PHYLOGENY OF THE AMERICAN GENERA OF SOLVIDAE (XYLOMYIDAE) (DIPTERA), WITH ILLUSTRATIONS OF THE FEMALE SPERMATHECA*

FILOGENIA DE LOS GENEROS AMERICANOS DE SOLVIDAE (XYLOMYIDAE) (DIPTERA), CON ILUSTRACIONES DE LA ESPERMOTECA DE LAS HEMBRAS

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ABSTRACT

A brief history of the taxonomy of the family Solvidae is given and a phylogeny presented for the three American genera: Solva (s.l.) is considered the sister-group of Arthropeina Lindner, and the ancestral species of both genera is considered as the sister-group of the ancestral species of Macrocercomys Bigot. The female spermatheca offers valuable characters for the distinction of these three genera.

KEYWORDS America, Diptera, Solvidae, Xylomyidae, Phylogeny, Spermatheca.

RESUMEN

Se presenta una breve historia de la taxonomía de la familia Solvidae con una propuesta de filogenia de los tres géneros americanos: Solva (s.l.) se considera el grupo hermano de Arthropeina Lindner y la especie ancestral de esos dos géneros como el grupo hermano de la especie ancestral de Macroceromys Bigot. Las espermatecas de las hembras brindan valiosos caracteres para la distinción de los tres géneros.

PALABRAS CLAVES América, Diptera, Solvidae, Xylomyidae, Filogenia, Espermateca.

A BRIEF HISTORY OF THE TAXONOMY OF THE SOLVIDAE

In 1820 Meigen created the genus Subula to include some of the species he had previously described in Xylophagus (varius, marginatus and maculatus). Xylophagus varius was subsequently designated by Rondani (1856:172) as the type-species of Subula Meigen. This species has a two-segmented palpus, the hind femur is more or less elongated and cylindrical and bears no denticles on its ventral surface, the first abdominal tergite has a very wide membranous area. M_2 ends

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before the wing margin, $C$ ends in $M_1$, the transverse crossvein $m-cu$ is present, and the antenna has elongated flagellomeres (cf. Hennig, 1967: figs. 20 (wing), 24 (abdominal tergites 1 and 2 and hind leg). 30 (antenna)).

Walker (1859) erected Solva for his Oriental species inamoena; Solva has an incrassate hind femur bearing a row of denticles on its ventral surface.

As Subula Meigen was preoccupied (Subula Schumacher, 1817), Rondani rebaptized it as Xylophagus; the type-species is, therefore, Xylophagus varius Meigen (automatically). Apparently unaware of this fact, Williston also proposed a new name for Subula Meigen-Subulaomyia.

Bigot (1877) described the first American representative of this group-Macroceromys (type-species, fulviventris Bigot, mon.: from Mexico). This species has very slender and elongate hind femora without denticles on the ventral surface, the first abdominal tergite has a very narrow membranous area, elongated antennal flagellum and a one-segmented palpus.

Enderlein (1913) started the confusion within this group of flies. He wrongly designated Xylophagus maculatus Meigen as the type-species of Xylomya Rondani; he erected two genera more, Prista (Oriental) and Subulonia (Neotropical), related to Solva Walker; he ignored Macroceromys Bigot. He distinguished those genera by the following key (slightly modified):

"1. $m_3$ und $cu_1$ nahe der Basis durch Querader verbunden [i.e., crossein $m-cu$ present] .......... 2

$m_3$ und $cu_1$ nahe der Basis eine Strecke weit verschmolzen (Mediocubitalquerader fehlt).
Fühler 10 gliedrig, normal. $m_3$ nicht verkürzt. (Hinterschenkel etwas verdickt, verbreitert um längs des unteren Randes fein gezähnelt) .................. Prista Enderlein

2. Fühlerglied wohl länger als die übrige, aber niemals gross und dick; 4.6. Glied nicht quer, $m_3$ nicht verkürzt .................................................. 3

3(2). Interschenkel nicht verdickt und ohne Zähnelung ........................................... "Xylomya"
Hinterschenkel etwas verbreitert und verdickt un längs des unteren Randes mit feiner körniger Zähnelung .................................................. Solva Walker"

Let it be noticed that in Enderlein's key "Xylomya" corresponds to Macroceromys Bigot, as can be seen by the characters given. Moreover, Xylophagus maculatus Meigen, which was erroneously fixed by Enderlein as the type-species of Xylomya sens Enderlein is clearly a Macroceromys (cf. Hennig, 1967: figs. 18 (wing), 22 (abdominal tergites 1 and 2 and hind leg), 27 (antenna)). From the on, "Xylomya" (we are going to indicate this concept by Xylomya sensu Enderlein) would be used by all subsequent authors in the meaning of Macroceromys Bigot.

Meijere (1914) erected the genus Ceratosolva (type-species, cylindricornis Meijere, Oriental). This genus is curiously "intermediary" between Xylomya Rondani (like this Ceratosolva has a slender, cylindrical hind femur) and Solva Walker (Ceratosolva has ventral denticles on the ventral surface of the hind femur, but is not incrassate as in Solva); in addition, it has $m-cu$ present and the antennal flagellum is elongate.

Enderlein (1920) described Hanadua (for Xylophagus marginatus Meigen); like Solva, this species has an incrassate hind femur with a row
of denticles on the ventral surface; m-cu, in *Hanauia*, is reduced to a mere point.

Brunetti (1920) created *Pararthropeas* (type-species, *thereviformis* Brunetti, Oriental), also apparently related to *Solva* Walker (i.e., hind femur incrassate, with denticles on the ventral surface).

Pleske (1925) described, from the Palaeartic, the genus *Nematoceropsis* (type-species, *ibex* Pleske), apparently related (or the same as?) to *Macrocercromys* Bigot.

James (1939) erected the subgenus *Formosolva* (of *Solva*) (type-species, *concavifrons* James, Oriental), declaring that it can “be distinguished from *Ceratosolva* [Meijere] by the longer antenna, the broad, concave front and the long first antennal segment”, *Formosolva* has, like *Ceratosolva*, a more or less slender and elongate hind femur with a series of denticles on the ventral surface, and m-cu is present.

Hull (1944) added to *Solva* the subgenus *Philoophila* (type-species, *pallipes* Loew, Nearctic); it has the hind femur incrassate, with ventral denticles (therefore belonging to the *Solva*-group); m-cu is reduced to a point (differing in this aspect from *Subulonia* Enderlein, which has a distinct m-cu).

Stey skal (1947) revised the Nearctic species of Solvidae, accepting only two genera, and introduced some interesting new morphological characters, as can be seen in his key:

"Hind femora swollen and furnished beneath with minute teeth, flagellum of antennae with the joints distinctly although but slightly separated, the terminal joint twice as long as the preceding one, with a short but distinct conical bare shining tip, the first joint sometimes considerably enlarged; the second abdominal tergite membranous medianly except the posterior margin, allowing itself to fit closely to the metanotum when the abdomen is greatly upflexed; wings with at least one branch of the media not reaching margin, crossvein m-cu short or absent; all veins microsetate above .......................................................... *Solva* Walker.

Hind femora not markedly thicker than the others and lacking teeth below; flagellum with the joints apparently fused, the first joint never enlarged; the second abdominal tergite not membranous anteromedianly; wing with all branches of media strong and reaching margin, crossvein m-cu well developed; wing veins posterior to radius not microsetate .......... ‘Xylomya’"

Frey (1960) recognized three groups of species within the family Solvidae:

1. Hind femur cylindrical, without denticles on the ventral surface - *'Xylomya'* (i.e., *Macroceromys* Bigot; *Nemotoceropsis* Pleske was synonymized here);
2. Hind femur incrassate, with denticles on the ventral surface - *Solva* Walker.
3. Hind femur cylindrical, with denticles below - *Ceratosolva* Meijere.

**THE CONTRIBUTION OF NAGATOMI & TANAKA (1971)**

A major advance in the knowledge of the Solvidae as contributed by Nagatomi & Tanaka (1971), in their revision of the Japanese species. The two authors accepted as valid the genera *Arthropeina* Lindner (1949; this genus differs from all other genera in the shape of the antennal flagellum; Lindner described it from the Neotropics; type-species, *fuva* Lindner), *Ceromyiodes* Brunetti (we doubt this genus belongs here) and *Solva* Walker, with two "subgenera" - *Solva* proper and *Macroceromys* Bigot. Nagatomi & Tanaka included in the synonymy of *Solva* s.s. the genera *Xylomya* Rondani, *Subulonia* Enderlein, *Prista* Enderlein, *Ceratosolva* Meijere, *Pararthropeas* Brunetti, *Hanalia* Enderlein, and the subgenera *Formosolva* James and *Phoophila* Hull; *Nemotoceropsis* Pleske was considered a synonym of *Macroceromys* Bigot.

The best contribution of Nagatomi & Tanaka is the careful study of the male terminalia of the Japanese species; the terminalia affords many important and clearcut characters for the separation of the species. This can be resumed in the following manner (we are reinterpreting here some of the original data; numbers of figures cited in parentheses refer, of course, to Nagatomi & Tanaka's 1971 paper):

1. Hypandrium present, its mid-anterior margin deeply concave, free from base of basistyli (4E) or fused to bases of basistyli (3E, 5E, 6E, 7E, 9B). *Epeandrium with a pair of laterodistal processes* (3E, 4F, 5F, 6F, 7F, 9C). *Aedeagus large* (3D, 4D, 5D, 6D, 7D, 9D). Dististylus large and broad, its base more or less constricted (3D, 4D, 5D, 6D, 7D, 9A). "Interbases" present (3D, 4D, 5D, 6D, 7D, 8A). *Sternite 8 with a pair of apical flat processes* (3G, 4G, 5G, 6G, 7G, 9D) .......... *Macroceromys* Bigot. 

   **Hypandrium absent** (12E, 13E, 14E, 15F). Epeandrium without a pair of laterodistal processes (12F, 13F, 14F, 15G) ................................................................. 2


   "Interbases" present, very large (long and broad) (15E-F). Sternite 8 with a pair of apical flat processes (15H). Dististylus absent (15E). Aedeagus small. Antennal flagellum elongate. Hind femur incrassate, but with very small denticles beneath, "which may be overlooked" ............................................................. **Solva**, group 2.
Characters in italics represent, according to us, apomorphic characters (polarized by outgroup comparison, the outgroup being all the other Brachycera).

It is interesting to note that the presence of a pair of apical flat processes on sternite 8 is probably homoplastic, having independently evolved in *Macroceromys* and group 2 (*Solva procera* (Frey)) of *Solva*. It becomes manifest, from the above list of characters, that at least three sound (phylogenetic) groups of species (let's say general) exist in Japan.

The same should be made for the rest of the Solvidae in the world. Dissections of male terminalia are needed, to decide on the validity of the nominal genera and subgenera thus far proposed. It is very likely that many of them will prove to be valid concepts, or that new genera may be needed.

To resume the present situation within the Solvidae, we may say that this family can be divided in the following manner (pointing out at the same time the open taxonomic problems):

1. A group of species with tergite 1 with a small, reduced membranous area; palpus with only one segment; hind femur cylindrical, elongate, without denticles on the ventral surface - *Macroceromys* Bigot (=? *Nematoceropsis* Pleske; the latter should be better studied in order to show whether it really belongs to the Solvidae and, in the affirmative case, whether it is distinct or not from *Macroceromys*).

2. A group of species with very large membranous area on tergite 1; palpus two-segmented:

   2.1. Basal 6 antennal flagellomeres fused, 8th flagellomere elongate; hind femur cylindrical, without ventral row of denticles - *Arthropeina* Lindner;

   2.2. Antennal flagellum never as above; other combinations of characters:

      2.2.1. Hind femur cylindrical, elongate, without denticles on ventral surface; m-cu present - *Xylomya* Rondani (with *Xylophagus varius* Meigen as type-species);

      2.2.2. Hind femur cylindrical, more or less elongate, with denticles on ventral surface; m-cu present - *Ceratosolva* Meijere and *Formosolva* James;


Notice that *Xylomya* Rondani is entirely based on plesiomorphic characters. Only dissections of male terminalia and female spermathecae could help to clarify the situation above.

PHYLOGENY OF THE AMERICAN GENERA

We are considering here the groups *Macroceromys* Bigot, *Arthropeina* Lindner and *Solva* authors. Dissection of the female spermathecae showed some very beautiful characters, which help extraordinarily well in the construction of the phylogeny. Our hypothesis is shown in Textfig. 2.

The characters employed in the phylogenetic reconstruction are the following (characters in italics are in the apomorphic condition; polarization was made taking the remaining groups of Brachycera as the outgroup):
1. Palpus two-segmented (*Palpus one-segmented*)

2. Tergite 1 without membranous area or, if membranous area present, very small (*Tergite 1 with very large membranous area, almost reaching margin of tergite 1*)

3. Three spermathecae present (*Two spermathecae present*)

4. C present beyond *M*₁ (*C absent beyond *M*₁*)

5. Antennal flagellomere clearly separated (*Basal 6 antennal flagellomeres fused, 8th elongate*)

6. Spermathecal capsule not showing layers (*Spermathecal capsule 3-layered*)

7. Remnant of middle spermathecal duct present (*No vestige of duct of middle spermatheca*)

8. Crossvein *m-cu* present (*Crossvein *m-cu* absent*)

Most unfortunately, the male terminalia of the American "Solva" and *Arthropeina* are not known (there are no males in the collections seen); in the future they may add valuable characters for the phylogeny.

**KEY TO THE AMERICAN GROUPS OF SOLVIDAE**

1. Palpus one-segmented. Membranous area at base of tergite 1 not evident or ending far away from posterior margin of that tergite (cf. Hennig, 1967: figs. 22-23 [p. 19]). Hind femur long and slender, narrower than hind coxa and without a series of denticles on ventral surface. Crossvein *m-cu* present. Costa ending in *M₂* or *M₁*. Three spermathecae present, the lateral ones with a long duct (reaching first abdominal segment and then bending backwards to segment 5) and more or less ovoid capsules, the median one with a very short duct and an exceedingly voluminous capsule (twice or more volume of lateral ones) (Figs. 1-4). Male with hypandrium present .............................................. *Macroceromys* Bigot

Palpus one-segmented. Abdominal tergite 1 with a more or less large, semicircular, basal, membranous (the integument very thin and transparent), anteriorly concave, pale area, which extends almost to the posterior margin of that tergite (cf. Hennig, 1967:figs. 24-25 (p. 19)). Posterior femur either slender or incrassate, either with or without denticles on ventral surface. Costa ending in *M₁*. Crossvein *m-cu* either present or absent. Only two
spermathecae present, the central one either absent or reduced to a short, whip-like filament (Figs. 6, 9) ........................................ 2

2(1). Antennal flagellum with 8 distinct flagellomeres, which become gradually narrower towards apex. Hind femur incrassate, almost as wide as hind coxa, with a row of small, short denticles on ventral surface, except in the immediate basal portion. Crossvein m-cu absent. Central spermatheca totally absent, not even vestige of duct left, the lateral spermatheca with an extremely long duct, which performs seven and a half bends inside the abdomen (Figs. 5-7). Male terminalia with hypandrium absent ......................... **Arthropeina** Lindner

**CATALOGUE OF NEOTROPICAL SOLVIDAE**

**(XYLOMYIDAE)**

**Genus Arthropeina** Lindner

**Arthropeina** Lindner, 1949: 189. Type-species, **fulva** Lindner (mon.).

**fulva** Lindner, 1949: 789, fig. 3 (antenna). Type-locality: not stated (but undoubtedly Brazil, Santa Catarina, Nova Teutônia). Ref.- Lindner, 1969.

**Genus Macraceromys** Bigot

**Macraceromys** Bigot, 1877: lxxiii. Type-species, **fulviventris** Bigot (mon.).

**Xylomya**, authors, not Rondani.

**americanus** (Wiedemann), 1821a: 1 (1821b: 51) (*Xylophagus*). Type-locality: “North America”. Distr.- Wyoming to Quebec, s. to Texas and Mississippi; Mexico. **N. COMB.**

**elongatus** (Osten Sacken), 1886: 62 (*Subula*). Type-locality: Guatemala, Capetillo. Distr.- Guatemala. **N. COMB.**


**fulviventris** Bigot, 1877: lxxiii (nomen nudum).

**prista** (Enderlein), 1913: 541 (*Xylomya*). Type-locality: Mexico, Chiapas. Distr.- Mexico (Chiapas). **N. COMB.**

**Genus Solva** Walker, *sensu lato*

?-**Subula** Meigen, 1820: 15 (preocc. Schumacher, 1817). Type-species, **Xylophagus varius** Meigen (Rondani 1856: 172) (Palearctic).

**Solva** Walker, 1859: 98. Type-species, **inamoenal** Walker (mon.) (Oriental).

?-**Xylomya** Rondani, 1861: 11 (nom. nov. for **Subula** Meigen). Type-species, **Xylophagus varius** Meigen (aut.).

?-**Subulaomyia** Williston, 1896: 43 (as **Subula Omyia** nom. nov. for **Subula** Meigen, but deleted in Corrigenda, p. iv). Type-species, **Xylophagus varius** Meigen (aut.).

?-**Subulonia** Enderlein, 1913: 545. Type-species, **truncativena** Enderlein (orig. des.) (Neotropical).

?-**Prista** Enderlein, 1913: 546. Type-species, **Subula viitata** Doleschall (orig. des.) = vittipes Bezzi (Oriental).

?-**Ceratosolva** Meijere, 1914: 21. Type-species, **cylindricornis** Meijere (mon.) (Oriental).

?-**Hanauia** Enderlein, in Brohmer, 1920: 281. Type-species, **Xylophagus marginitas** Meigen (Enderlein, 1921c: 170) (Palearctic).

?-**Pararthropeas** Brunetti, 1920: 108. Type-species, **thereviformis** Brunetti (orig. des.) (Oriental).

?-**Solva** subg. **Formosolva** James, 1939: 32. Type-
species, \textit{concavifrons} James (orig. des.) (Oriental).


\textit{?brasiliana} (Lindner), 1949: 791 (\textit{Subulonia}). Type-locality: Brazil, Santa Catarina, Nova Teutônia.

\textit{?flavicoxis} (Enderlein), 1921: 172 (\textit{Hanauia}). Type-locality: Paraguay, San Bernardo.

\textit{?pallipes} (Loew), 1863: 6 (Centuria 3, n° 9) (\textit{Subula}). Type-locality: USA, Illinois, Wisconsin. Distr.- USA, Canada, "Middle America".

\textit{?truncattiva} (Enderlein), 1913: 545 (\textit{Subulonia}). Type-locality: Costa Rica.

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