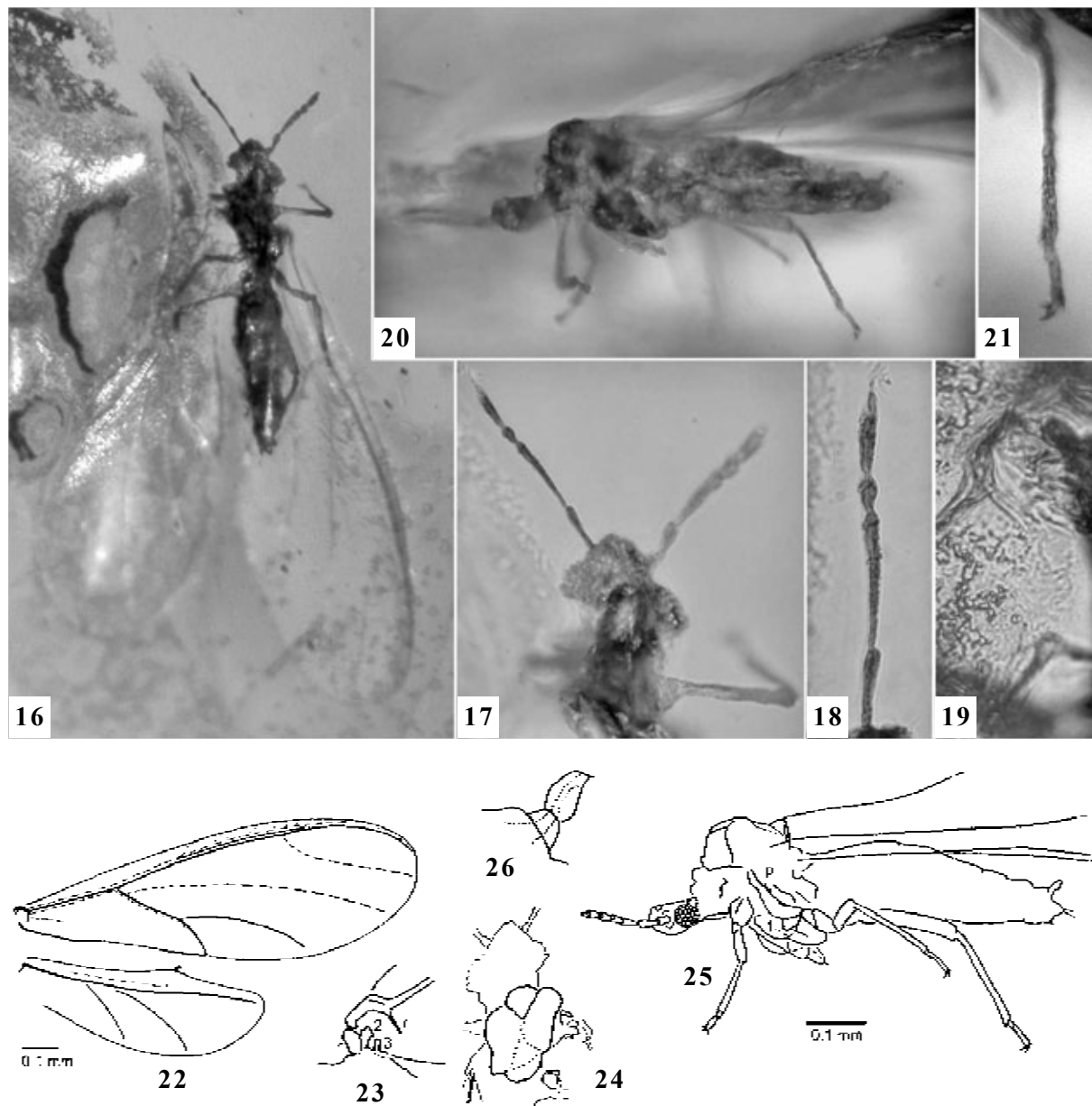
Figs 16–26

MATERIAL. Holotype: PIN 3387/34, slightly deformed insect in amber (rumenite), probably somewhat desiccated before burial — near Starodubskoe, eastern coast of southern Sakhalin; Upper Paleocene, Lower Due Formation; amber collected at sea shore [Zherikhin, 1978: 116; Eskov, 2002].

DESCRIPTION. Body 0.70 mm long. Forewing 0.98–1.04 mm long, 0.38–0.36 mm wide, elongate (mean 2.73:1; left and right wings are of slightly different shape due to amber distortion). R(+M) nearly straight at CuA origin. Indistinct proximal limit of pterostigma at ca. 0.44 of wing length. RS leaving beyond midlength of R–R1. Proximal portions of RS and especially of M feeble, latter obviously fold-like. CuA1 arched forwards, shortly interrupted at base. Claval fold traceable at base only, coupling fold just reaching CuA2 apex. Membrane divided by a network of indistinct dark lines into small polygonal units (individual hypodermal cells). Axillary sclerites of coccid type: 1st largest, its distal margin articulated with 2nd sclerite; the latter subtriangular with two projections towards base of R+M, its caudal tip articulated with anterior one of a L-shaped 3rd sclerite. R+M bent near base forming a zigzag and giving rise to a thin rib directed to Pcu+1A base (the rib is homologous to proximal border of additional sclerite).

Hindwing 0.65 mm long, 0.23 mm wide, 1.5 times shorter than forewing. R+M elbowed near base at almost right angle, anterior margin angulate at hamuli (at 0.65 of wing length), concave Sc traceable along main vein (R–R1), distal oblique vein arched, proximal one nearly straight. Both fore- and hindwing covered with sparse and very short microtrichia, more dense at wing margins.

Head 0.13 mm wide, 0.06 mm high, very flat, projecting between eyes and slightly emarginate at apex. Eyes prominent (largest diameter 0.06 mm), somewhat displaced ventrad, each of about 35 large spaced hemispherical ommatidia;



Figs 16–26. *Naibia zberichini* gen. et sp.n., holotype: PIN 3387/34, Paleocene Sakhalin amber: 16, 20, 25 — habitus; 17 — head; 18 — right antenna; 19 — bases of right pair of wings; 21 — left hind tibia and tarsus; 22 — fore- and hindwing venation; 23 — жилкование переднего и заднего крыла; 23 — основание переднего крыла (аксиллярные склериты пронумерованы); 24 — среднеспинка; 26 — анальная трубка; 16–19 — снизу; 20–21, 25–26 — сбоку; 23–24 — сверху; латероплеурит показан точками; *p* — плеуральный шов; *r* — ребро; *t* — поперечный вентральный шов.

Рис. 16–26. *Naibia zberichini* gen. et sp.n., голотип: ПИН 3387/34, палеоценовый сахалинский янтарь: 16, 20, 25 — общий вид; 17 — голова, 18 — правый усик, 19 — основания правой пары крыльев; 21 — левая задняя голень и лапка; 22 — жилкование переднего и заднего крыла; 23 — основание переднего крыла (аксиллярные склериты пронумерованы); 24 — среднеспинка; 26 — анальная трубка; 16–19 — снизу; 20–21, 25–26 — сбоку; 23–24 — сверху; латероплеурит показан точками; *p* — плеуральный шов; *r* — ребро; *t* — поперечный вентральный шов.

ocular tubercle with 3(?) ommatidia. Three light spots visible in the same places as aphid ocelli. Antennae ca. 0.19 mm long, of 5 segments (length ratio 6:10:22:7:11), 3rd subdivided; each of 4 rhinaria in subapical position on its own (sub)segment of flagellum, processus terminalis 3.5 times shorter than base of 5th segment and bearing 2 short apical setae; flagellum transversely grooved, rhinaria elevated. Loroclypeus narrow, sunken between eyes (hardly visible in profile). Rostrum 0.18 mm long, basally hidden in midventral

depression, directed caudad and reaching mid coxae, of no less than 3 (probably 4) segments, ultimate one 0.04 mm long with a pair of apical setae, penultimate 0.05 mm long with proximal boundary oblique, preceding the longest one and less sclerotized than two distal segments. Stylet bundle partly extracted from labial groove.

Pronotum reduced to a narrow transverse strip separated from head by membranous zone. Mesothorax well sclerotized, compressed laterally, 0.14 mm wide and 0.20 mm high.

Steeply humped mesonotum divided into a subtriangular prescutum, lateral lobes separated by a pale (desclerotized?) triangular depression, and a transverse crest-like scutellum. Mesopleuron with pleural suture and lateropleurite traceable; epimeron narrow; ventral area ('mesosternum') divided into four quarters by deep median (discrimen) and transverse (paracoxal?) sutures. Metathorax diminished, its notum broadly membranized. Legs rather short, fore femur 0.10 mm long, tarsus 0.05, hind femur 0.11, tibia 0.18, tarsus 0.06 mm long. Tibiae covered with sparse short suberect setae, at least hind tibia with 2 (or more?) tiny apical spurs. 1st tarsomere very short with a pair of ventroapical setae, 2nd with a pair of longer dorsoapical setae, claws inflated in proximal half at inner and ventral sides.

Abdomen ca. 0.42 mm long, 0.11 wide, slender and feebly sclerotized, of no less than 8 fully developed segments. Its apex formed by 9th segment bearing a small pointed ventral projection (penis? ovipositor?), a pair of very long apical setae, and anal tube attached dorsally. The tube 0.03 mm long with central canal visible, of two segments, basal one (10th abdominal) shorter and narrower than apical (11th abdominal), the latter with a pair of short apical setae, slightly emarginate between them in plane.

REMARKS. The sex of the holotype remains uncertain, because the ventral projection of the 9th abdominal segment may be interpreted as either a rudimentary spine-like ovipos-

itor (like those of Palaeoaphididae from the Upper Cretaceous Canadian amber [Richards, 1966]) or tip of the penis protruding from the penial sheath (compare with *Steingelia* and *Pseudococcus* as figured by Theron [1958]). Nevertheless, in either case the situation (flying female or feeding male) is quite dissimilar to that met with in coccids. The presence of large eyes displaced ventrad and concealing the clypeus from the sides in the specimen rather agrees with the second assumption. If the holotype really is a male, another, twice larger specimen from the same locality described below may well represent a conspecific female.

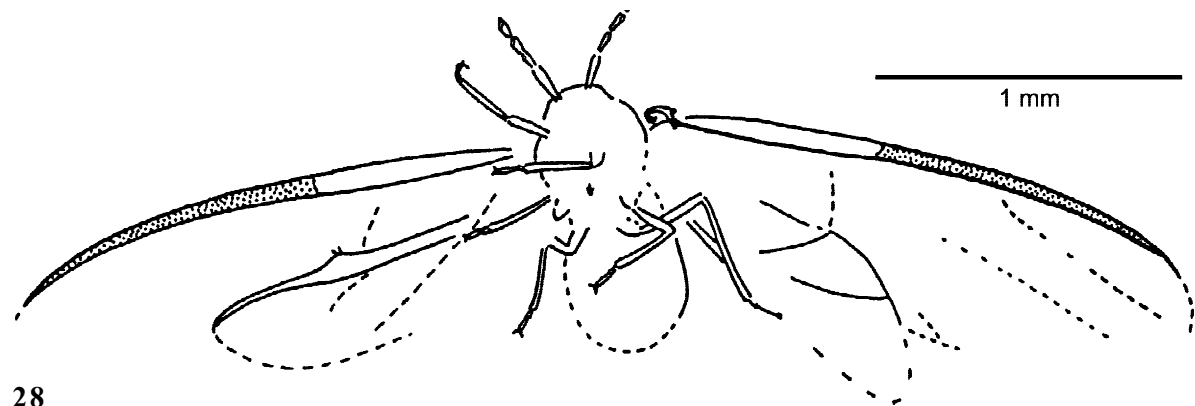
ETYMOLOGY. To the memory of Dr Vladimir V. Zherikhin, paleoentomologist, one of collectors of Sakhalin amber.

Naibiidae gen.sp.

Fig. 27–28

MATERIAL. PIN 3387/35, insect in rumenite; wings and abdomen exposed to amber surface and partly eroded away (venation mostly untraceable), body structure obscured with a froth-like layer of gas bubbles — same locality as for *N. zherichini* sp.n.

DESCRIPTION. Forewing ca. 1.9 mm long, 0.6 mm wide, elongate (3.2:1). Costal space rather wide. R+M with a basal zigzag bend, nearly straight at CuA origin. Pterostigma well pigmented, far not reaching wing apex, with a clear



Figs 27–28. Naibiidae gen. sp., PIN 3387/35, Paleocene Sakhalin amber: habitus, ventral view (poorly visible structures in broken line).

Рис. 27–28. Naibiidae gen. sp., ПИН 3387/35, палеоценовый сахалинский янтарь: общий вид снизу (плохо различимые структуры прерывистой линией).

proximal limit at 0.37 of wing length. Hindwing ca. 1.1 mm long, 1.7 times shorter than forewing, with anterior margin angulate and sclerotized at 2 hamuli (at 0.64 of wing length). Antenna ca. 0.3 mm long, of 6 segments, 3rd longest, 4–6th subequal and distinctly widening towards subapical rhinaria (like 4th segment in *N. zherichini* sp.n.), processus terminalis shorter than diameter of a rhinarium, with short apical setae. Apex of rostrum visible in front of mid coxae, between hind quarters of ventral mesothoracic area. Body 0.93 mm long, stout, mesothorax ca. 0.35 mm, abdomen ca. 0.40 mm wide. Legs like in *N. zherichini* sp.n.: short, tibiae setose, 2nd tarsomeres with a pair of dorsoapical setae, claws proximally inflated.

REMARKS. Differs from *N. zherichini* sp.n. in the larger size, stouter body, 6-segmented antennae, shorter processus terminalis, wider costal space, relatively shorter hindwing, and (also from other genera) in the pterostigma terminating at a longer distance from the wing apex. This fossil may well represent one more, yet undescribed genus. However, the possibility cannot be excluded that this specimen and the *N. zherichini* sp.n. holotype are merely a conspecific female and male, respectively, especially because naibiids (as well as boreoscytids) might have possessed sexual dimorphism more pronounced than in aphids, affecting important characters such as the antennal segment number and (like in *Dinoscyta*) wing venation.

Discussion

Systematic position of Simulaphididae

This monobasic family is most similar to Pincombeidae and symplesiomorphous with it in the quite long M+CuA stalk, and the claval vein remote from posterior margin. It is symplesiomorphous with Pincombeidae and some Triassic aphid genera in the M branches quite long (M1 much longer than M1+2; with *Triassoaphis* Evans, 1956) and RS originating before the nodal line and convex up to it (with *Creaphis* Shcherbakov et Wegierek, 1991). However, it differs from pincombeids and is synapomorphous with Aphido+Coccomorpha in the *r-m* lost, M proximally fold-like, and CuA1 not crossed by nodal line. In the enlarged pterostigma *Simulaphis* resembles most aphids, few coccids (Margarodidae s.str.), and Archescytinidae, but so far as the bend of R1 at the base of pterostigma is characteristic of archescytinids (and of pincombeid genus *Madygenopsyllidium* with small pterostigma) rather than of higher Aphidinea, the similarity to aphids could be homoplastic. Unusually small CuA fork (CuA1 is not shorter than the CuA stem in all other Aphidinea retaining this fork) and quite long M+CuA stalk of Simulaphididae exclude direct relationships to Aphidomorpha: CuA1 is much longer than the CuA stem in all pre-Cretaceous aphids, and moderate shortening of the fork in the Late Cretaceous genera of Palaeoaphididae is secondary (M is not stalked with CuA even in these latter). One may interpret small fork in simulaphidids as a last step towards its loss in scale insects, but this loss probably occurred much later, with the hindwing reduction in Coccomorpha s.str. (see below). In simulaphidids the whole fork (rather than only CuA2)

gives support for the coupling fold, like in the naibiid genus *Coccvus*, and this character may eventually turn out to be a synapomorphy of Simulaphididae and Coccomorpha s.l. (if so, the marginal position of the claval vein was acquired by aphids and coccids independently). The genus *Simulaphis* resembling aphids and precoccids may represent a group directly ancestral to the latter, or to both extant infraorders of Aphidinea, but there are no sufficient reasons to associate it with either. Its assignment to paraphyletic infraorder Pincombeomorpha as a third, the most derived family is at present the only plausible solution.

Systematic position of Naibiidae

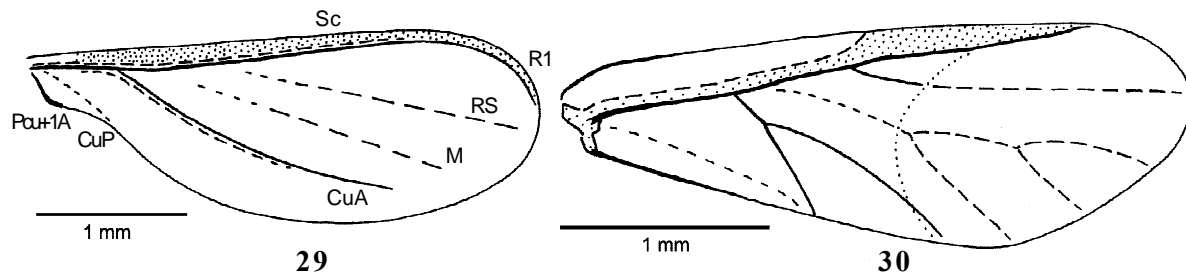
(i) *Naibia* and its relatives demonstrate several **symplesiomorphies with aphids** but not coccids. As shown below, all these characters may be interpreted as inherited from more or less distant ancestors by both aphids and naibiids and secondary lost in Coccomorpha s.str. Some are obvious plesiomorphies, e.g. the absence of coccid sexual dimorphism and retention of two tarsal claws.

Rounded subapical rhinaria are observed on flagellar segments in some Early Permian Archescytinidae (pers. obs.), the group ancestral to all the other Hemiptera [Shcherbakov, 1996; Shcherbakov & Popov, 2002], therefore the condition can be assumed primitive for the order. The processus terminalis (a narrowed post-rhinarial part of the ultimate antennal segment) is characteristic, besides naibiids, of two distantly related hemipteran groups, whiteflies and aphids, and seems to have been formed in both cases independently from fused terminal flagellomeres losing their rhinaria. Scale insects may have lost rhinaria (which at least in alate female aphids serve as distant chemoreceptors for searching host plant [Pettersson, 1973]) and hence the processus terminalis due to female aptery and male aphagy (some rhinaria are lost or replaced by sensorial cones in whiteflies [Gill, 1990]). The increase of the antennal segment number up to 13 (more than in any other Hemiptera) in some coccid males is secondary [Koteja, 1996], and it agrees with an opinion that the structure of coccid antenna is far from primitive for Hemiptera. The 7-segmented antennae of *Neomargarodes* with flagellomeres largely devoid of long setae [Hodgson & Foldi, 2006] probably hint that in the direct ancestors of Coccomorpha s.str. antennae were not much unlike the 7-segmented antennae common in Mesozoic aphids (see Shaposhnikov [1979]).

A transverse ventral suture of the mesothorax, shared by naibiids and aphids but unknown among male coccids, is probably homologous to the paracoxal one belonging to the pleural groundplan.

CuA fork with CuA2 supporting coupling fold in the forewing (the condition appearing in the earliest Aphidinea and first described in aphids [Börner, 1910]) has been lost in scale insects when the fold shifted basad due to hindwing diminution.

A functional hindwing with two convex oblique veins characteristic of aphids and naibiids is much more primitive than coccid hamulohaltere (minute haltere-like hind-



Figs 29–30. Forewing venation: 29 — *Orthezia urticae* (Linnaeus, 1758), Recent (modified after Koteja [1986]); 30 — *Creaphis theodora* Shcherbakov & Wegierek, 1991, Middle or Upper Triassic of Kyrgyzstan.

Рис. 29–30. Жилкование переднего крыла: 29 — *Orthezia urticae* (Linnaeus, 1758), современный (по Koteja [1986] с изменениями); 30 — *Creaphis theodora* Shcherbakov & Wegierek, 1991, средний или верхний триас Киргизии.

wing retaining hamuli for coupling to forewing but lacking oblique veins) and can be considered an initial condition for Aphido+Coccoomorpha, because it is easily derivable from the hindwing of their presumable common ancestors, Pincombeidae, by reduction of one of three oblique veins, obviously RS.

(ii) Among numerous **synapomorphies of Aphidomorpha + Coccoomorpha** [Theron, 1958; Schlee, 1969a, b] or of all the **Aphidinea**, some are evident in the body structure of *Naibia*: mesepisternum with lateropleurite, coxae widely separated, pretarsal lobes lost, tarsi two-segmented, and larval eyes persisting in imago. The tarsi of two segments, with 1st segment short and triangular, are met with, besides aphids, in the males of Margarodidae s.l., Pseudococcidae, Eriococcidae and Kermesidae [Morrison, 1928, Lobdell, 1937, Koteja & Žak-Ogaza, 1972]. Larval eyes (known also as ocular tubercles, triommatidia, lateral ocelli and stemmata) consist of 3 ommatidia each (up to 15 in *Orthezia* [Koteja, 1986]), in male coccids united under a common cornea [Pflugfelder, 1936], and are innervated from the optical lobes, but not from the protocerebrum as true dorsal ocelli [Pflugfelder, 1937] which seem to be completely lost in scale insects [Theron, 1958] (probably retained in *Naibia*).

Synapomorphies of Aphidomorpha + Coccoomorpha in the forewing structure are: C trachea lost [Patch, 1909], *r-m* lost, Pcu+1A (sub)marginal, and probably also M concave throughout and fold-like in its proximal part. In more primitive insects, M is a tubular structure, convex (raised) or almost neutral up to the nodal flexion line and turning concave (depressed) beyond it. In aphids, proximad of this line (inconspicuous but nevertheless constant) M is transformed into a light concave fold, probably allowing easier changes in the wing camber during the upstroke [Shcherbakov & Wegierek, 1991]. A similar condition occurs in naibiids and *Orthezia* males (Fig. 29); so far as known in other coccids M is fold-like throughout ('1st light line' of Morrison [1928]) or lost. Distal RS origin in the forewing may be considered as a common trend (underlying synapomorphy [Saether, 1986]) for Aphidomorpha + Coccoomorpha, being characteristic of all the aphids except *Creaphis* (Fig. 30) [Shcherbakov & Wegierek, 1991], naibiids, and some archaeococcids retaining RS (*Matsucoccus matsumurae*, *Ultracoelostoma* [Morrison, 1928]),

the more so that in some others, with a proximal origin of RS, its trachea leaves distally (*Orthezia* [Koteja, 1986]). Another underlying synapomorphy of these two infraorders is the aptery at imaginal stage (in females, sometimes in males; imago is always winged in Psyllinea and never completely wingless in Auchenorrhyncha [Szelegiewicz, 1971]).

Some wing synapomorphies introduced by Schlee [1969b] have been confirmed but some others rejected (see Szelegiewicz [1971]) as resulting from parallel evolution, e.g. the hypertrophied pterostigma of Margarodidae s.str. and most aphids. Enlargement of pterostigma follows costalization (i.e. anterior concentration of veins [Rohdendorf, 1946: 34]) and correlates with size decrease, as shown for Hymenoptera by Rasnitsyn [1969].

(iii) The anal tube of *Naibia* is rather comparable to those of Auchenorrhyncha (10th and 11th abdominal segments free and more or less tubular [Emeljanov, 1987]), both being more **primitive** than modified or reduced perianal structures of extant sternorrhynchan groups. In *Naibia*, the tube is constricted basally and looks (at least in profile) like a prolonged knobbed cauda considered primitive for aphids [Heie, 1987]. The knobbed cauda has been revealed in Mesozoic Oviparosphidae [Wegierek, 1990], the earliest undoubted members of Aphidoidea s.str. [Shcherbakov & Popov, 2002]. The supposition that the aphid cauda was derived from the anal tube (i.e. from 10+11th segments) is confirmed by the condition found in the sexuparae of some *Prociphilus* spp. (Pemphigidae, Aphidoidea): protruded anal plate (belonging to the 9th segment) forms a collar between the 8th tergite and the base of the cauda [Smith, 1969]. If this hypothesis is true, the most primitive aphids (such as Triassic ones) with the body structure unknown might still have retained an anal tube. A short unsegmented remnant of the anal tube persists also in some male scale insects (e.g. *Newsteadia* [Koteja, 1986]). The anal ring of female coccids is probably homologous to the 11th abdominal segment [Koteja, 1996], especially as in *Naibia* the 10th segment is much shorter than the 11th. An invaginated 'anal tube' in the females of Monophlebidae and some coccoid families is not homologous to the anal tube of other insects [Danzig, 1980].

(iv) Several naibiid characters can be interpreted as true or underlying **synapomorphies with scale insects**:

both fore- and hindwing with R+M bent near base, forewing with both Sc and R1 extending far distally, M unbranched, CuA twofold (with posterior groove), and membrane tuberculate or corrugate (listed as coccid autapomorphy by Koteja [1996]); head flattened dors-oventrally, eyes of rather few spaced ommatidia, both pro- and metanotum somewhat reduced. If *N. zherichini* **sp.n.** holotype is a male, its sunken loroclypeus may be considered a first step to the reduction of mouthparts completing in coccid males, and its genitalia should be interpreted (like those of scale insects) as lacking parameres and consisting of a penis enclosed proximally in a penial sheath. If it is a female, its spine-like ovipositor represents one more synapomorphy of naibiids and primitive aphids.

A zigzag bend of R+M base in the forewing and an elbow-like one in the hindwing are lost in most aphids (except for Triassic ones), but occur among archaeococcids: in the forewings of Margarodidae and Monophlebidae, in the hindwings of *Steingelia* and (to a lesser degree) of *Margarodes* [Theron, 1958] and *Orthezia* [Koteja, 1986]. Sc+R+M is already elbowed basally in most Pincombeomorpha (forewings of boreoscytids and *Madygenopsyllidium*, hindwing of *Dinoscyta*). Configuration of the forewing axillaries in *Naibia* is also rather coccid than aphid one, closely resembling that of *Pseudaspidothroctus* (Monophlebidae [Theron, 1958]).

A combination of R1 almost reaching the forewing apex with simple M is diagnostic of naibiids, neither of these two characters being known in aphids until the Late Cretaceous when they appear (never combined) in two or three unrelated aphid lineages [Kononova, 1976, 1977]. In naibiids the CuA stem is continued with either CuA1 or CuA2 (in the latter case CuA1 interrupted at base or turning concave), whereas in aphids retaining the stem it is forked symmetrically (or rarely continued by CuA2: *Triassoaphis*) and both branches are convex.

In the forewings of Coccoomorpha s.l., both Sc+R and CuA are twofold, i.e. consisting of convex discal and concave peripheral components [Morrison, 1928]. Concave-convex Sc+R is a hemipteran apomorphy lost by all descendants of Archescytinidae other than Aphidinea. Convex-concave CuA may have been patterned after Sc+R in naibiids.

(v) A remarkably doubled CuA2 of most *Coccavus* specimens, unique among the Hemiptera, reflects its destabilization before reduction and/or the need of supporting the coupling fold (still in aphid position) when CuA2 turns weak and CuA–CuA1 becomes a straight vein (already a coccid condition, **synapomorphy of Coccavinae + Coccoomorpha s.str.**). It is doubtless the last step towards the simple CuA of scale insects, pointing out *Coccavus* as the genus nearest to coccid ancestors.

(vi) The peculiar humped profile of *Naibia* formed by a flat head, a distinct neck constriction, a short prothorax, a deep mesothorax, and a highly convex scutellum resembles the habitus of ortheziid and (to a lesser degree) matsucoccid males. A combination of the above features with the subtriangular prescutum, R1

reaching the wing apex, M not fold-like distally, well-developed CuA and narrow clavus is characteristic set of **plesiomorphies within Coccoomorpha**, opposing both Naibiidae and Ortheziidae to the other scale insects.

(vii) Klimaszewski and Wojciechowski [1992] argued that Naibiidae belong to aphids and have no close relations to coccids. Their conclusions are based on plesiomorphies and misinterpreted naibiid characters, such as: pterostigma ‘absent’ (in fact present), Sc ‘absent’ (in fact present at least as a weak groove), clavus ‘lost’ in *Naibia* (in fact claval fold reduced except base).

Systematic position of Naibiidae is indeed two-edged: the family combines numerous plesiomorphies shared with aphids and several not so evident coccid apomorphies, i.e. belongs to the coccid clade remaining at the aphid grade. There are few aphid synapomorphies in respect to coccids, and they are either unknown in the Triassic aphids (anal tube transformed into cauda) or not yet acquired by them (loss of the R+M basal bend and of the posterior claval angle). Therefore these earliest members of Aphidomorpha (*Creaphis*, *Triassoaphis* and several undescribed genera) may well represent the group ancestral to both Coccoomorpha s.l. and other aphids. The earliest known aphids and naibiids are of Triassic age, hence these groups diverged prior to radiation of aphid families beginning in the Jurassic [Wegierek, 1990; Shcherbakov & Popov, 2002]. In this case we prefer to stress coccid affinities of Naibiidae by including it in Coccoomorpha s.l. as a third superfamily, Naibioidea.

Phylogeny of Aphidinea

Paraphyletic (ancestral) taxa are no less natural and legitimate than holophyletic (monophyletic s.str.) ones [Rasnitsyn, 1996] and inherent in the Linnean classification [Brummitt, 2003], so taxonomists and paleontologists will continue to use such concepts as Reptilia, Blattodea or Pincombeomorpha. The proposed phylogram of Aphidinea (Fig. 31) is based chiefly on the wing characters (body structure is much less known in compression fossils). Boreoscytidae, Pincombeidae, Simulaphididae and Naibiidae (especially Triassic *Coccavus*) form together quite a continuous transformation series linking Archescytinidae to scale insects.

Besides **Aphidinea**, two other primary hemipteran lineages known since the Permian are shown in the phylogram, with some of their apomorphies listed, **Auchenorrhyncha** (= Cicadinea [Shcherbakov, 1996]) and **Psyllinea** (Psyllomorpha with their offshoot Aleyrodomorpha known since the Jurassic [Shcherbakov, 2000]), as well as the stem lineage **Paleorrhyncha** Carpenter, 1931 (= Archescytininea) that shows apomorphies of neither major lineage of the order and merits a subordinal rank as well. Two remaining hemipteran suborders, **Coleorrhyncha** (= Peloridiinea) and **Heteroptera** (= Cimicinae), descended from primitive Auchenorrhyncha later, separately and somewhat in parallel [Popov & Shcherbakov, 1996; Shcherbakov & Popov, 2002], all three united under the name Hemelytrata Fallen, 1829 (= Euhemiptera Zrzavy, 1990)

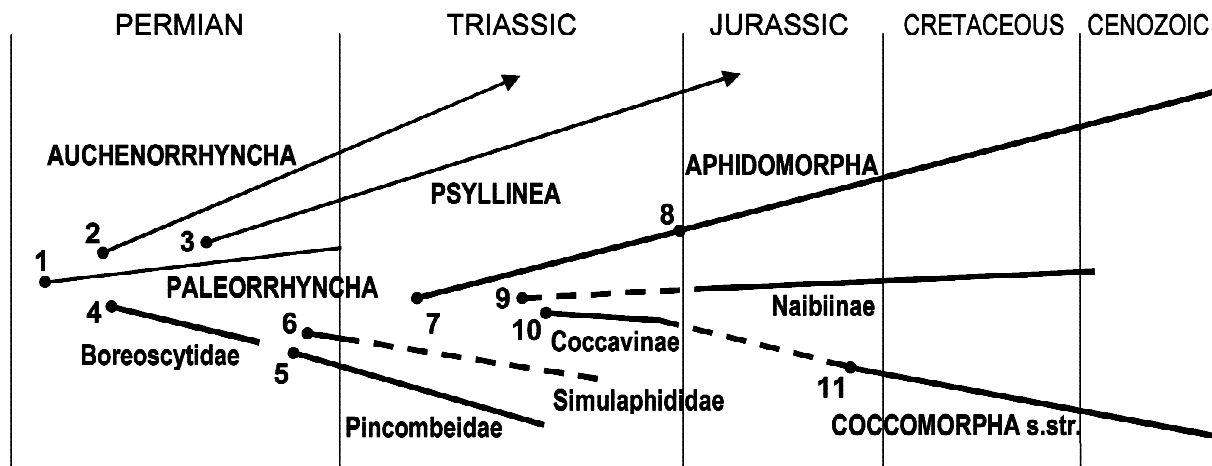


Fig. 31. Phylogram of Aphidinea (key to lettering in text).
Рис. 31. Филограмма Aphidinea (обозначения в тексте).

[Shcherbakov, 2005]. Extant Sternorrhyncha are diphyletic, but the transition from Paleorrhyncha to Hemelytrata is not as gradual as those from Paleorrhyncha to Psyllomorpha and to Pincombeomorpha, so one may include Paleorrhyncha in Sternorrhyncha s.l., which thus become paraphyletic with respect to Hemelytrata [Popov, 1980].

Phylogram internodes are numbered, and apomorphies are listed below for each lineage (for each paraphyletic taxon marked with '+' these are synapomorphies of it and some or all its descendants):

1 (Hemiptera = Paleorrhyncha+): (a) mouthparts of rhynchotous type; (b) hind legs with apical pectens of teeth and somewhat enlarged first two tarsomeres, being modified for jumping (pers. obs.); associated plesiomorphy: coxae contiguous along midventral line; (c) concave Sc running (except for the apex termed dSc) close to convex R (lost by all descendants of Archescytinidae other than Aphidinea, thus characteristic of the latter along with associated plesiomorphy: forewing not tegminized with C thin and ecarinate). One more character of Archescytinidae is an autplesiomorphy among Hemiptera: fore- and hindwing homonomous (i.e. of equal size and structure), uncoupled in flight.

2 (Hemelytrata = Auchenorrhyncha+): (a) fore- and hindwing coupled in flight, coupling fold in forewing clavus, claval veins (Pcu and 1A) forming Y-vein; (b) forewing tegminized with C carinate and middle section of Sc fused to R (Sc trachea in more primitive extant forms is associated with R as well); (c) hindwing anojugal area enlarged; etc. (see Shcherbakov [1996], Shcherbakov & Popov [2002]).

3 (Psyllinea; first two apomorphies are partly homoplastic with Auchenorrhyncha and oppose both lineages to Aphidinea): (a) fore- and hindwing coupled in flight, coupling fold in forewing clavus, Pcu and 1A forming Y-vein; (b) forewing tegminized with C thickened and middle section of Sc fused to R (but Sc trachea associated with C in extant forms); (c) M and CuA forming common stalk in forewing; etc.

4 (Aphidinea = Boreoscytidae+): (a) fore- and hindwing coupled in flight, coupling fold beyond forewing clavus supported by nearly straight CuA–CuA2, nodal line shifted from CuP to CuA2 apex; (b) R–R1 in forewing nearly straight, costal space and pterostigma narrow; (c) clavus narrow with posterior angle obtuse, Pcu and 1A forming Y-vein; (d) hindwing much smaller than forewing; (e) coxae widely separated.

5 (Pincombeidae+): (a) free CuA base lost; (b) Pcu and 1A fused throughout; (c) *m-cu* lost in forewing; (d) hindwing with 3 oblique veins and no crossveins.

4–7 (apomorphies gained not earlier than in Boreoscytidae and not later than in the last common ancestors of Aphido- and Coccoomorpha): (a) C trachea lost in forewing; (b) processus terminalis formed (associated plesiomorphy: rhinaria rounded, subapical on flagellomeres); (c) larval eyes persisting in imago; (d) mesepisternum with lateropleurite.

5–7 (not earlier than in Pincombeidae and not later than in ancestors of Aphidomorpha + Coccoomorpha): (a) pretarsal lobes lost; (b) ovipositor somewhat reduced.

6 (Simulaphididae+): in forewing (a) *r-m* lost, (b) M concave throughout, fold-like proximally, and (c) nodal line shifted to CuA1 apex.

7 (Aphidomorpha + Coccoomorpha): (a) Pcu+1A (sub)marginal in forewing; (b) RS lost in hindwing; (c) tarsi two-segmented; also underlying synapomorphies: (d) occurrence of wingless imagines; (e) RS originating distally in forewing; (f) viviparity.

8 (Aphidoidea + Phylloxeroidea): (a) bend of R+M base reduced; in forewing (b) Sc trachea lost [Patch, 1909] and (c) posterior claval angle lost; (d) anal tube transformed into cauda.

9 (Coccoomorpha s.l. = Naibiidae+): in forewing (a) Sc and R1 extending distally, (b) M simple, (c) CuA two-fold (with posterior groove), (d) membrane tuberculate to corrugate; (e) head dorsoventrally flattened; (f) ommatidia of compound eye spaced, not numerous (underlying synapomorphy); (g) pro- and metanotum re-

Table. Vein nomenclature and homology in coccids
Таблица. Номенклатура и гомология жилок крыла червецов

vein	nomenclature and homology after Morrison [1928]	structure
Sc+R	costal complex (=Sc+R)	concave-convex
RS	apical diagonal vein (=RS)	concave
M	1st diagonal light line (=MS)	concave, at least partly fold-like
CuA	basal diagonal vein (=Cu+CuS)	convex-concave
CuP (claval fold)	2nd light line (?=1AS)	concave fold
Pcu+1A	fold or pocket	convex, marginal, rudimentary, with coupling fold

duced; possibly also (h) penis proximally enclosed in sheath, parameres reduced.

10 (Coccavinae+): in forewing CuA–CuA1 in straight line,

11 (Coccomorpha s.str.): (a) hindwing reduced to hamulohaltere, coupling fold displaced basad (onto posterior angle of short clavus), CuA2 lost; (b) rhinaria and processus terminalis lost; (c) true ocelli lost; (d) rostrum in male and wings in female lost; (e) transverse ventral suture of mesothorax lost; (f) one of two claws lost; (g) ovipositor lost.

As shown above, Aphidinea evolved towards diminution of the body size and costalization in coupled wings, and therefore to reduction of the clavus and hindwing up to subdiptery and true diptery in male coccids, whereas both Psyllinea and Auchenorrhyncha transformed forewings into tegmina, probably due to improvement of jumping ability [Rohdendorf, 1949: 66] first arising in archescytinids. Such evolutionary transformations of coccid forewing as narrowing of the wing stalk, formation of two-fold cubital spar (CuA of convex and concave components, the latter more persistent), basal shift of RS origin and secondary expansion of claval region are same as associated with acquisition of diptery in true flies, and were probably formed through transfer of the hindwing pattern onto forewings [Shcherbakov et al., 1995]

Implications to scale insect morphology and phylogeny

Accepting the naibiid forewing as an initial point for coccid wing evolution, we come to the conclusion that the wing of *Orthezia* is the most primitive among the known scale insects, since it retains all the elements of the coccid groundplan venation (Table).

The direct comparison of *Coccavus* and *Orthezia* largely confirms the homology proposed by Morrison [1928], except for the veins posterior to CuA.

A set of plesiomorphies characteristic of *Orthezia* includes: Sc+R extending (as R1) towards wing apex, CuA well-developed, claval fold reaching margin, clavus narrow, coupling fold elongate. There are no wing apomorphies in the genus other than those of all the *Coccomorpha* s.str. The other extant *ortheziid* genus with the wing structure described, *Newsteadia*, had lost the hindwing and coupling fold and M in the forewing.

Wings of other archaeococcids and all neococcids are more derived. The apomorphies of coccid taxa in the wing structure are listed below (ranks of taxa after Koteja [1974, 1996]) and mapped onto a tentative phylogram (Fig. 32):

- (a) Margarodidae s.l.: claval region expanded.
- (b) Xylococcidae & Matsucoccidae: no posterior claval angle; CuA reduced to diffuse sclerotization; corrugation pinnate across RS and CuA.
- (c) Matsucoccidae: CuA lost; RS normally lost.
- (d) Kuwaniidae & Callipappidae: claval fold parallel to (but remote from) CuA, far not reaching margin.
- (e) Coelostomidiidae, Monophlebidae & Margarodidae s.str.: claval fold shifted to CuA, long but not reaching margin; posterior claval angle projecting, with short coupling fold; CuA usually shortened.
- (f) Monophlebidae & Margarodidae s.str.: Sc+R somewhat shortened.
- (g) Margarodidae s.str.: pterostigma hypertrophied; convex component of CuA reduced to diffuse sclerotization or lost.
- (h) Steingeliidae, Phenacoleachiidae, Putoidae & Coccoidea s.str.: RS lost; posterior claval angle projecting, with short coupling fold.
- (i) Steingeliidae; Coccoidea s.str.: claval fold lost.

Most phylogenetic schemes show archaeococcids as paraphyletic with respect to neococcids [Koteja, 1974; Danzig, 1980; Miller, 1984; Foldi, 1997]. Recent molecular analysis agrees with this view and show relationships among Archaeococcoidea+Putoidae unresolved [Cook et al., 2002].

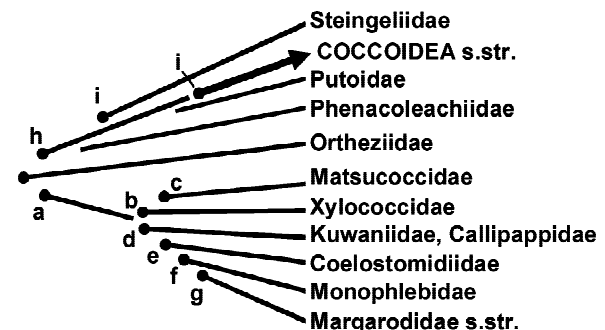


Fig. 32. Tentative phylogram of selected coccid taxa (key to lettering in text).

Рис. 32. Предположительная филограмма некоторых таксонов червецов (обозначения в тексте).

The affinities of Ortheziidae have been variously assessed: the family was regarded either as the most primitive coccid group [Borchsenius, 1958], an early blind offshoot from ancestral coccids [Koteja, 1974], or as the first side branch of the neococcid lineage and then either retained in the same superfamily as the rest of archaeococcids [Danzig, 1980] or placed in Coccoidea s.str. [Miller, 1984]. However, the supposed synapomorphies of Ortheziidae + Coccoidea s.str. mostly seem doubtful: one-segmented female tarsus might have appeared several times (like the same condition in males), and the setigerous anal ring of the female [Danzig, 1980] is rather a plesiomorphy [Borchsenius, 1958], especially as the ring probably derived from the 11th abdominal segment; of five synapomorphies listed by Foldi [1997] four show abundant reversals or are known in margarodids and even aphids. Borchsenius and Koteja's opinions look plausible since reliable synapomorphies of Ortheziidae with either Margarodidae s.l. or Coccoidea s.str. are lacking. The primitiveness of ortheziids, apart from the set of plesiomorphies shared with Naibiidae (see above), is further stressed by the fact that the male pupa (i.e. the last preimaginal instar) of *Orthezia* is able to move and, moreover, bears fully developed and clearly separated tarsal claws, unlike other coccid pupae (J. Koteja, pers. comm. 1990). Ortheziids often live in forest litter, the life mode being hypothesized for the ancestral coccids [Koteja, 1985]. Of two still undescribed Late Jurassic scale insect males (the earliest known *Coccomorpha* s.str.) one may be associated with ortheziids (J. Koteja, pers. comm. 1999).

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