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**Holarctic genus *Pseudoseioptera* Stackelberg
(Diptera: Ulidiidae (=Otitidae)).
Part I.
Phylogenetic relationships and taxonomic position¹**

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Голарктичний рід *Pseudoseioptera* Stackelberg (Diptera: Ulidiidae (=Otitidae)).
Частина I. Філогенетичні стосунки та таксономічне положення роду. Каменєва О.П.,
Корнєєв В.О. — За допомогою програми HENNIG'86 аналізуються філогенетичні
стосунки роду *Pseudoseioptera* Stackelberg з іншими родами стрічкокрилок. Обговорю-
ється надродова таксономія Ulidiidae. Як молодший синонім Ulidiidae розглядається на-
зва родини Otitidae **syn.n.** Родину Ulidiidae поділено на дві підродини: Ulidiinae (з трьо-
ма трибами: Seiopterini **trib.n.**, Lipsanini **stat.n.** (= Euxestini, **syn.n.**) та Ulidiini **stat.n.**)
та Otitinae (також з трьома трибами, Pterocallini **stat.n.**, Cephalini **stat.n.** та Otitini **stat.n.**)
До складу Seiopterini (Ulidiinae) переміщено *Seioptera* Kirby, *Homalocephala* Zetterstedt
та *Pseudoseioptera*. Наведено таблиці для визначення підродин та триб Ulidiidae, а також
родів Seiopterini.

Голарктический род *Pseudoseioptera* Stackelberg (Diptera: Ulidiidae (=Otitidae)).
Часть I. Филогенетические взаимоотношения и таксономическое положение
рода. Каменева Е.П., Корнеев В.А. — С помощью программы HENNIG'86 анализируются
филогенетические взаимоотношения рода *Pseudoseioptera* Stackelberg с другими
родами лентокрылок. Обсуждается надродовая таксономия Ulidiidae. Как младший
синоним Ulidiidae рассматривается название семейства Otitidae **syn.n.** Семейство
Ulidiidae разделено на два подсемейства: Ulidiinae (с тремя трибами: Seiopterini **trib.n.**,
Lipsanini **stat.n.** (= Euxestini, **syn.n.**) и Ulidiini **stat.n.**) и Otitinae (также с тремя трибами,
Pterocallini **stat.n.**, Cephalini **stat.n.** и Otitini **stat.n.**). В состав Seiopterini (Ulidiinae)
перемещены *Seioptera* Kirby, *Homalocephala* Zetterstedt и *Pseudoseioptera*. Приводятся
таблицы для определения подсемейств и триб Ulidiidae, а также родов Seiopterini.

Introduction. Stackelberg (1955) established the genus *Pseudoseioptera* for a single new species, *P. ingraca* Stack. based upon two female specimens from the Leningrad region. Steyskal (1956) reviewed six species assigned to the genus *Seioptera* Kirby, but Krivosheina and Kovalev (1972) transferred three of them to *Pseudoseioptera*. They also described reared males and larvae of *P. ingraca* breeding under the bark of fallen trees in Russian Far East. Thus, four species were included in the genus; two of them, *P. ingraca* and *P. demonstrans* (Hennig) Palaearctic, and the other two, *P. albipes* (Cresson) and *P. dubiosa* (Johnson) Nearctic. We will recognize only one Palaearctic species in the Part two of this paper, thus the number of species is to be reduced to three.

The family Ulidiidae belongs to the superfamily Tephritoidea, as was defined by McAlpine (1989). It forms a monophyletic cluster of families jointly with Pyrgotidae, Tachiniscidae, Platystomatidae and Tephritidae, in which all male protandrial (6th and 7th) spiracles are reduced². This character is synapomorphic for the families above. Species of Lonchaeidae, Piophilidae, Pallopteridae and Richardiidae usually have these spiracles well-developed, and form another group within Tephritoidea.

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² Korneyev (1987) reported *Homalocephala* to have 6th spiracle, but his suggestion was based upon an artifact.

Recent use of the family name Ulidiidae is somewhat controversial. It was applied only to its nominal subfamily, by several authors who treated it as a separate family (e.g., Hennig, 1940; Zaitzev, 1984). Another name commonly used recently for the family (*sensu latiorum*) was Otitidae. This one was proposed by Aldrich (1932) as a replacement name for Ortalidae Fallén, 1820, as the latter name was shown to be derived from a preoccupied generic name. Another family group name derived from *Otites* is Otitides Westwood, 1840. If Ulidiidae and Otitidae are united in one family, the oldest name Ulidiidae Macquart, 1835 must be used instead of Otitidae. Nevertheless, it was overlooked by all the authors, including Rohdendorf (1977), who published a list of family names and their authors for Diptera. We suggest Otitidae (s. lat.) to be a junior synonym of Ulidiidae. It may be retained only for a taxon of tribal or subfamilial rank.

As stated by McAlpine (1989), Ulidiidae (as Otitidae) are the sister-group to Pyrgotidae + Tachiniscidae + Platystomatidae + Tephritidae, and remain closer to the ground plan of this subgroup. Of the autapomorphies McAlpine listed for the Ulidiidae, only the reduced dorsal notch of the pedicel and absence of the presutural supraalar bristles are undoubtedly apomorphic character states.³ Moreover, Ulidiidae very often have an inconspicuous subcostal break in the costal vein, whereas in many Piophilidae, Pallopteridae, Pyrgotidae and Tephritidae it is strong. This character state may be treated as an autapomorphy of the most of genera of Ulidiidae. Other characters listed by McAlpine need additional re-evaluation.

No generally accepted suprageneric classification of the family exists. Loew (1868, 1873) was the first who had divided Ortalidae (= Ulidiidae) into «sections» Pyrgotina Loew, 1873, Platystomina Loew, 1873, Cephalina Loew, 1873, Ortalina Fallén, 1820, Pterocallina Loew, 1873, Ulidina Macquart, 1835 and Richardiina Loew, 1873. Since that time, Hendel (1916) proposed family rank for the Pyrgotidae, Platystomidae (= Platystomatidae), Richardiidae, Pterocallidae and Ulidiidae. Three more suprageneric names, Myrmecomyina Hendel, 1914, Lipsaninae Enderlein, 1938 and Euxestinae Hennig, 1940 were proposed hitherto (primarily within the Platystominae, Ortalidae and Lonchaeidae). Hennig (1939) synonymized Pterocallidae, Cephalidae and Myrmecomyiidae with Otitidae, and Steyskal (1961) considered Ulidiidae a subfamily of Otitidae. Hennig (1973) has shown that the only significant distinction between them is the presence or absence of modified bristles on the aedeagus. Later, Richter (1970a; 1970b), Soós (1984) and Zaitzev (1984) follow his previous point of view, and treated Otitidae and Ulidiidae (with two subfamilies, Euxestinae and Ulidiinae) as separate families. The subfamily Lipsaninae with the only monotypic genus *Lipsana* Enderlein from Easter Island was transferred into this family by J.F. McAlpine (in: Evenhuis, 1989). Recently, Kameneva (1992) proposed to divide Palaearctic Otitidae into three subfamilies, Euxestinae, Ulidiinae and Otitinae. Since Pterocallidae was synonymized with Otitidae, no new rank was formally proposed to this clearly monophyletic taxon, though Steyskal (1982) noted that this name is «entitled to no more than a possible tribal status».

3 Several Pyrgotidae also have these characters, but they appear independently.

Krivosheina and Kovalev (1972) noted that the taxonomic position of both *Seioptera* and *Pseudoseioptera* is isolated within Otitidae and considered them as transitional genera between Otitidae and Ulidiidae. Both genera have two katepisternal bristles and the stipe of the aedeagus setulose. In *Pseudoseioptera* the 1st radial vein is setulose, whereas in *Seioptera* it is bare, as in most Ulidiinae. To decide, if Ulidiinae, Otitinae and several other suprageneric taxa of Otitidae are monophyletic and supported with synapomorphic characters, we tested various hypotheses of phylogenetic relationships between the main groups of genera in the family.

Materials and Methods. Specimens were examined from the following collections: Deutsche Entomologisches Institut, Eberswalde-Finow, Bundesrepublik Deutschland (DEI), National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM), Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia (ZISP) and Zoological Museum of Moscow University, Russia (ZMMU).

To obtain cladograms of the main suprageneric taxa of Otitidae, character state matrices were analysed using the HENNIG86 © computer program (Farris, 1988). Fourteen characters were used in the phylogenetic analysis (Table 1). Trees were calculated from the character data matrix (Table 2) using the **mhennig** option to build multiple parsimonious trees. Then, with the option **nelsen**, a Nelson consensus tree (Table 3) was obtained from four **mhennig** trees. This part of the work and English translation were made by V.A.Korneyev, the rest was prepared by the senior author.

The morphological terminology used in this paper follows McAlpine (1981). English transliteration of geographical names follows recommendations by Kerzhner and Nartshuk (1992).

Relationships. *Pseudoseioptera* Stackelberg clearly belongs to Ulidiidae. It has the general body and wing habitus of the family, and lacks pre-sutural supraalar bristles. It appears to be close to the ground plan of Ulidiidae in several morphological features, e.g., body subshining black, R_1 completely setulose, cup with a short lobe, aedeagus moderately long and covered with small and rather fine setulae. Within the family, *Pseudoseioptera* fits closely to *Seioptera* Kirby and *Homalocephala* Zetterstedt. Synapomorphies of these three genera are the following: anepisternal bristles reduced; 2 pairs of katepisternal bristles present; in females 2 pairs of spermathecae developed. Both *Pseudoseioptera* and *Homalocephala* live in the forests of the temperate zone in the Holarctic Region, and their larvae breed under the bark of fallen trees, that also belong to ground plan of biological features in Tephritoidea as well as in Ulidiidae.

From Tables 3 and 4, it may be considered, that *Seioptera* is the sister-group of *Homalocephala*. Actually, there is no good synapomorphy in addition to those given above, so the branch 12 in Table 3 is to be polytomic. Autapomorphies of *Seioptera* are the following: white pilosity of katepisterna is very short (in *S. vibrans*) or completely absent (in *S. colon* Lw.), vein R_1 bare, cell r_{4+5} narrowed apically, and surstyli directed ventrally rather than posteroventrally. Autapomorphies of *Homalocephala* may be recognized as follows: body slender, head extremely wide and low in profile, face concave, antennal grooves indistinct, cup without any lobe or extension. The elongate, rather than spherical, shape of spermathecae is the only character of *Pseudoseioptera* considered here to be autapomorphic.

Relationships of this monophyletic group to other ulidiid taxa are shown in Tables 3 and 4. These cladograms should be considered provisional, as there is little information on the morphology of male and female terminalia in Lipsaninae and ulidiine genera. There is evidence that *Pseudoseioptera* and related genera belong to the same branch, as *Physiphora* and *Euxesta*. Its monophyly is supported by at least one synapomorphy. The epandrium in most of Ulidiinae species is expanded in antero-caudal direction rather than short and ovoid, as in Pterocallinae (= Otitinae). In some genera, such as in *Chaetopsis* it is shortened, but this state of character seem to be secondary.

Classification of Ulidiidae

In this paper we consider the family Ulidiidae to be divided into two subfamilies, Ulidiinae Macquart, 1835 and Otitinae Westwood, 1840, in the main features corresponding to Ulidiidae and Otitidae sensu Hennig (Hennig, 1939, 1940). The subfamily Ulidiinae here is divided into three tribes, Ulidiini Loew, 1873, stat.n., Lipsanini Enderlein, 1938, stat.n., and Seiopterini trib.n.

We consider *Lipsana insulaepaschalis* Enderlein, 1938 to belong to the same tribe as *Euxesta* Loew, *Neoeuxesta* Malloch and *Pseudeuxesta* Coq. and fit close to these genera, those are common in most of East Pacific islands. The subcostal break of the costa that Enderlein considered the character of Lonchaeidae (versus Ulidiidae), is more or less expressed in these related genera. Several important characters were omitted in the original description of *Lipsana*, and no materials were available, so we can neither synonymise, nor locate this genus and species more precisely. Nevertheless, the Lipsanini (= Lipsaniinae Enderlein, 1938) is undoubtedly a senior synonym of Euxestini (= Euxestinae Hennig, 1940).

The subfamily Otitinae includes three tribes: Otitini Westwood, 1840, stat.n., Pterocallini Loew, 1873, stat.n., and Cephalini Loew, 1873, stat.n. They may be recognized as follows.

Key to subfamilies and tribes of Ulidiidae

- 1(2) Vein R_1 bare, as a rule; if sometimes setulose, then anepisternal bristles absent and 2 pairs of katepisternal bristles are developed, and aedeagus bare or, at most, pubescent or short spinulose 3
 - Ulidiinae**..... 3
- 2(1) Vein R_1 always setulose, at least in its apical portion. Aedeagus strong and long spinulose 7
 - Otitinae**..... 7
- 3(4) Anepisternal bristles absent and 2 pairs of katepisternal bristles are developed. Four spermathecae **Seiopterini, trib.n.**
- 4(3) Anepisternal bristles present and no more than one pair of katepisternal bristles is developed 5
 - Ulidiini**..... 5
- 5(6) Face with deep, oval antennal grooves and broad carina between them. Aedeagus long and wide, with apically expanded and partially sclerotized preglans. Three spermathecae **Ulidiini**
- 6(5) Face at most with indistinctive antennal grooves and linear carina, or often without them. Aedeagus short and narrow, without preglans. Two spermathecae **Lipsanini**
- 7(8) Face concave; antennal grooves and carina indistinctive. Pterostigma and lobe of cup often very long. In males an impaired lobe of sternum 10 is developed anteromedially from surstyli **Pterocallini**
- 8(7) Face not concave; antennal grooves and carina distinctive. Pterostigma and lobe of cup less than 3,5 times longer than wide. Sternum 10 without such lobe 9
- 9(10) Proepisternal bristle seta-like or absent. Cell cup never with a pointed extension on lower apex. Form ant-like **Cephalini**

- 9(10) Proepisternal bristle strong. Cell cup with a pointed extension on lower apex.
Form not ant-like **Otitini**

Tribe SEIOPTERINI Kameneva et Korneyev, trib.n.

Diagnosis. Vein R_1 setulose or bare; anepisternal bristles absent and two pairs of katepisternal bristles present;⁴ epandrium expanded in antero-caudal direction; aedeagus pubescent or short spinulose in its medial part; no sclerotized preglans or long spinulae; in females two pairs of spermathecae.

Contains three genera as follows: *Seioptera* Kirby, 1817, with two species: *S. vibrans* (L.) and *S. colon* Lw., *Homalocephala* Zetterstedt, 1838, with seven species: *H. albitarsis* Ztt. (Holarctic), *H. angustata* (Wahlberg, 1839) (Palearctic), *H. apicalis* (Wahlberg, 1839) (Holarctic), *H. bimaculata* (Wahlberg, 1839), *H. bipunctata* (Loew, 1854) (Holarctic), *H. biseta* (Frey, 1908) (Palearctic) and *H. similis* (Cresson, 1924) (Nearctic), and *Pseudoseioptera* Stackelberg, 1955, with four nominal species; *P. demonstrans* (Hennig, 1941), *P. ingrlica* Stackelberg, 1955 (Palearctic), *P. albipes* (Cresson, 1919) and *P. dubiosa* (Johnson, 1921) (Nearctic).

Seioptera importans Hennig, 1941, from Central Chile, assigned to *Seioptera* also by Steyskal (1956; 1968; 1982), has R_1 bare, cell r_{4+5} not narrowed apically, 2 pairs of supraalar, 2 pairs well-developed anepisternal and one katepisternal bristle, and is believed to belong elsewhere.

Immature Stages. Larvae of *Seioptera vibrans* and *Pseudoseioptera demonstrans* were described by Lobanov (1958) and by Krivosheina and Kovalev (1972), respectively. In the main features they are very similar to those of some Lonchaeidae, Platystomatidae and Tephritidae.

Biology. *Pseudoseioptera ingrlica* was reported to breed under the bark of rotten trees; its larvae are saprophagous (Krivosheina, Kovalev, 1972). Nearctic species of this genus live in temperate zone forests and are believed to have similar bionomics. *Homalocephala albitarsis*, *H. apicalis* and *H. bimaculata* breed in mountain forests of North Caucasus under the bark of fallen aspens (light brown to dark brown stages of wood rotting) and larvae of *H. angustata* were found under the bark of birches (latest stages of decaying, together with larvae of Tipulidae) (Lukasheva, 1987). Larvae of *Seioptera vibrans* feed in decaying onions of various wild Liliaceae (Hennig, 1939), and very often can be found in cesspools feeding in rotten vegetable remainders (Lobanov, 1958).

Key to the genera of Seiopterini

- 1(2) Vein R_1 completely bare; cell r_{4+5} narrowed apically. Anepisterna very short and whitish pilose or bare. Lower apex of cell cup short lobate ***Seioptera* Kirby**
 2(1) Vein R_1 setulose from its base to apex; cell r_{4+5} not narrowed apically. Anepisterna rather long and dark setulose 3
 3(4) Face wider than high. Eyes longer or as long as high. Cell cup without any lobe ***Homalocephala* Ztt.**
 4(3) Face higher than wide. Eyes higher than long. Cell cup with a short but distinctive lobe ***Pseudoseioptera* Stack.**

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4 In some species of *Homalocephala* one or both katepisternals are absent.

Table 1 Characters used in analysis of phylogenetic relationships between the suprageneric groups of Ulidiidae

State 0 is hypothesized as plesiomorphic, states 1 and 2 as apomorphic

1. Frontal bristles — 0) seta-like or inconspicuous; 1) strong.
2. Presutural supraalar bristles — 0) present; 1) absent.
3. Anepisternal bristles — 0) developed; 1) absent.
4. Katepisternal bristles — 0) one pair; 1) two pairs.
5. Vein R₁ — 0) completely setulose; 1) bare basally; 2) completely bare.
6. Extension of cell cup — 0) short; 1) absent; 2) long (non-additive character).
7. Gonites — 0) with long setulae; 1) with inconspicuous setulae.
8. Parameres — 0) produced; 1) plate-like, small.
9. Epandrium — 0) as high as long, or higher than long; 1) longer than high.
10. Surstyli — 0) ventral; 1) ventrocaudal.
11. Medial portion of aedeagus stipe dorsally — 0) fine and/or short setulose; 1) bare; 2) long spinulose.
12. Spermathecae — 0) - three; 1) two; 2) four.
13. Glans of aedeagus — 0) well-developed, sclerotized; 1) indistinctive, membranous; 2) secondary apical sclerotized preglands developed.
14. Subcostal break of costal vein — 0) distinctive; 1) indistinctive.

Table 2 Matrix of character state distribution in Ulidiidae and families of Tephritoidea

Character No:	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Taxa														
Richardiidae	0	0	0	2	2	0	1	1	0	0	0	1	0	0
Pyrgotidae	1	0	0	0	0	0	1	1	0	0	0	0	0	0
Pallopteridae	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Physiphora	0	1	0	0	2	2	?	1	1	1	0	0	2	1
Chaetopsis	1	1	0	0	2	0	0	0	0	0	0	1	1	1
Euxesta	1	1	0	0	2	2	0	1	1	1	0	1	1	0
Homalocephala	0	1	1	1	0	1	0	1	1	1	0	2	1	1
Pseudoseioptera	0	1	1	1	0	0	0	1	1	1	0	2	1	1
Seioptera	0	1	1	1	2	0	0	1	1	0	0	2	0	0
Myennis	0	1	0	0	1	2	1	1	0	0	2	0	1	1
Otites	0	1	0	0	0	0	0	1	0	0	2	?	1	1
Herina	0	1	0	0	1	0	0	1	0	0	2	0	1	1

Table 3 Treeplot of phylogenetic relationships between the genera of Ulidiidae and families of Tephritoidea

nelsen file 0 from mhennig 4 trees, tplot file 0 from nelsen 1 tree

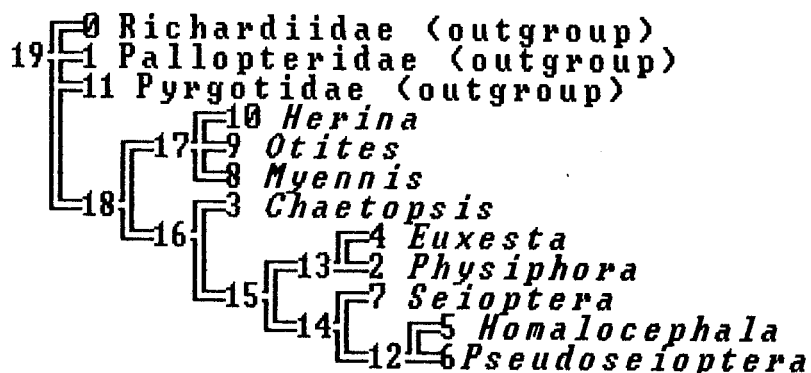
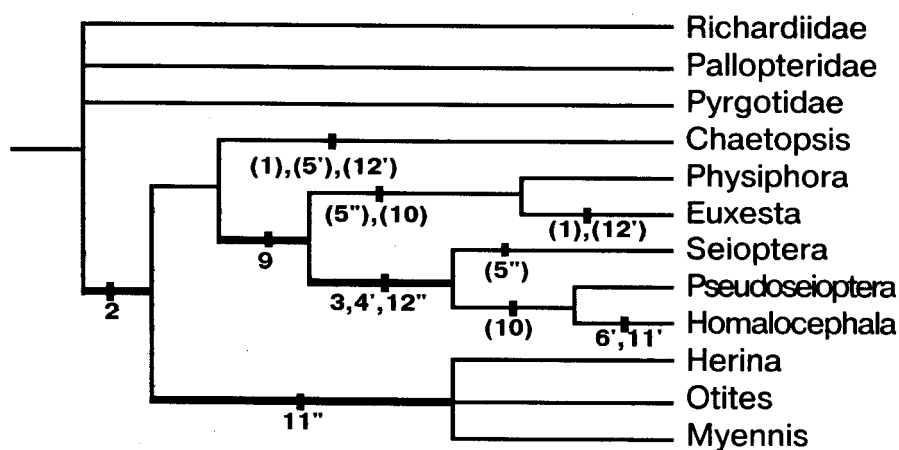


Table 4
Hypothesized phylogenetic relationships of some genera
of Ulidiidae and families of Tephritoidea, with distribution
of the most sufficient apomorphies
(a modification of Table 3)



Apomorphies showing homoplasy are given in parentheses. Clades, based on good synapomorphies, are performed with bold line. Numbers of characters with strokes mean various degrees or conditions of apomorphies, e.g. 5' = Character 5, State 1, 12'' = Character 12, State 2 (see table 1)

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