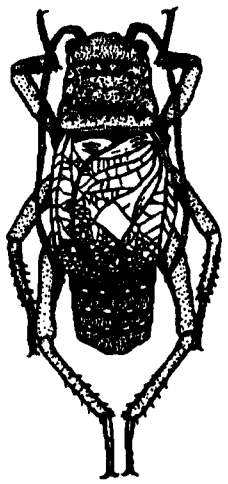

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PHYLOGENY OF THE TRIBE *STEGANINI* HENDEL AND SOME RELATED TAXA (DIPTERA, DROSOPHILIDAE)

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Phylogenetic relationships of the tribe Steganini and some related taxa of the subfamily Steganinae were analysed. 31 species of Steganinae as ingroup and 3 species representatives of three ephydroid families as outgroup were studied. 78 adult morphological characters (from the head to the male and female terminalia) were extracted for the analysis. The data matrix was subjected to a cladistic analysis by PAUP 4.0b8 and gilded a consensus tree (length of 328 steps, CI – 0.3865, HI – 0.6135, RI – 0.06311, RC – 0.2439). Results of analysis support the former suprageneric classification (Grimaldi, 1990) but taxonomic status of some genera and subgenera must be changed. New subgenus *Anastega* Sidorenko, **subgen. n.** of the genus *Stegana* is described. Subgenus *Nankangomyia* Maca et Lin, 1993, **comb. n.** is transferred from genus *Leucophenga* (tribe Steganini) to genus *Cacoxenus* (tribe Gitonini), therefore new combinations are proposed: *C.* (*N.*) *academicus* (Maca et Lin, 1993), **comb. n.**; *C.* (*N.*) *leucophengoides* (Sturtevant, 1927), **comb. n.**; *C.* (*N.*) *parallelinervis* (Duda, 1924), **comb. n.**; *C.* (*N.*) *philippinensis* (Sidorenko, 1998), **comb. n.** *Parastegana* Okada, 1971, **stat. n.** is considered as distinct genus of tribe Gitonini with follow species: *P. drosophiloides* Toda et Peng, 1992, **comb. n.**; *P. femorata* (Duda, 1923), **comb. n.**; *P. maculipennis* Okada, 1971, **comb. n.** *Pseudostegana* Okada, 1978, **stat. n.** is considered as distinct genus of tribe Gitonini with follow species: *P. albinotata* Okada, 1982, **comb. n.**; *P. campanularia* Okada, 1982, **comb. n.**; *P. fleximidiata* Takada, Momma et Shima, 1973, **comb. n.**; *P. grandipalpis* Takada et Momma,

1975, **comb. n.**; *P. hirta* Okada, 1982, **comb. n.**; *P. javana* Okada, 1978, **comb. n.**;*P. lacrymaria* Okada, 1982, **comb. n.**; *P. latipalpis* Sidorenko, 1998, **comb. n.**; *P. latiparma* Okada, 1982, **comb. n.**; *P. latizonaria* Okada, 1982, **comb. n.**; *P. lineoparma* Okada, 1982, **comb. n.**; *P. malayana* Okada, 1978, **comb. n.**; *P. zonaria* Okada, 1982, **comb. n.** Among the studied species of the subgenus *Steganina* three species-groups were established (two of them for the first time).

KEY WORDS. Drosophilidae, *Stegana*, phylogeny, taxonomy.

Â. Ñ. Ñèäîðåíêî. Ôèëîãåíåçèò òðèáû *Steganini* Hendel è íåêîòîðûõ áëèçêèõ òàêñîíîâ (Diptera, Drosophilidae) // Äàëüíåâîñòî÷íûé ýíòîìîëîã. 2001. N 111. Ñ. 1-20.

Ïðîâåäåíî èçó÷åíèå ôèëîãåíåòè÷åñêèõ âçàèìîîòíîøåíèé òðèáû Steganini è íåêîòîðûõ áëèçêèõ òàêñîíîâ èç ïîäñåì åéñòâà Steganinae. Èññëåäîâàí 31 âèä èç ïîäñåì åéñòâà Steganinae (ingroup) è 3 âèäà èç áëèçêîðîäñòâåííûõ ñåì åéñòâ (outgroup). Ì àòðèöà äàííûõ ñäåëàíà íà îñíîâå 78 ìîðôîëîãè÷åñêèõ ïðèçíàêîâ è îáñ÷èòàíà ïðè ïîìîùè ïðîãðàìì PAUP 4.0b8. Õàðàêòåðèñòèêà ïîëó÷åííîãî äåðåâà (äëèíà 328 ø àãà, CI – 0.3865, HI – 0.6135, RI – 0.06311, RC – 0.2439). Ðåçóëüòàòû àíàëèçà ñîãëàñóþ òñÿ ñ íàäðîäîâîé êëàññèôèêàöèåé ïîäñåì åéñòâà Steganinae, ïðåäëîæåííîé Ãðèì àëüäè (1990). Î ïèñûâàåòñÿ íîâûé ïîäðîä *Anastega* Sidorenko **subgen. n.** â ðîäå *Stegana*. Ïîäðîä *Nankangomyia* Maca et Lin, 1993, **comb. n.** ïåðåíåñåí èç ðîäà *Leucophenga* (òðèáà Steganini) â ðîä *Cacoxenus* (òðèáà Gitonini), ïîýòîìó ïðåäëàãàþ òñÿ íîâûå êîìáèíàöèè: *C.* (*N.*) *academicus* (Maca et Lin, 1993), **comb. n.**; *C.* (*N.*) *leucophengoides* (Sturtevant, 1927), **comb. n.**; *C.* (*N.*) *parallelinervis* (Duda, 1924), **comb. n.**; *C.* (*N.*) *philippinensis* (Sidorenko, 1998), **comb. n.** *Parastegana* Okada, 1971, **stat. n.** ðàññìàòðèâàåòñÿ êàê ñàì îñòî ÿòåëüíûé ðîä â òðèáå Gitonini è âêëþ÷àåò ñëåäóþ ùè å âèäû: *P. drosophiloides* Toda et Peng, 1992, **comb. n.**; *P. femorata* (Duda, 1923), **comb. n.**; *P. maculipennis* Okada, 1971, **comb. n.** *Pseudostegana* Okada, 1978, **stat. n.** ðàññìàòðèâàåòñÿ êàê ñàì îñòî ÿòåëüíûé ðîä â òðèáå Gitonini è âêëþ÷àåò ñëåäóþ ùè å âèäû: *P. albinotata* Okada, 1982, **comb. n.**; *P. campanularia* Okada, 1982, **comb. n.**; *P. fleximidiata* Takada, Momma et Shima, 1973, **comb. n.**; *P. grandipalpis* Takada et Momma, 1975, **comb. n.**; *P. hirta* Okada, 1982, **comb. n.**; *P. javana* Okada, 1978, **comb. n.**; *P. lacrymaria* Okada, 1982, **comb. n.**; *P. latipalpis* Sidorenko, 1998, **comb. n.**; *P. latiparma* Okada, 1982, **comb. n.**; *P. latizonaria* Okada, 1982, **comb. n.**; *P. lineoparma* Okada, 1982, **comb. n.**; *P. malayana* Okada, 1978, **comb. n.**; *P. zonaria* Okada, 1982, **comb. n.** Ñõåìè èçó÷åíû âèäîâ ïîäðîäà *Steganina* âûäåëåíû òðè ãðóïïû âèäîâ (äâå èç íèõ óñòàíîâëåíû âïåðâûå).

Áèîëîãî-ïî÷âåííûé èíñòèòóò, Äàëüíåâîñòî÷íîå îòäåëåíèå Ðîññèéñêîé Àêàäåìèè íàóê, Âëàäèâîñòîê-22, 690022, Ðîññèÿ.

INTRODUCTION

The Drosophilidae is one of the largest families of muscomorphan Diptera, including about 3000 species around the world (Wheeler, 1981, 1986). All previous studies on drosophilid phylogeny came to conclusion that family Drosophilidae is divided into two sister-group subfamilies, Steganinae and Drosophilinae, and that Steganinae retains more plesiomorphic characters than Drosophilinae (Grimaldi, 1990). In some phylogenetic studies on drosophilines, steganines were selected as outgroup species (DeSalle, Grimaldi, 1991). The revealing of the phylogenetic relationships among steganine species is important not only to estimate the origin of Drosophilidae, but also to obtain reliable results for drosophiline phylogeny. At present, there are three hypotheses of phylogenetic relationships among the Drosophilidae (Throckmorton, 1975; Okada, 1989; Grimaldi, 1990). As to Steganinae phylogeny, only a few studies have been attempted.

Okada (1989) made a phenetic analysis with fourteen adult morphological characters for sixty-two genera of Drosophilidae, of which only eight characters concerned the nineteen steganine genera studied. Based on the result, he proposed to establish tribes for this family, including Steganini and Leucophengini for Steganinae. The tribe Steganini included genera *Electrophortica* Hennig, 1965; *Soederbomia* Hendel, 1938; *Pyrgometopa* Kertesz, 1901; *Eostegana* Hendel, 1913; *Stegana* Meigen, 1830; *Amiota* Loew, 1862; *Crincosia* Bock, 1982; *Apenthecia* Tsacas, 1983; *Mayagueza* Wheeler, 1960; *Cacoxenus* Loew, 1858 and *Gitona* Meigen, 1830 and tribe Leucophengini included genera *Acletoxenus* Frauenfeld, 1869; *Luzonimyia* Malloch, 1926; *Leucophenga* Mik, 1886; *Paraleucophenga* Hendel, 1914; *Pseudiastata* Coquillett, 1908; *Trachyleucophenga* Hendel, 1917; *Pararhinoleucophenga* Duda, 1924 and *Rhinoleucophenga* Hendel, 1917.

Grimaldi (1990) made a cladistic analysis extracting 217 adult morphological characters from a set of 158 species (but only 120 species subjected to the analysis) representing most genera and subgenera of Drosophilidae. Twenty-seven (but eighteen subjected to the analysis) steganine species representing eighteen (sixteen) genera and subgenera with sixty-seven characters were included in his study. He proposed the tribes Steganini and Gitonini among Steganinae. The tribe Steganini included genera *Stegana, Eostegana* (subtribe Steganina) and *Leucophenga* (subtribe Leucophengina), and tribe Gitonini included *Pararhinoleucophenga, Rhinoleucophenga, Pseudiastata, Mayagueza, Acletoxenus* (subtibe Acletoxinina), *Paraleucophenga, Crincosia, Cacoxenus, Gitona, Amiota* and *Apenthecia* (subtribe Gitonini) and genera *Electrophortica, Trachyleucophenga,*. However, either study did not guarantee the monophyly for each of these genera: Okada extracted the characters as generic features, and Grimaldi chose in principle only the type species as a representative of each genus or subgenus. The monophyly seems to be questionable for some of these steganine genera.

The major objective of this report is to establish phylogenetic relationships of genera and subgenera in the subfamily Steganinae, focusing on *Stegana*-related taxa, especially of subtribe Steganina defined by Grimaldi (1990).

MATERIALS AND METHODS

Thirty four species from nine genera have been studied for the obtaining of morphological characters and their distribution among the steganine high taxa. The list of studied species is given herein according to the Grimaldi's (1990) classification of Drosophilidae (Final position of studied taxa see belowin taxonomic results).

OUTGROUP: *Campichoeta griseola* (Zetterstedt, 1855) (♂,♀) – Campichoetidae; *Diastata vagans* Loew, 1864 (♂, ♀) - Diastatidae; *Curtonotum anus* Meigen, 1830 (♂, ♀) - Curtonotidae.

INGROUP: Tribe **Gitonini** Grimaldi. **Amiota** genus group. *Amiota* (*A.*) *albilabris* (Roth, 1860) (♂, ♀); *Amiota* (*A.*) *stylopyga* Wakahama et Okada, 1958 (♂, ♀); *A.* (*Apsiphortica*) *lini* Okada, 1971 (♂); *A.* (*Phortica*) *kappa* Maca, 1977 (♂, ♀).

Subtibe **Gitonina** Grimaldi. *Cacoxenus* (*Gitonides*) *kaszabi* (Okada, 1973) (♂, ♀); *C.* (*Paracacoxenus*) *perspicax* Knab, 1914 (♂, ♀); *Gitona distigma* Meigen, 1830 (♂, ♀); *Paraleucophenga emeiensis* Sidorenko, 1998 (♂).

Tribe **Steganini** Hendel. Subtribe **Leucophengina** Okada. *Leucophenga* (*L.*) *angusta* Okada, 1956 (♂, ♀); *L.* (*Nankangomyia*) *philippinensis* Sidorenko, 1998 (♂, ♀).

Subtribe **Steganina** Hendel. *Stegana* (*Oxyphortica*) *watabei* Sidorenko, 1998 (♂); *S.* (*O.*) *convergens* (de Meijere, 1911) (♂, ♀); *S.* (*Parastegana*) *femorata* (Duda, 1923) (♂, ♀); *S.* (*Pseudostegana*) *latipalpis* Sidorenko, 1998 (♂); *S.* (*P.*) *fleximediata* Takada, Momma et Shima, 1973 (♂); *S.* (*Stegana*) *antlia* Okada, 1991 (♂); *S.* (*S.*) *furta* (Linnaeus, 1766) (♂, ♀); S. (S.) *nartshukae* Sidorenko, 1997 (♂); *S.* (*S.*) *sibirica* Duda, 1934 (♀); *S.* (*S.*) *singularis* Sidorenko, 1990 (♂, ♀); *S.* (*Steganina*) *baechlii* Lastovka et Maca, 1982 (♂, ♀); *S.* (*S.*) *belokobylskiji* Sidorenko, 1997 (♂); *S.* (*S.*) *ctenaria* Nishiharu, 1979 (♂, ♀); *S.* (*S.*) *longifibula* Takada, 1968 (♂, ♀); *S.* (*S.*) *masanoritodai* Okada et Sidorenko, 1992 (♂, ♀); *S.* (*S.*) *nigrithorax* Strobl, 1898 (♂, ♀); S. (S.) *nigrolimbata* Duda, 1924 (♂, ♀); *S.* (*S.*) *ornatipes* Wheeler et Takada, 1964 (♂, ♀); S. (S.) *vietnamensis* Sidorenko, 1997 (♂); *S.* (*S.*) *chitouensis* Sidorenko, 1998 (♂, ♀); S. (S.) *undulata* de Meijere, 1911 (♂, ♀).

The 78 following characters from the head to terminalia of male and female adult morphology were used to analyse phylogenetic relationship. Their resulting matrix is given in Table 1. Some transformation series were adopted from Griffiths (1972), Chandler (1987), Grimaldi (1990) and indicated in parentheses as G#, C# and Gr# respectively. Polarity is indicates in parentheses; (0) is primitive state; (1,2,3,4) are derived states and (?) is the data unknown. The data matrix was

subjected to parsimony analysis using PAUP, version 4.0b8 (Swofford, 2001). All characters states were treated as unweighted. Heuristic search gave Adams consensus tree (Fig. 1) by length 328 steps from 1512 most parsimonius trees with length 328 steps (CI = 0.3865, HI = 0.6135, RI = 0.6311, RC = 0.2439).

Head

1 (partly C1; Gr68, 73). Proclinate orbital seta situated postero-externally to anterior reclinate orbital (1), antero-externally (0), antero-internally (2). Defined type – [0(1,2)]; CI – 0.667; RI – 0.667; RC – 0.444; HI – 0.333.

2 (Gr69). Posterior reclinate orbital situated near to proclinate orbital than to inner vertical (0), posterior reclinate orbital situated near to inner vertical than to proclinate orbital (1). Unordered; CI – 0.500; RI – 0.000; RC – 0.000; HI – 0.500.

3 (Gr70). Anterior reclinate orbital seta long (1/3 or more of the length of other orbital) (0), short (1/4 or less) (1). Unordered; CI – 0.500; RI – 0.500; RC – 0.250; HI – 0.500.

4 (Gr74). Ocellar triangle not elongated, extending to about the middle of the frons (0), ocellar triangle elongated, extending to anterior margin of the frons (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

5 (Gr61). Interfrontal setulae – 15 or more (0), 7-13 (1), 5 or less (2). Ordered; CI – 0.333; RI – 0.600; RC – 0.200; HI – 0.667.

6 (partly Gr75). Ocellar setae situated inside of ocellar triangle (0), outside of ocellar triangle (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

7 (C5). Postocellar setae present (0), postocellar setae absent (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

8 (Gr3). Postocular setae 12-19 per side (0), 20-29 per side (1), 30-34 per side (2). Ordered; CI – 0.400; RI – 0.250; RC – 0.100; HI – 0.600.

9 Frons and face making obtuse angle in profile (0), making acute angle in profile (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

10 (Gr1, 44, 46 partly). Arista short pubescent (0), plumose (with 2 or more ventral rays) (1), plumose (with 1 ventral ray) (2), plumose only dorsally (3), micropubescent (4). Defined type – [0(1(2(3)),4)]; CI – 0.444; RI – 0.500; RC – 0.222; HI – 0.556.

11 (Gr94). Subvibrissa not differentiated (0), differentiated but shorter than vibrissa (1), as long as vibrissa (2). Unordered; CI – 0.400; RI – 0.500; RC – 0.200; HI – 0.600.

12 (Gr11). Postgena broad (0), postgena somewhat narrow (1). Unordered; CI – 0.250; RI – 0.786; RC – 0.196; HI – 0.750.

13 (Gr2). Supracervical setae blunt (0), tapered, thin with curved apex (1). Unordered; CI – 0.500; RI – 0.800; RC – 0.400; HI – 0.500.

14 (Gr4, 6 partly, 7 partly). Dorsolateral tentorial apodemes divergent (0), parallel or slightly convergent (1). Unordered; CI – 0.125; RI – 0.417; RC – 0.052; HI – 0.875.

15 (Gr5). Bases of dorsolateral tentorial apodemes situated rather far from each other (distance between bases of apodemes 3/4 or more than length of apodemes (0),

dorsolateral tentorial apodemes closely situated to each other at base (distance between bases of apodemes 1/2 or less than length of apodemes) (1). Unordered; CI – 0.250; RI – 0.769; RC – 0.192; HI – 0.750.

16 (Gr8, 9 modified). Dorsomedial tentorial apodeme short (less 1/2 of length dorsolateral) (0), long (more than 3/4 of length of dorsolateral) (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

17 (Gr10). Base of ventrolateral tentorial apodemes narrow (0), broad (1). Unordered; CI – 0.500; RI – 0.500; RC – 0.250; HI – 0.500.

18 (Gr26). Posterior cibarial sensillae 15 or less per side (0), 16 or more per side (1). Unordered; CI – 0.500; RI – 0.000; RC – 0.000; HI – 0.500.

19 (Gr28). Anterior cibarial sensillae situated as quadrate (0), as rhomb (1), as stright line (2). Ordered; CI – 0.667; RI – 0.000; RC – 0.000; HI – 0.333.

20 Cibarium truncate at anterior end (0), slightly protruted at anterolateral corner (1), distinctly protruded here (2). Ordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

Thorax

21 (Gr104). Thorax without spots at bases of each setae (0), with spots at bases of each setae (1). Unordered; CI – 0.333; RI – 0.000; RC – 0.000; HI – 0.667.

22 (Gr100). Postpronotal lobe with 1 seta (0), with 2 setae (1), with 3 setae (2). Unordered; CI – 0.500; RI – 0.000; RC – 0.000; HI – 0.500.

23 (Gr101). Acrostichal setulae in line with and anterior to dorsocentral the same in size as others (0), thicker and longer than others (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000. One or few setulae just before the transverse suture are usually thicker and longer than others. The innermost one is situated just lateral to the dorsocentral line but is not counted in this transformation series.

24 (Gr98). Acrostichal setulae situated in 8 or more rows (0), in 6 rows (1). Ordered; CI – 1.000; RI – 0/0; RC – 0/0; HI – 0.000. Grimaldi (1990) defined seven states according to the numbers of rows of acrostichals, but I lumped the two state with 8 rows into the plesiomorphic state. It is difficult to count accurately the number of rows due to irregularity of arragement and/or intraspecific variation.

25 (Gr103). 2 pairs of dorsocentral setae present (0), 1 pair present (1). Irreverrsible; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

26 (Gr95). Prescutellar setae present (0), absent (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000. Grimaldi (1990) discriminating two states in the relative length of prescutellars to the dorsocentrals. However, it varies continuously among taxa so that it is difficult to define them objectively.

27 Scutellum pubescent (0), bare (1). Unordered; CI – 0.500; RI – 0.000; RC – 0.000; HI – 0.500.

28 (Gr102). Dorsalmost setae between two katepisternals nearly the same in size (0), longer than other but shorter than anterior katepisternal (1), as long as or longer than katepisternals (2). Ordered; CI – 0.200; RI – 0.429; RC – 0.086; HI – 0.800. Grimaldi's definition (1990) did not concern the relative length of the katepisternals.

29 (Gr99). 2 long katepisternal setae present (0), 1 seta present (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

30 (C3). Anepisternum pubescent (0), bare (1). Ordered; CI – 0.500; RI – 0.500; RC – 0.250; HI – 0.500.

Wing

31 Longitudinal veins of wing not became thin transversally (0), longitudinal veins of wing became thin transversally (1). Unordered; CI – 0.500; RI – 0.933; RC – 0.467; HI – 0.500.

32 (Gr109 partly). Costa with long spine-like setae (0), with thorn-like warts (1), without spines and thorn-like warts (2). Ordered; CI – 0.667; RI – 0.900; RC – 0.600; HI – 0.333.

33 (C3; G5). Humeral break of costa present (0), absent (1). Ordered; CI – 1.000; RI – 0/0; RC – 0/0; HI – 0.000.

34 (G6a; G6). *Sc* is close to R_1 and more or less fused apically to it (0), *Sc* parallel with R_1 and distinct from the costa (1). Unordered CI – 1.000; RI – 0/0; RC – 0/0; HI – 0.000.

35 (Gr108, 115). R_{4+5} and M_1 parallel or slightly divergent (0), R_{4+5} and M_1 slightly convergent apically (1), strongly convergent apically (2). Unordered; CI – 0.400; RI – 0.727; RC – 0.291; HI – 0.600.

36 (C7). Crossvein *bm-cu* present (0), absent (1). Unordered; CI – 0.250; RI – 0.250; RC – 0.063; HI – 0.750.

37 (C2, G7). Anal cell with rounded closing vien (0), with angulate closing vein (1). Unordered; CI – 0.500; RI – 0.000; RC – 0.000; HI – 0.500.

38 C-index - 2.5 or less (0), 2.5-3.5 (1), 3.5 or more (2). Unordered; CI – 0.333; RI – 0.600; RC – 0.200; HI – 0.667.

39 5x-index – 1.0 or less (0), 1.2 or more (1). Unordered; CI – 0.125; RI – 0.300; RC – 0.037; HI – 0.875.

40 4V-index – 1.5 or less (0), 1.5-2.5 (1), 2.5 or more (2). Unoredred; CI – 0.333; RI – 0.333; RC – 0.111; HI – 0.667.

41 C3F-index less than 0.5 (0), 0.5 or more (1). Unordered; CI – 0.167; RI – 0.000; RC – 0.000; HI – 0.833.

Legs

42 (Gr1). Ctenidial spines on anterior femora present (0), absent (1). Ordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

43 Mid femora without sharp spine-like setae apically (0), with such setae (1). Irreversible; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

Male terminalia

44 (Gr177). Epandrium with setae not only on ventral portion but also on other portions (0), only on ventral portion (1). Unordered; CI – 0/0; RI – 0/0; RC – 1.000; HI – 0.000.

45 Ventral part of epandrium without any sclerotized or not protrunings (0), with such protrudings (1).; Unordered; CI – 0.333; RI – 0.333; RC – 0.111; HI – 0.667.

46 (Gr127). Surstylus separated from but articulating with epandrium (0), fused to epandrium (1). Unordered; CI – 0.250; RI – 0.000; RC – 0.000; HI – 0.750.

47 (C15). 1 pair surstylus present (0), additional pair of surstylus present (1). Unordered; CI – 1.000; RI – 0/0; RC – 0/0; HI – 0.000.

48 (partly Gr155, 178, 186, 187, 200). Surstylus without peg-like prensisetae (0), with 1 peg-like prensisetae apecally (1), with peg-like ones in irregular rows (2), with peg-like ones arranged in 1 row (3). Unordered; CI – 0.300; RI – 0.588; RC – 0.176; HI – 0.700. Grimaldi (1990) treated various morphologies and arrangements of prensisetae on the surstylus in different TSs. However, there is no reason for designating of different TSs with respect to homologous characters. I defined them as different characters in a single TS.

49 Surstylus without stout setae on caudoventral margin to caudal inner surface (0), with such setae (1). Unordered; CI – 0.250; RI – 0.727; RC – 0.182; HI – 0.750.

50 Surstylus without stout setae on outher mesal surface (0), with such setae (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

51 Cercus nearly entirely pubescent (0), partly pubescent (1), not pubescent (2). Unordered; CI – 0.400; RI – 0.800; RC – 0.320; HI – 0.600.

52 Cercus caudoventrally without any ornamentation (0), with ornamentation or tuft of fine setae (1). Unordered; CI – 0.333; RI – 0.000; RC – 0.000; HI – 0.667.

53 Hypandrium without paramedian setae (0), with 1 pair (1), with 2 pairs of paramedian setae (2). Unordered; CI – 0.286; RI – 0.375; RC – 0.107; HI – 0.714.

54 (Gr167). Hypandrium pubescent in a very small portion (0), not pubescent (1). Unordered; CI – 0.250; RI – 0.000; RC – 0.000; HI – 0.750. Grimaldi (1990) regarded the paramere with small patch of dense microtrichia on the ventral surface as a synapomorphic character. Since sternites are usually pubescent and partly pubescent hypandrium (sternite IX) such a character is considered here to be plesiomorphic.

55 Aedeagal guide present (0), absent (1). Irreversible; CI – 0.250; RI – 0.250; RC – 0.063; HI – 0.750.

56 Paramere ventrobasally not articulating with hypandrium (0), articulating with small expansion of hypandrium (1). Ordered; CI – 0.250; RI – 0.500; RC – 0.125; HI – 0.750.

57 Paramere articulating with aedeagus (0), fused to aedeagus (1), fused to aedeagal guide (2). Defined type – [0(1,2)]; CI – 0.500; RI – 0.867; RC – 0.433; HI – 0.500.

58 (Gr201 partly). Paramere partly pubescent (0), not pubescent (1). Unordered; CI – 0.333; RI – 0.333; RC – 0.111; HI – 0.667. Grimaldi (1990) defined his apomorphy 201 as the paramere bearing a field or patch of fine, dense microtrichia on its lateral, broad surface. According to his figures 482, 485, 488, 489, however, this character can not be distinguished frim his apomorphy 167 and the pubescent portion reffered to by him should be a part of hypandrium. The partly pubescent paramere is regarded here as plesiomorphic.

59 (Gr145 partly). Paramere with minute sensillae arranged nearly longitudinally (0), with small sensilla in a patch (1), with long sensillae apically (2), without sensilla (3), with sensilla each on peg-like tooth (4). Unordered; CI – 0.364; RI – 0.417; RC – 0.152; HI – 0.636. Grimaldi (1990) designated two or more long setae on the paramere as his apomorphy 145. According to the his figure 415, he seemed to misjudge the setae on the caudolateral processes of hypandrium as those on the paramere. I descriminated the five different characters in the arrangement, number, and length of sensilla on the paramere.

60 Paramere ventrally without processes (0), with processes (1). Unordered; CI – 1.000; RI – 0/0; RC – 0/0; HI – 0.000.

61 Paramere caudally without processes (0), with processes (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

62 Gonopods fused to each other, forming plate or ventral rod situated dorsally to distiphallus (0), fused to each other, forming bridge connecting caudal ends of hypandrium (1), almost degenerated (2). Unordered; CI – 0.286; RI – 0.583; RC – 0.167; HI – 0.714. McAlpine (1981) reviewed, much confusion has been existing with respect to the interpretation and naming of processes on the posterior margin of sternite IX (hypandrium), which he called gonopods, throughout the endopterygote orders. In the drosophilid taxonomy the consistent term and interpitation have not been conventionally called posterior paramere. According to the terminology and interpretation recently revised by Zhang and Toda (1992) and Cheng and Toda (1994), I define here the organ that articulates anteriorly with the hypandrium and posteriorly with 10th sternite and bridges the caudal edges of hypandrium as gonopods. Grimaldi (1990) refereed to an organ lying over the aedeagus as folded, dorsal process and recognized it as anapomorphy (Gr130-1) for the genus *Leucophenga*. Okada (1968) termined is posterior. The relative position of this organ is completely consistent with the above definition of gonopods and supports Okada' interpretations. The apically curved, median rod of this organ (hooked piece in Okada or "der Haken" in Bachli (1971) is homologous to dorsal mantle (Okada, 1977) and vertical lobe (Toda, Peng, 1992) of posterior paramere in the subgenera *Phortica* and *Amiota*, respectively. Grimaldi (1990) recognized Okada's "dorsal mantle" as an autopomorphy (Gr154-1) for the subgenus *Phortica* and considered it to be " a huge extension of the floor of the decasternum". He pointed out that there is a similar organ articulating with 10th sternite also in *Cacoxenus* (*Paracacoxenus*). According to the above definition, these organs are all to be gonopods.

63 Aedeagal apodeme shorter than aedeagus (0), as long as aeeagus (1), longer than aedeagus (2), degenerated (3). Defined type – [0(1(2),3)]; CI – 0.250; RI – 0.571; RC – 0.143; HI – 0.750.

64 (Gr153 partly). Aedeagal apodeme rod-like (0), laterally flat (1), horizontally flat (2). Unordered; CI – 0.400; RI – 0.571; RC – 0.229; HI – 0.600. In TS Gr153, Grimaldi (1990) reffered to variations in the morphology of aedeagal apodeme only within the genus *Amiota*, designating the horizontally flat aedeagal apodeme as an apomorphy for the subgenus *Amiota*.

65 Aedeagus articulating with aedeagal apodeme (0), fused to it (1). Irreversible; CI – 0.143; RI – 0.455; RC – 0.065; HI – 0.857.

66 1 pair of simple rod-like processes extending posteriorly from base of aedeagus, apically articulating with gonopod (0), aedeagal basal processes connected to gonopods with membrane bearing finger-like or conical processes (1), aedeagal basal processes free from gonopods (2), absent (3). Unordered; CI – 0.300; RI – 0.364; RC – 0.109; HI – 0.700.

67 (Gr128, 132). Aedeagus without hair crown or tentackle-like processes (0), with hair crown, tentackle-like processes or microtrichia (1). Unordered; CI – 0.167; RI – 0.545; RC – 0.091; HI – 0.833. Grimaldi (1990) designated mictotrichia or tentackle-like processes on the distal portion of aedeagus as separate apomorphies. However, it is somewhat difficult to distingiush clearly between microtrichia and tentackle-like processes on the aedeagus throughout the Steganinae.

68 Distiphallus connected to gonopods with membrane (0), free from gonopods or gonopods absent (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

69 Aedeagus sclerotized (0), pale, membranous (1). Unordered; CI – 0.333; RI – 0.500; RC – 0.167; HI – 0.667.

Female terminalia

70 Tergite VII dorsally broad (0), separated on 2 lobes connected by membrane (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

71 Tergite VIII dorsally pubescent (0), not pubescent (1). Unordered; CI – 0.333; RI – 0.778; RC – 0.259; HI – 0.667.

72 Cercus pubescent (0), not pubescent (1). Irreversible; CI – 0.250; RI – 0.625; RC – 0.156; HI – 0.750.

73 (Gr211 partly) Oviscapt simple plate resembling the other tergites (0), caudally partly bilobed (1), bilobed but connected by membrane (2), pear-shaped (3). Defined type – [0(1,2),3)]; CI – 0.500; RI – 0.250; RC – 0.125; HI – 0.500. Although Grimaldi (1990) recognized a natural progression in the morphology of oviscapt from a simple sternite VIII to almost bilobed one with peg-like ovisensilla, he designated only two characters corresponding to the plesiomorphy (0) and the apomorphy (2) in our TS. I designated the partly bilobed oviscapt seen in *A. (Ph.) kappa* and *S. (O.) convergens* as well as pear-shaped one in *L. (N.) philippinensis*.

74 Oviscapt pubescent at least partly (0), not pubescent (1). Irreversible; CI – 0.250; RI – 0.400; RC – 0.100; HI – 0.750.

75 Oviscapt with only trichoid sensilla (0), with peg-like sensilla (1). Unordered; CI – 0.333; RI – 0.600; RC – 0.200; HI – 0.667.

76 Spermathecal duct not introverted into capsule (0), introverted into capsule (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

77 Spermathecal capsule without apical indentation (0), with apical indentation (1). Unordered; CI – 1.000; RI – 1.000; RC – 1.000; HI – 0.000.

78 Spermatheca present (0), atrophied (1). Irreversible; CI – 1.000; RI – 0/0; RC – 0/0; HI – 0.000.

RESULTS

According to the final dendrogramm (fig. 1) I obtain the following taxonomic results. Subfamily Steganinae consists of two tribes Steganini and Gitonini. But composition of tribes has been changed considerably. The present study supporte classification of Steganinae tribes proposed by Grimaldi (1990) in spite that a part of steganine genera were included in our analysis. However, the monophyly of tribe Steganini proposed by Grimaldi (1990) was supported.

Tribe Steganini Hendel, 1917

Steganina Hendel, 1917: 43 (as generic group).
Steganini: Okada, 1989: 396 (as tribe).

DIAGNOSIS. Dorsolateral tentorial apodemes closely situated to each ther at base (15-1); cibarium truncated at anterior end or slightly protruded at anterolateral corner (20-1, 2); aedeagus with hair crown, tentacle-like processes or microtrichia (67-1).

REMARKS. According to the article 30 of ICZN (1999), Hendel (1917) is the author of subfamily Steganinae, tribe Steganini and subtribe Steganina.

Subtribe Steganina Hendel, 1917

DIAGNOSIS. Postgena broad (12-0, not recorded in *Oxyphortica*); cibarium truncate at anterior end (20-0); longitudinal veins of wing became thin transversally (31-1); R_{4+5} and M_1 strongly convergent apically (35-2, see above for the homoplasies); mid femora with sharp spine-like setae apically (43-1); parameres fused to aedeagal guide (57-2); spermathecal capsule with apical indentation (77-1).

INCLUDED GENERA. *Stegana* and *Eostegana* Hendel (latter not examined at present study).

Genus *Stegana* Meigen, 1830

Stegana Meigen, 1830: 79. Type species: *Stegana nigra* Meigen, 1830: 79 (= *furta* (Linnaeus, 1767)).

DIAGNOSIS. The same as in subtribe.

SUBGENERA INCLUDED. *Agastega* Sidorenko, subgen. n., *Stegana*, *Steganina* Wheeler, *Oxyphortica* Duda *Orthostegana* Hendel, 1913, *Ceratostylus* Enderlein, 1922 (two latters not examined at present study).

DISCUSSION. Before the present analysis the genus *Stegana* was considered as paraphyletic one. The results of this study are not in agreement with those of Okada (1978), in that *Parastegana+Pseudostegana* was a sister group to the rest of *Stegana*. According to the present study these subgenera should be elevated to the generic rank and transferred to the tribe Gitonini (see below). The studied species of the subgenus Steganina are devided, at least, into three spesies-groups. One of

them is *S. coleoptrata* species-group established by Lastovka and Maca (1982). It includes *S. nigrithorax* Strobl, *S. longifibula* Takada, *S. baechlii* Lastovka et Maca, *S. masanoritodai* Okada et Sidorenko and *S. ctenaria* Nishiharu. This species-group can be separated into two species-subgroups: first species-subgroup includes (*S. nigrithorax* Strobl, *S. longifibula* Takada, *S. baechlii* Lastovka et Maca) and second one with *S. masanoritodai* Okada et Sidorenko and *S. ctenaria* Nishiharu which differs from the first subgroup by number of peg-like prensisetae on surstylus (48-3). This subdivision of *S. coleoptrata* species-group is in agreement with just published results of phenetic analysis of the subgenus *Steganina* (Okada, Sidorenko, 1992). *S. undulata* species-group (or "group 2" in Okada (1971)) contains single species *S. undulata* de Meijere è has following characters: face broadened ventrally with conspicuous black band below; interfrontal setulae – 7-13 (5-1); postpronotal lobe with 2 setae (22-1); hypandrium with 1 pair of paramedian setae (53-1). *S. nigrolimbata* species-group (or "group 3" in Okada (1971)) units *S. ornatipes*, S. *vietnamensis*, *S. chitouensis*, *S. belokobylskiji*, *S. nigrolimbata* and has following characters: palpus dark brown or blackish; thorax without stripes; scutellum unicolorous; mesopleuron with dark bands; cercus partly pubescent (51-1); aedeagus articulating with apodeme (65-0); cercus not pubescent (72-1); oviscapt not pubescent (74-1); oviscapt with trichoid and peg-like sensillae. Monophyly of the subgenus *Stegana* is supported by following synapomorphies: frons and face making obtuse angle in profile (9-0); paramere with long sensillae apically (59-2); gonopods fused to to each other, forming bridge connecting caudal ends of hypadrium (62-1). Subgenus *Oxyphortica* derived from *Stegana* s. str. has the following apomorphies: postgena somewhat narrow (12-1); longitudinal veins of wing not became thin transversally i. e. wing not curved down in resting position (31-0); C-index – 2.5-3.5 (38-1). New subgenera *S.* (*Anastega*) subgen. n. is described below. Results of cladistic analysis of the genus *Stegana* similar with results of Okada' phenetic analysis (1971).

Subgenus Anastega Sidorenko, subgen. n.

Type species: *Stegana* (*Stegana*) *singularis* Sidorenko, 1990

DIAGNOSIS. Palpus yellow; surstylus fused with epandrium (46-1); pair of simple rod-like processes extending posteriorly from base of aedeagus, apically articulating with gonopod (66-0); oviscapt not pubescent (74-1) and with peg-like sensilla (75-1).

SPECIES INCLUDED. *S.* (*A.*) *singularis* (Sidorenko, 1990), comb. n.

NOTES. New subgenus is closely related to *Stegana* s. str. in having of frons and face making the obtuse angle in profile (9-0); paramere with small sensillae in a patch (59-1); spermatheca almost globular but differs from it by yellow palpus (character seen in *S. crescentica* Gupta et Panigraphy, 1987 from India); surstylus without peg-like prensisetae (48-0) (homoplasy seen in *S. nartshukae*) and without stout setae on caudoventral margin to caudal inner surface (49-0) (homopasy seen in *S. furta*). On the other hand, *Anastega* subgen. n. possesses some subgenus *Steganina*' characters: anterior cibarial sensillae situated as quadrate (19-0);

paramere with small sensillae in a patch but differs from it by oviscapt not pubescent (homoplasy seen in *S. nigrolimbata*, *S. ornatipes*, *S. chitousensis* and *S. (O.) convergens*) and with peg-like sensilla (homoplasy seen in *S. nigrolimbata*, *S. ornatipes* and *S. chitousensis*). The unique combination of these characters gave a possibility to select a new subgenus which is sister group to other *Stegana'* subgenera.

Subtribe Leucophengina Okada, 1989

Leucophengini Okada, 1989: 392 (as tribe).
Leucophengina: Grimaldi, 1990: 112 (as subtribe).

DIAGNOSIS. Crossvein *bm-cu* absent (36-1); paramere ventrobasally articulating with small expansion of hypandrium (56-1); longitudinally arranged sensilla on paramere (59-0); aedeagal apodeme degenerated (63-3).

GENUS INCLUDED. *Leucophenga* Mik.

Genus *Leucophenga* Mik, 1886

Leucophenga Mik, 1886: 317. Type species: *Drosophila maculata* Dufour, 1839: 50.

DIAGNOSIS. The same as in subtribe.

SUBGENERA INCLUDED. *Leucophenga* Mik and *Neoleucophenga* Oldenberg.

NOTES. Maca and Lin (1993) described *Nankangomyia* as a subgenus of *Leucophenga* regarding the following characters as diagnostic for genus *Leucophenga*. "middle orbital bristle close to lower orbital bristle" and "wing veins R_{4+5} and M parallel". In the present study, however, the former character varied continuously among the studied species, and the latter was regarded as plesiomorphic in *Nankangomyia* but as a secondary reversal in *Leucophenga*. The topology of most parsimonious cladograms was inconsistent with Maca and Lin's (1993) classification of *Nankangomyia* as a subgenus of *Leucophenga*, but suggested its inclusion in genus *Cacoxenus*. I concluded that subgenus *Nankangomyia* should be transferred from genus *Leucophenga* to genus *Cacoxenus*.

Tribe Gitonini Grimaldi, 1990

Gitonini Grimaldi, 1990: 112 (as tribe).

DIAGNOSIS. See in Grimaldi (1990)

GENERA INCLIDED. According to Grimaldi (1990) – 13 genera (see Introduction above) plus *Parastegana* and *Pseudostegana*, which are transferred from tribe Steganini below.

Genus *Parastegana* Okada, stat. n.

Parastegana Okada, 1971: 91 (as subgenus of *Stegana*). Type species: *Parastegana femorata* Duda, 1923: 33.

DIAGNOSIS. Postpronotal lobe with 3 setae (22-3); acrostichal setulae in line with and anterior to dorsocentral the same in size as others (23-0); acrostichal setulae situated in 6 rows (24-1); epandrium with setae only on ventral portion (44-1); hypandrium with 2 pairs of paramedian setae (53-2); gonopods almost degenerated (62-2).

SPECIES INCLUDED. *P. drosophiloides* Toda et Peng, 1992, comb. n.; *P. femorata* (Duda, 1923), comb. n.; *P. maculipennis* Okada, 1971, comb. n.

NOTES. Synapomorphies: anterior reclinate orbital seta short (3-1); dorsolateral tentorial apodemes closely situated to each other at base (15-1); postpronotal lobe with 2 setae (22-2); acrostichal setulae situated in 6 rows (24-1); dorsalmost seta between two katepisternals as long as than katepisternals (28-2); R_{4+5} and M_1 strongly convergent apically (35-2, homoplasy seen in *Pseudostegana* and subgenera of *Stegana*); C3F less than 0.5 (41-0); epandrium with setae only on ventral portion (44-1); ventral part of epandrium with sclerotizing or other protrudings (45-1); hypandrium pubescent (54-0); parameres fused to aedeagus (57-1); parameres without sensillae (59-3); gonopods almost degenerated (62-2) are supported monophyly of *Parastegana*. Position of this genus within the tribe Gitonini is still unclear.

Genus *Pseudostegana* Okada, stat. n.

Pseudostegana Okada, 1978: 392 (as subgenus of *Stegana*). Type species: *Stegana* (*Parastegana*) *grandipalpis* Takada et Momma, 1975: 12.

DIAGNOSIS. Ocellar triangle elongated, extending to anterior margin of the frons (4-1); ocellar setae situated outside of ocellar triangle (6-1); 1 pair of dorsocentral setae present (25-1); prescutellar setae absent (26-1).

SPECIES INCLUDED. *P. albinotata* Okada, 1982, comb. n.; *P. campanularia* Okada, 1982, comb. n.; *P. fleximidiata* Takada, Momma et Shima, 1973, comb. n.; *P. grandipalpis* Takada et Momma, 1975, comb. n.; *P. hirta* Okada, 1982, comb. n.; *P. javana* Okada, 1978, comb. n.; *P. lacrymaria* Okada, 1982, comb. n.; *P. latipalpis* Sidorenko, 1998, comb. n.; *P. latiparma* Okada, 1982, comb. n.; *P. latizonaria* Okada, 1982, comb. n.; *P. lineoparma* Okada, 1982, comb. n.; *P. malayana* Okada, 1978, comb. n.; *P. zonaria* Okada, 1982, comb. n.

NOTES. Anterior reclinate orbital seta short (3-1, homoplasy seen in *Parastegana*); ocellar triangle elongated, extending to anterior margin of the frons (4-1); interfrontal setulae 5 or less (5-2); ocellar setae situated outside of ocellar triangle (6-1); postocellar setae absent (7-1); subvibrissa as long as vibrissa (11-2); 1 pair of dorsocentral setae present (25-1); prescutellar setae absent (26-1); R_{4+5} and M_1 strongly convergent apically (35-2, homoplasy seen in *Parastegana* and subgenera of *Stegana*); aedeagal apodeme longer than aedeagus (63-2) supported monophyly of *Pseudostegana*.

Genus *Cacoxenus* Loew, 1858

Cacoxenus Loew, 1858: 217. Type species: *Cacoxenus indagator* Loew, 1958: 218.

DIAGNOSIS. Aedeagal apodeme lobe-shaped, horizontally flat (64-2); oviscapt not pubescent (74-1).

SUBGENERA INCLUDED. *Cacoxenus*, *Paracacoxenus* Hardy, *Phragmitoxenus* Gornostaev, *Gitonides* Knab and *Nankangomyia* Maca et Lin.

NOTES. The monophyly of genus *Cacoxenus* was supported by the following synapomorphies: aedeagal apodeme lobe-shaped, horizontally flattened (64-2; homoplasy seen in Diastatidae and Curtonotidae); cercus pubescent (72-0). Within genus *Cacoxenus,* subgenus *Nankangomyia* regards as monophyletic, based on the following synapomorphies: arista shortly pubescent (10-0; regarded as a secondary reversal); postgena broad (12-0); at least one acrostichal setula between posterior dorsocentral and prescutellar setae thicker and longer than others (23-1); oviscapt pear-shaped (73-3). Subgenera *Nankangomyia* and *Gitonides* formed a monophyletic group supported by distal margin of subscutellum not swollen in lateral view (26-1; homoplasies seen in genera *Paraleucophenga and Amiota*); cercus caudoventrally with ornamentation or tuft of fine setae (52-1) and longitudinally arranged sensilla on paramere (59-0; secondary reversal also occurred in genus *Leucophenga*).

Subgenus *Nankangomyia* Maca et Lin, 1993, comb. n.

Nankangomyia Maca et Lin, 1993: 7 (as a subgenus of *Leucophenga).* Type species: *Leucophenga (Nankangomyia) academica* Maca et Lin, 1993: 8.

DIAGNOSIS. Postocular setae 12-19 per sedie (8-0); arista shortly pubescent (ch. 10-0); postgena broad (12-0); at least one acrostichal setula between posterior dorsocentral and prescutellar setae thicker and longer than others (23-1); oviscapt pear-shaped (73-3).

SPECIES INCLUDED. *C.* (*N.*) *academicus* (Maca et Lin, 1993), comb. n.; *C.* (*N.*) *leucophengoides* (Sturtevant, 1927), comb. n.; *C.* (*N.*) *parallelinervis* (Duda, 1924), comb. n.; *C.* (*N.*) *philippinensis* (Sidorenko, 1998), comb. n.

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Table 1

Characters matrix for 31 species of Drosophilidae and 3 outgroups used in cladistic analysis

Òàõà	Characters			
	01	11	21	31
Ca. griseola	1000100000	0111000002	0000001101	0000001211
D. vagans	1100000000	1010000012	0000001010	0010001200
Cu. anus	0000200101	0110001022	0100000010	0011010200
A. albilabris	2100000101	0100001022	0010001001	0210100101
A. stylopyga	2100000201	2100001022	0010001101	0210100012
A. lini	2100000101	0101011022	0010001000	0210100111
A. kappa	2100000102	0101011022	1010001001	0210100112
C. kaszabi	2100000104	0101011022	0010001001	0210000111
C. perspicax	2100000104	0101011022	1010001001	0210000001
G. distigma	2100000104	0011011022	1010001101	0210010112
L. angusta	2100000101	0101101021	0010001001	0110010011
L. philippinensis	2100000200	0000011022	0010001001	0210010101
P. emeiensis	2100000?03	01?010????	0010000201	0210010200
S. watabei	2100000101	11001????2?	0010001101	0110200111
S. femorata	2110100001	0110100022	0201001201	0110200011
S. latipalpis	2111211102	2111001???	0010111101	0110200002
S. fleximediata	2111211?02	21?100????	0010111001	0110200002
S. antlia	2100000201	000110??2?	0010001101	1110200011
S. furta	2100000101	1000101120	0010001101	1110200011
S. nartshukae	2100000101	000110??2?	0010001101	1110200011
S. sibirica	2100000101	1000101120	0010001001	1110200011
S. singularis	2100000101	0001101020	0010001001	1110200011
S. baechlii	2100000111	0001101020	0010001001	1110200011
S. belokobylskiji	2100100111	000?1????2?	0010001101	1110200011
S. ctenaria	2100000111	0001101020	0110001001	1110200011
S. longifibula	2100100111	0000101020	0010001001	1110200011
S. masanoritodai	2100000111	0001101020	0010001001	1110200011
S. nigrithorax	2100000111	00011?1?20	0010001001	1110200011
S. nigrolimbata	2100100111	0000001020	0010001101	1110200001
S. ornatipes	2100000111	0001101020	0010001001	1110200001
S. vietnamensis	2100?00111	000?????20	0010001001	1110200011

S. chitouensis	2100000111	000?????20	0010001101	1110200001
S. undulata	2100100111	0001101020	0110001001	1110200011
S. convergens	2100000101	1100101020	0010001101	0110200111

Table 1 (continued)

Òàõà	Characters			
	41	51	61	71
Ca. griseola	0000000000	0021010100	0110130100	00100000
D. vagans	1000001000	0001010111	0002001100	00200??1
Cu. anus	1000000000	1120110130	0102131100	00000000
A. albilabris	1100000300	0001000110	10210???11	10001000
A. stylopyga	1100000310	0001001110	10010???11	10001000
A. lini	1100100000	0001100130	002001000?	????????0
A. kappa	1100000200	0000010040	0000000000	00100100
C. kaszabi	0100010000	0001100110	0012101100	01000100
C. perspicax	1100000210	0101100100	0002130110	01000100
G. distigma	0100010300	0011110020	0200030110	00000100
L. angusta	1100000000	0001010000	003?01100	00000000
L. philippinensis	1100000000	0100010000	0002120100	11310100
P. emeiensis	0100000300	0001000110	000112011?	????????0
S. watabei	1110000011	0001000130	0120130102	????????0
S. femorata	0101100000	0020001130	0201131100	00000000
S. latipalpis	1100000000	0011000120	0020020102	????????0
S. fleximediata	1100000000	0011000120	0020020102	????????0
S. antlia	0110000110	2001002120	0120121102	?????010
S. furta	1110010300	2001002120	0120131100	00100010
S. nartshukae	1110000010	2001002120	0120131102	?????010
S. sibirica	111???????	??????????	?????????0	00000010
S. singularis	1110010000	2001002110	0020101100	00011010
S. baechlii	1110000100	2001002110	0020131100	11000010
S. belokobylskiji	1110100110	1011002110	0120020102	?????010
S. ctenaria	1110000300	2001002110	0020131100	00000010
S. longifibula	1110000100	2001002110	0020131100	11000010
S. masanoritodai	1110000300	2001002110	0020131100	00000010
S. nigrithorax	1110000100	20110?21??	?020131100	11000010
S. nigrolimbata	1110100210	2011002110	0120020100	11011010
S. ornatipes	1110000110	1001002110	0120131100	11011010
S. vietnamensis	1110000110	1001002110	0120031102	?????010
S. chitouensis	1110000110	1001002110	0120031100	11011010
S. undulata	1110000110	2011002110	0120131100	10000010
S. convergens	1110000211	2001000120	0010121100	00110010

Notes. Generic position of species follows Materials: A. – *Amiota*; Ca. – *Campichoeta*; C. – *Cacoxenus*; Cu. – *Curtonotum*; G. – *Gitona*; L. – *Leucophenga*; P. – *Paraleucophenga*, S. – *Stegana*.
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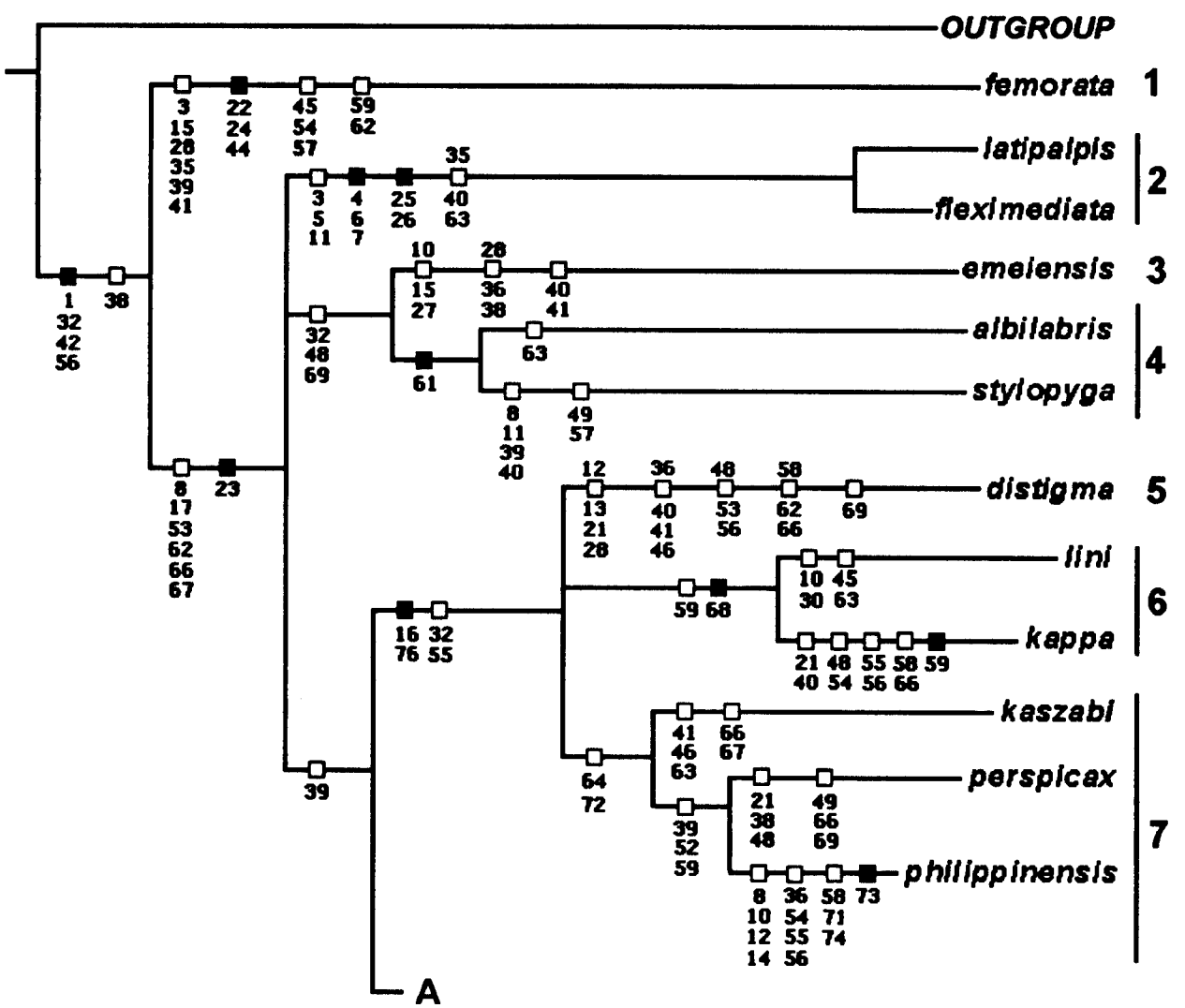

Fig. 1. The Adams consensus tree (length of 328 steps, CI – 0.3865, HI – 0.6135, RI – 0.06311, RC – 0.2439) of 1512 maximum parsimony trees resulting from cladistic analysis by PAUP (4.0b8) with indication of apomorphies ( ) occurring only once on the tree; homoplasies ( ). Outgroup – Diastatidae + Campichoetidae + Curtonotidae; tribe Gitonini (1-7): 1 – *Parastegana*; 2 – *Pseudostegana*; 3 – *Paraleucophenga*; 4 – *Amiota* s. str.; 5 – *Gitona*; 6 – *Amiota* (subgenera *Apsiphortica* and *Phortica*); 7 – *Cacoxenus*. Tribe Steganini (8-11): subtribe Leucophengina (8): 8 – *Leucophenga*; subtribe Steganina (9-12): 9-12 – *Stegana* (subgenera *Anastega* – 9; *Steganina* - 10; *Stegana* - 11; *Oxyphortica* – 12).

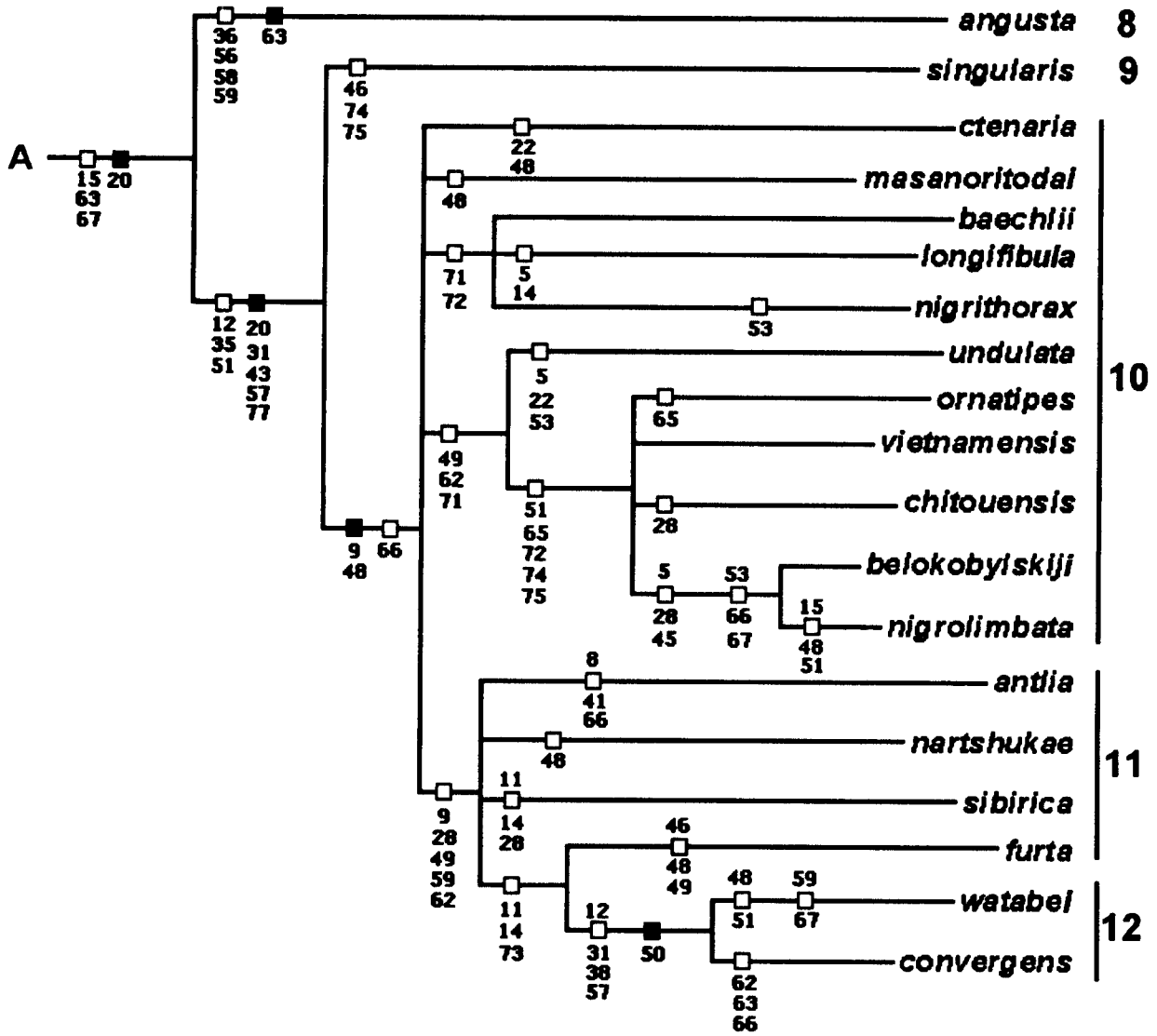

Fig. 1 (continue). The Adams consensus tree of 1512 maximum parsimony trees resulting from cladistic analysis of tribe Steganini by PAUP (4.0b8) with indication of apomorphies ( ) occuring only once on the tree; homoplasies ( ).

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