

THE PHYLOGENY OF THE SUBGENUS *TIPULA* (*MEDIOTIPULA*) (DIPTERA: TIPULIDAE)

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The phylogeny of the species of the subgenus *Tipula* (*Mediotipula* Pierre) (Diptera: Tipulidae) is discussed, based on the examination of 24 morphological characters of the adults of the currently recognized 11 species. The synonymy of *aragoniensis* Theowald under *cataloniensis* Theowald is established. A short discussion on the distribution of the species is given.

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Key words. – Diptera, Tipulidae, *Mediotipula*, phylogeny, distribution.

This paper presents an analysis of the phylogeny of the species of the subgenus *Tipula* (*Mediotipula* Pierre, 1924) as part of a research project dealing with the historical biogeography of the western Mediterranean. About half of the species of *Mediotipula* are confined to the western Mediterranean and could provide clues for a better understanding of the historical biogeography of the area.

Pierre (1924) introduced *Mediotipula* as a genus to accommodate his new species *fulvogrisea* from northern Algeria. As recorded by Theowald (1978), the study of type material of *fulvogrisea* enabled Mannheims to recognize this species as a member of the *Tipula stigmatella* species group sensu Lackschewitz (1934). Correspondence on these findings with Mannheims led Theowald (1957) to use the name *Mediotipula* for the species of the *stigmatella* group. In the text of Theowald's 1957 paper, *Mediotipula* was used in the subgeneric sense, while Theowald's table 2, which presented a proposal for a new classification of the western Palearctic Tipulidae, listed *Mediotipula* as a genus. Following Savchenko (1961), *Mediotipula* is usually considered a subgenus of *Tipula* Linnaeus. Savchenko, dealing with five species of *Mediotipula*, distinguished two species groups within the subgenus. A revision of *Mediotipula* was provided by Theowald (1978), who recognized a total of 12 species divided over four species groups. The arrangements of both authors will be commented upon in the 'Discussion of adopted phylogeny', below. In Appendix A of the present paper, the synonymy of *aragoniensis* Theowald under *cataloniensis* Theowald is established, thus reducing the number of valid species to 11. A list of the species of *Mediotipula* as recognized in this paper is given in table 1.

Mediotipula has a strictly western Palearctic distribution, with about half of the species being confined to the western Mediterranean. The general distribution of *Mediotipula* is given in fig. 1. More detailed maps with the ranges of individual species will be provided in a forthcoming paper on the historical biogeography of the western Mediterranean. A short discussion on the distribution of the species of *Mediotipula* is given at the end of the present paper. A synopsis of their distribution can also be found in Oosterbroek & Theowald (1992).

MATERIAL, METHODS AND TERMINOLOGY

With the exception of the female of *fulvogrisea*, material of both sexes of all species of *Mediotipula* was examined. The majority of specimens studied originate from the collection of the Institute for Systematics and Population Biology (Zoological Mu-

Table 1. The species of *Tipula* (*Mediotipula*) as recognized in this paper. +: examined; -: not examined.

	♂	♀
<i>anatoliensis</i> Theowald, 1978	+	+
<i>brolemanni</i> Pierre, 1922	+	+
<i>cataloniensis</i> Theowald, 1978	+	+
<i>caucasiensis</i> Theowald, 1978	+	+
<i>fulvogrisea</i> Pierre, 1924	+	–
<i>galiciensis</i> Theowald, 1978	+	+
<i>mikiana</i> Bergroth, 1888	+	+
<i>nitidicollis</i> Strobl, 1909	+	+
<i>sarajevensis</i> Strobl, 1898	+	+
<i>siebkei</i> Zetterstedt, 1852	+	+
<i>stigmatella</i> Schummel, 1833	+	+

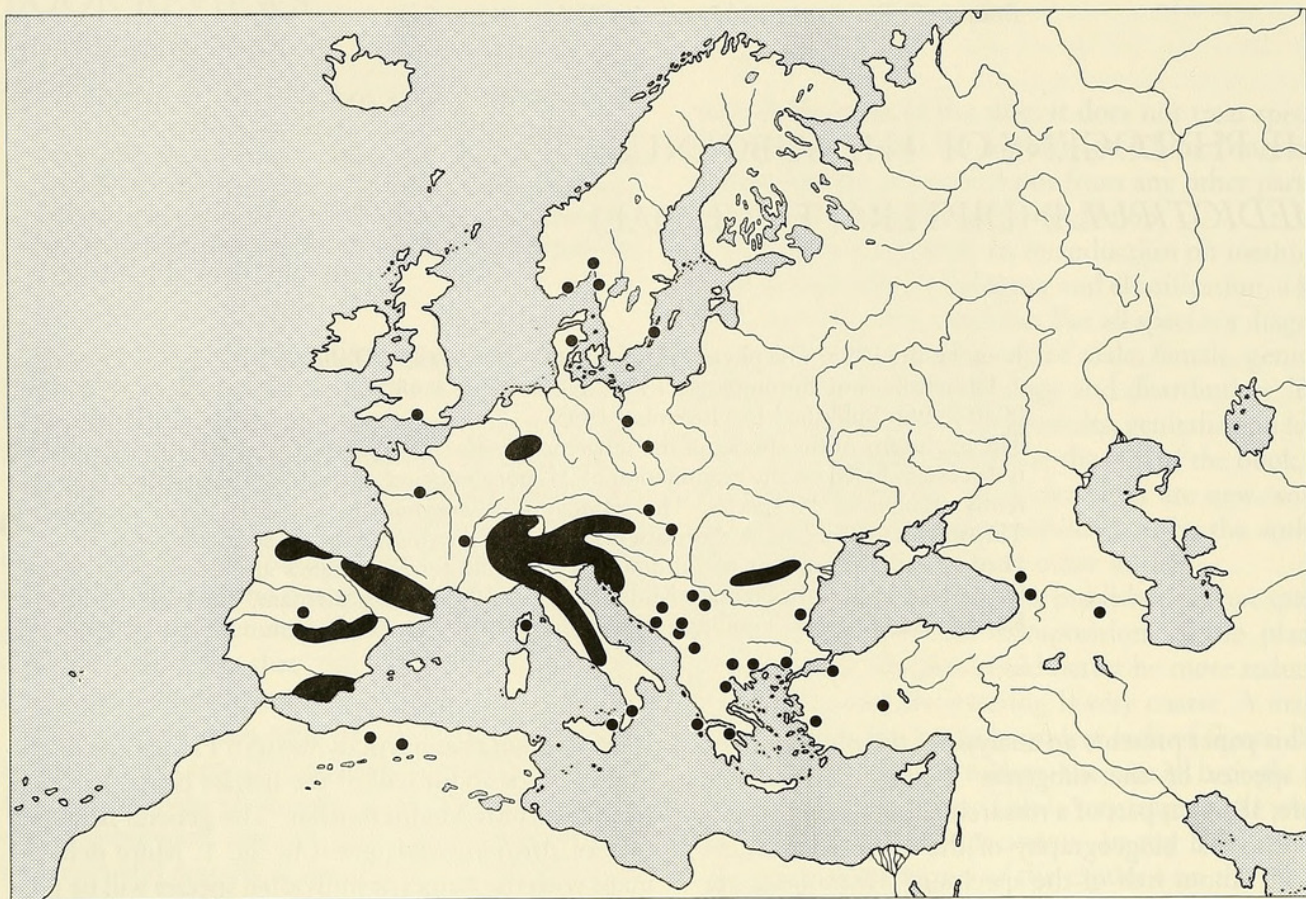


Fig. 1. Distribution of *Tipula* (*Mediotipula*).

seum), Amsterdam (ZMAN). This material consisted of dry pinned and alcohol preserved specimens. A male paratype and the female paratype of *caucasiensis* were borrowed from the Zoological Institute of the Academy of Sciences, St. Petersburg, the female paratype of *anatoliensis* was borrowed from the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, and some material of *cataloniensis* was borrowed from the Musée d'Histoire Naturelle, Neuchâtel.

Only two female specimens of *fulvogrisea* are mentioned in the literature (Theowald 1978), viz., Pierre's female paratype in the Paris Muséum and another female in the collection in Vienna. Both specimens, however, are in a very bad condition and without terminalia (Matile in litt. and Contreras-Lichtenberg in litt., respectively). I did not examine the remaining parts of these females.

Preparations of the male and female terminalia were made by removing these parts and clearing them in a nearly boiling 10% KOH solution for about five minutes. After rinsing with water and 70% alcohol, the terminalia were transferred to glycerol. Examination of the specimens and their terminalia was carried out with a Wild stereo microscope, using a magnification of up to 100 ×. Drawings were made with the

aid of a drawing tube attached to the microscope. Illustrations of the genital structures were made from macerated specimens. For permanent storage, the terminalia were transferred to a microvial containing some glycerol. The microvial was pinned with the relevant specimen.

The parsimony programs Hennig86, version 1.5 (Farris 1988) and PAUP, version 3.1 (Swofford 1993) were used to analyze the phylogeny. More information on the procedures followed is given in 'Discussion of adopted phylogeny'.

The terms for the structures of *Mediotipula* as used in this paper are generally in accord with those employed by McAlpine (1981), with a few additions for particular features of Tipulidae. The terminology as adopted here is explained in figs. 3-6, 8. A recent overview of the morphology of the terminalia of Tipulidae was given by Tangelder (1985) to which paper I refer the reader for more information.

BIOLOGY

The most comprehensive information on the biology of adult *Mediotipula* – and of other adult Tipulidae occurring in the region – can be found in Dufour's 1986 monograph on the Tipulidae of

Switzerland. Three of the four Swiss species of *Mediotipula*, viz., *sarajevensis*, *siebkei*, and *stigmatella*, are usually found at the colline and montane levels. The species *mikiana* occurs primarily at the subalpine level. The occasional occurrence of *mikiana* at lower levels either suggests altitudinal movements or the availability of favourable habitats even at these lower altitudes. Adults of *mikiana* can be found at higher levels in moors on slopes and along the banks of rivers. The greater majority of localities of *mikiana* in Switzerland are situated in crystalline domains, and none on lime. Therefore, Dufour supposed that the geological substrate plays a determinant role in the occurrence of *mikiana*. The species is absent from the calcareous Alps of northern Tirol (cf. Mannheims & Pechlaner 1963), while its absence from the Carpathians is possibly related to the essentially sedimentary nature of the pertaining rock formations. The species *sarajevensis* is associated with open woods and hedges exposed to the sun, most often in steep terrains. It is seldom found in uniform plains and dark

woods. The few Swiss localities known of the relatively rare *siebkei* suggest a habitat of deciduous woods (*Quercus*, *Castanea*). The species *stigmatella* was found in Switzerland at two localities only, both very steep woods on thin and gravelly soil, one an oak grove, the other an *Ostrya* grove in the so-called *Querco-ostryetum* zone. Dufour supposed that the distribution of *stigmatella* in Switzerland is determined by the rarity of suitable habitats. Both sexes of the Swiss species of *Mediotipula* were captured in light traps. The non-Swiss species of *Mediotipula* are also found at colline to montane levels, with recorded altitudes ranging for *anatoliensis* from 430-1000 m, for *brolemanni* from 1000-1450 m, for *cataloniensis* from 1035-2000 m, for *galiciensis* from 200-700 m, and for *nitidicollis* from 350-900 m. The type couple of the Algerian *fulvogrisea* was captured on a wall in Mascara (Pierre 1924). Mascara lies at an altitude of about 600 m. The flight of the species of *Mediotipula* is swift and straight.

Theowald (1957, 1967) described and illustrated

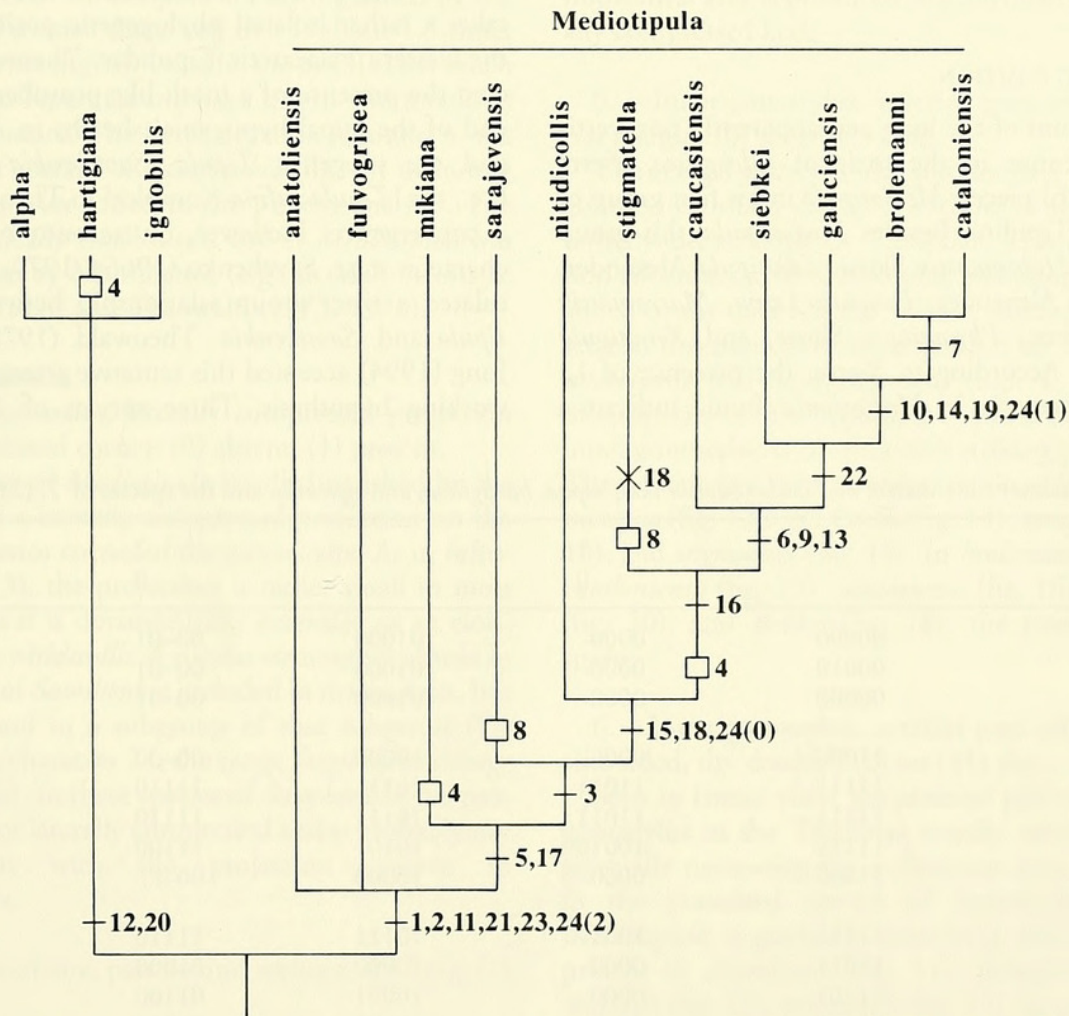


Fig. 2. Cladogram of *Tipula* (*Savtshenkia*) *alpha*, *hartigiana*, and *ignobilis*, and the species of *Tipula* (*Mediotipula*). Length 30, consistency index 0.83, retention index 0.93. See 'Discussion of adopted phylogeny' for further details. —: synapomorphy; □: homoplasy; ×: reversal.

the larvae and pupae of *mikiana* (as *stigmatella*), *sarajevensis*, and (1967) *stigmatella* (as *bidens* Bergroth). The larva and pupa of *stigmatella* were also treated in detail by Savchenko (1966a, 1966b; as *bidens*). Höchstetter (1963) described and illustrated the larva of *mikiana* (as *stigmatella*). The information provided by Höchstetter, Savchenko and Theowald suggests that the habitats of the larvae and pupae of *Mediotipula* species are restricted to moss cushions. Whereas Theowald recorded both stages of the species he dealt with from very moist moss on rocks in and along brooks, Savchenko characterized *stigmatella* as an obligate briobiont and xerophil, occurring under dry moss, especially *Brachythecium velutinum* (Hedwig). Höchstetter knew the larva of *mikiana* from dry moss in woods only.

Certain authors (e.g., Collin 1954; Stubbs 1992) referred to the occurrence of larvae of *siebkei* in rotting wood of alder (*Populus tremula* Linnaeus). This report goes back to Zetterstedt's description of *siebkei* (1852; 'Larva in Populo tremula capta, secundum Siebke'), but, as it has not been confirmed since, this reference should be considered with reserve.

SYSTEMATIC POSITION

On account of the long and apparently non-verticillate antennae in the male of *fulvogrisea*, Pierre (1924, 1926) placed *Mediotipula* in his first group of the tribus Tipulini. Besides *Mediotipula*, this group contained *Habromastix* Skuse, *Idiotipula* Alexander, *Leptotipula* Alexander, *Longurio* Loew, *Macromastix* Osten Sacken, *Phymatopsis* Skuse, and *Xenotipula* Alexander. According to Pierre, the presence of 12 antennal segments in *Mediotipula* should indicate a

close relationship with *Leptotipula*. However, distinct verticils among the long pubescence on the flagellomeres and a minuscule thirteenth apical antennal segment are actually present in the male of *fulvogrisea*. Both character states indicate a relationship with the more derived Tipulidae as are presently arranged in the genus *Tipula* and its near relatives. The structures of the male and female terminalia also show that there is no direct phylogenetic relationship between *Mediotipula* and the other taxa of Pierre's first group of Tipulini. With the exception of *Idiotipula*, the remaining taxa of this group are at present considered subgenera of *Leptotarsus* Guérin (cf. Hutson 1980, Oosterbroek 1989). *Leptotarsus* contains about 300 described species and has a primarily southern hemisphere distribution. The current systematics of *Leptotarsus* and its close relatives, which belong to the phylogenetically more primitive Tipulidae, are unsatisfactory and in need of a cladistic revision. At present, the monotypic South African *Idiotipula* is considered a genus. It is doubtless closely related to *Leptotarsus*.

According to Theowald (1957: 300), *Mediotipula* takes a rather isolated phylogenetic position among the western Palaearctic Tipulidae. Theowald considered the presence of a tooth-like protuberance at the end of the pupal hypogynial sheaths in *Mediotipula* and the subgenus *Tipula* (*Savtshenkia* Alexander) (i.e., the '*Tipula rufina*-Komplex' in Theowald 1957) a convergence. However, on account of the same character state, Savchenko (1966a, 1979, 1983) postulated a sister group relationship between *Mediotipula* and *Savtshenkia*. Theowald (1978) and De Jong (1994) accepted this tentative arrangement as a working hypothesis. Three species of *Savtshenkia*,

Table 2. Character state matrix of *Tipula* (*Savtshenkia*) *alpha*, *hartigiana*, and *ignobilis*, and the species of *T.* (*Mediotipula*).

Character		1 0		2 0	2 4
<i>alpha</i>	00000	0000-	01000	00-01	0000
<i>hartigiana</i>	00010	0000-	01000	00-01	0000
<i>ignobilis</i>	00000	0000-	01000	00-01	0000
<i>anatoliensis</i>	11000	0000-	10000	00-00	1012
<i>brolemanni</i>	11111	11011	10111	11110	1111
<i>cataloniensis</i>	11111	11011	10111	11110	1111
<i>caucasiensis</i>	11111	10010	10101	11100	1010
<i>fulvogrisea</i>	11000	0000-	10000	00-??	?? ??
<i>galiciensis</i>	11111	10011	10111	11110	1111
<i>mikiana</i>	11011	0000-	10000	01000	1012
<i>nitidicollis</i>	11101	0000-	10001	01100	1010
<i>sarajevensis</i>	11101	0010-	10000	01000	1012
<i>siebkei</i>	11111	10010	10101	11100	1110
<i>stigmatella</i>	11111	0010-	10001	11000	1010

viz., *alpha* De Jong, *hartigiana* Theowald, Dufour & Oosterbroek, and *ignobilis* Loew, are included in the phylogenetic analysis of *Mediotipula* given below. The phylogeny of the species of *Savtshenkia* was examined by De Jong (1994).

CHARACTER DISCUSSION

This section provides a discussion of the characters employed in the phylogenetic analysis of the species of *Mediotipula*. The character states recognized are briefly outlined, accompanied by their respective codes, after which a more detailed discussion follows. Table 2 gives the data set for the three supplementary *Savtshenkia* species, which are listed first, and the species of *Mediotipula*. The resultant cladogram (fig. 2) is discussed in the next section. Autapomorphies recognized for the species of *Mediotipula* are listed in Appendix B.

Wing

1. – Discal cell: (0) relatively large; (1) small.

All species of *Mediotipula* are distinguished by the presence of a small discal cell that is about 1.5 times as long as wide (fig. 6). Usually, the discal cell is much larger in the Tipulidae and has a length-width ratio of about 2 or more. The latter situation is found in the majority of species of *Savtshenkia* (fig. 7), including the three species added to the present analysis. The characteristically small discal cell of *Mediotipula* was noted before by Mannheims (e.g., in Mannheims & Pechlaner 1963) and Theowald (1973, 1978).

Male terminalia

2. – Gonocoxite, laterally compressed projection on posterodorsal corner: (0) absent; (1) present.

All species of *Mediotipula* are distinguished by the presence of a laterally compressed projection on the upper posterior corner of the gonocoxite. As in *fulvogrisea* (fig. 3), the projection is rather small in most species, but it is dorsoventrally extended as an elongate keel in *nitidicollis*. A similar structure is absent in the species of *Savtshenkia* included in the analysis, but can be found in a subgroup of that subgenus (De Jong 1994, character 24, the range *fragilina* to *subsignata cazorla*). In these species of *Savtshenkia*, the projection is not laterally compressed and is probably not homologous with the projection present in *Mediotipula*.

3. – Gonocoxite, part behind suture x: (0) long; (1) short.

In the Tipulidae, suture x usually separates a relatively large posterior section of the gonocoxite from the remainder of the gonocoxite, a situation found in all species of *Savtshenkia*. Within *Mediotipula*, the

posterior part of the gonocoxite is relatively long in *anatoliensis*, *fulvogrisea*, and *mikiana* (fig. 8, arrow). The remainder of species of *Mediotipula* are distinguished by a short caudal part of the gonocoxite (fig. 9).

4. – Gonocoxite, midventral area, ventral extension at midlength: (0) absent; (1) present.

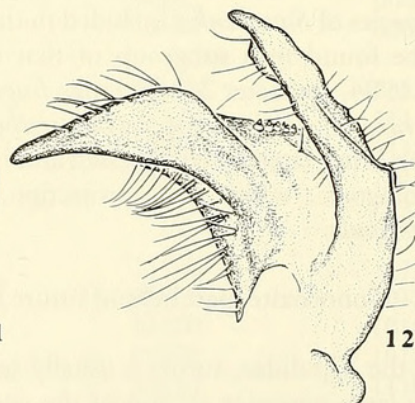
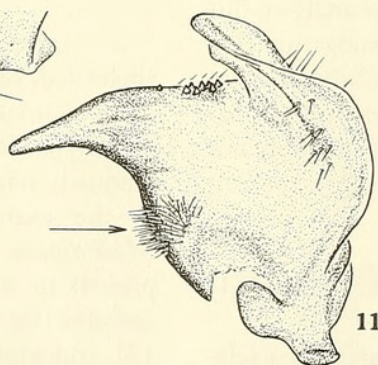
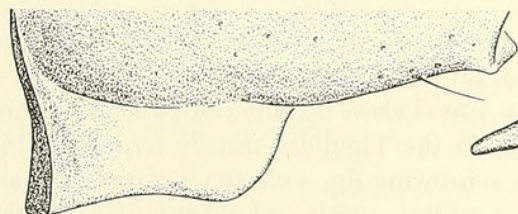
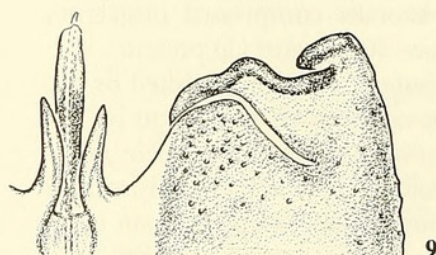
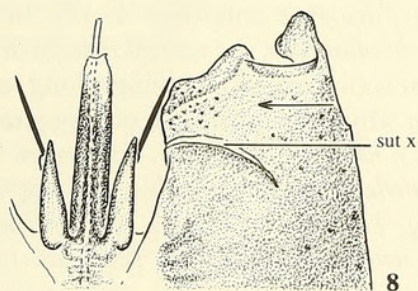
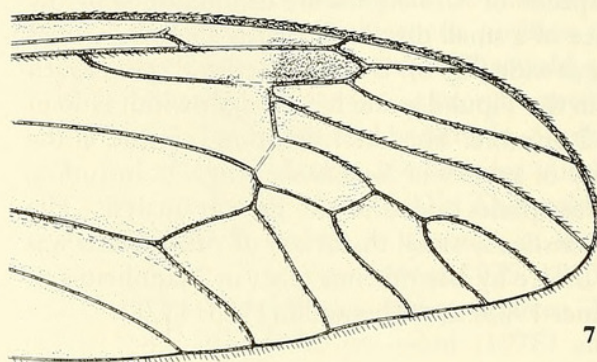
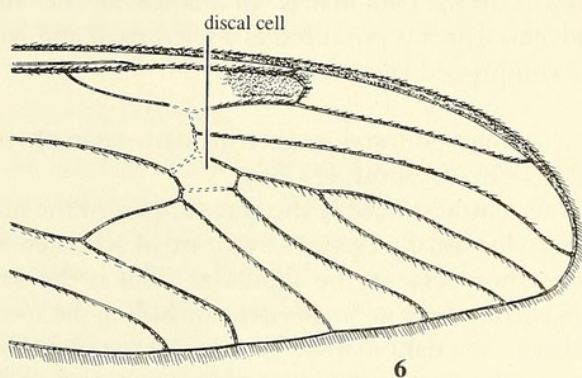
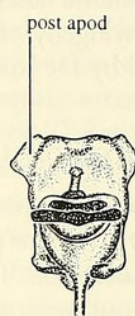
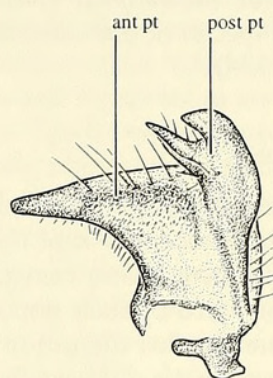
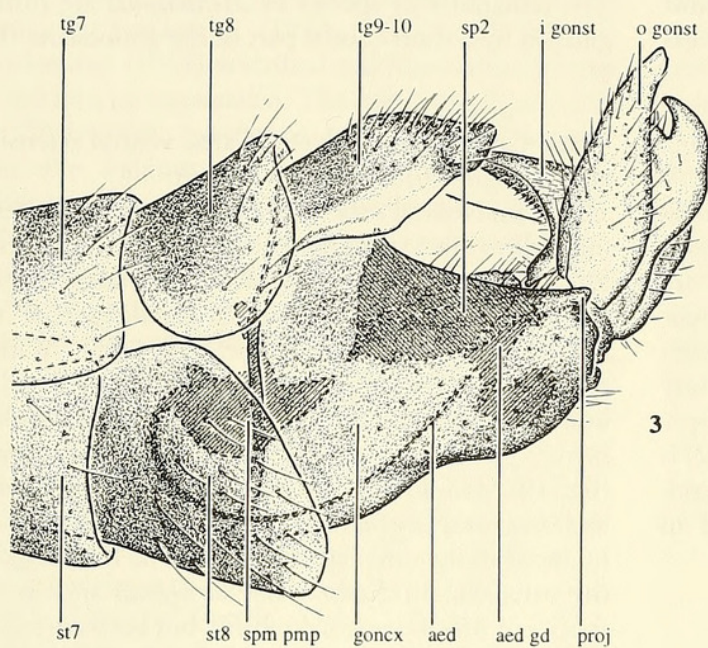
The midventral area in between the gonocoxites is unmodified in a minority of the species studied (fig. 3). *Savtshenkia hartigiana* carries a well-developed cone-shaped extension at about midlength of the midventral area (De Jong 1994, fig. 33). Within *Mediotipula* the midventral area is provided with a bulbous extension in *brolemanni*, *cataloniensis*, *caucasiensis*, *galiciensis*, *mikiana*, *siebkei*, and *stigmatella* (fig. 10). The lobe is relatively small in *caucasiensis*, *mikiana*, and *stigmatella*, whereas it is more pronounced in the other species listed. The homology of the extension in *Savtshenkia hartigiana* and in the species of *Mediotipula* is doubtful, but both are scored 'present' in the data matrix. In *anatoliensis* the entire midventral area is produced as a sclerotized and laterally compressed keel.

5. – Inner gonostylus, anterior part, setae on ventral margin: (0) short; (1) long.

The ventral surface of the anterior part of the inner gonostylus usually carries a vestiture of scattered and rather short setae in the Tipulidae. This is the situation encountered in *Savtshenkia*, including the species added to the data matrix. Within *Mediotipula*, short setae at this part of the inner gonostylus are found in *anatoliensis* and *fulvogrisea* only (figs. 4, 11). In the other species of *Mediotipula*, the ventral margin of the inner gonostylus is covered with strikingly long setae. There is a rather strong concentration of long setae in *mikiana* (fig. 12), *nitidicollis* (fig. 14), *sarajevensis* (fig. 13), and *stigmatella* (fig. 15). In *brolemanni* (fig. 22), *cataloniensis* (fig. 23), *caucasiensis* (fig. 16), *galiciensis* (fig. 20), and *siebkei* (fig. 18), the setae are more sparse.

6. – Inner gonostylus, anterior part, elongate, parallel sided, tip 'double': (0) no; (1) yes.

Seen in lateral view, the anterior part of the inner gonostylus in the Tipulidae usually terminates in a gradually narrowing tip, a character state found also in the examined species of *Savtshenkia*. Within *Mediotipula*, a gradually narrowing anterior part is present in *anatoliensis* (fig. 11), *fulvogrisea* (fig. 4), *mikiana* (fig. 12), *nitidicollis* (fig. 14), *sarajevensis* (fig. 13), and *stigmatella* (fig. 15). The species *brolemanni* (fig. 22), *cataloniensis* (fig. 23), *caucasiensis* (fig. 16), *galiciensis* (fig. 20), and *siebkei* (fig. 18) have a rostrally stretched anterior part of which the dorsal and ven-



tral sides run more or less parallel for some distance. The tip of the anterior part laterally carries a low extended rim that gives the apex a two fold appearance (fig. 16, upward arrow).

7. – Inner gonostylus, posterior part, dorsally directed crest: (0) absent; (1) present.

The dorsal margin of the posterior part of the inner gonostylus is usually rounded in the species of the Tipulidae. This situation is present in the studied species of *Savtshenkia* and in most species of *Mediotipula* (figs. 4, 11-16, 18, 20). Both *brolemanni* and *cataloniensis* are distinguished among the members of *Mediotipula* by the presence of a dorsally extended and laterally compressed crest on the posterodorsal surface of the posterior part at the point where the posterior parts curves anteriorly (figs. 22, 23, arrow). The actual size and shape of this crest can vary among specimens of the pertaining species, a feature that led Theowald (1978) to recognize the species *aragoniensi*s and *cataloniensis* (figs. 23-27; see Appendix A).

8. – Inner gonostylus, posterior part, posterolateral extension: (0) absent; (1) present.

Two of the species studied, viz., *sarajevensis* and *stigmatella*, are characterized by the presence of a posterolateral extension on the posterior part of the inner gonostylus (figs. 13, 15, arrows).

9. – Inner gonostylus, posterior part, posteromedial extension: (0) absent; (1) present.

The inner gonostylus of the majority of species examined is relatively simple and composed of an anterior and posterior part only. The species *brolemanni*, *cataloniensis*, *caucasiensis*, *galiciensis*, and *siebkei* are distinguished by the presence of a low placed posteromedial extension on the posterior part (figs. 16, 17, 19-23; see next character).

10. – Inner gonostylus, posterior part, posteromedial extension: (0) short; (1) elongate.

The posteromedial extension on the inner gonostylus varies in size between the species that show this structure. The extension is small in *siebkei* (fig. 19, arrow), somewhat more pronounced in *caucasiensis* (figs. 16, 17, downward arrows), and present as an el-

ongate structure in *brolemanni* (fig. 22), *cataloniensis* (fig. 23), and *galiciensis* (figs. 20, 21, arrows).

11. – Sperm pump, posterior apodemes, entirely fused, forming plate: (0) no; (1) yes.

The sperm pump carries a pair of separate posterior apodemes in the majority of species of Tipulidae, a situation found also in *Savtshenkia*, including the species added to the matrix. All species of *Mediotipula* show the total fusion of the posterior apodemes in the horizontal plane; a dorsoventrally flat blade connects the posterior apodemes from the body of the sperm pump up to their posterior apices (fig. 5).

12. – Sp2, medial margin blackish sclerotized: (0) no; (1) yes.

All species of *Savtshenkia* are characterized by the blackish sclerotized medial margin of sp2 (De Jong 1994). Within *Mediotipula*, sp2 is moderately, and usually uniformly, sclerotized throughout (figs. 28-31).

13. – Sp2, dorsal vaulting at anterior margin: (0) absent; (1) present.

Sp2 usually is present as a relatively flat structure, a situation found in all species of *Savtshenkia*. A relatively flat sp2 is present also in about half of the species of *Mediotipula* (fig. 28). The species *brolemanni*, *cataloniensis*, *caucasiensis*, *galiciensis*, and *siebkei* are distinguished by the presence of a dorsal vaulting at the anterior margin of sp2. The resulting lobe is relatively low and broad-based in *caucasiensis* (fig. 29, arrow), it is more pronounced and relatively narrow-based in *brolemanni*, *cataloniensis*, *galiciensis* (fig. 31), and *siebkei* (fig. 30, arrow).

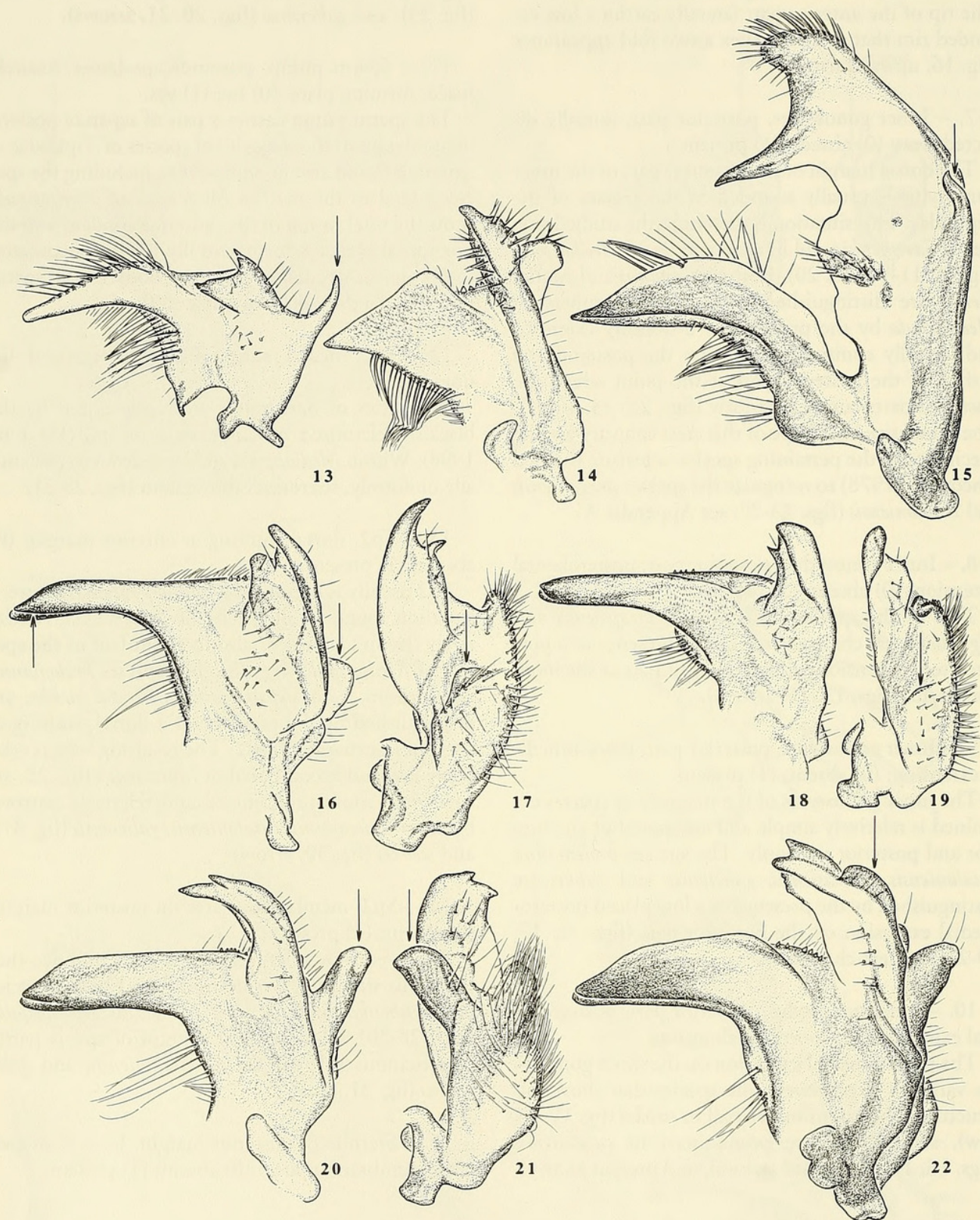
14. – Sp2, membranous area on posterior margin: (0) absent; (1) present.

Sp2 is entirely sclerotized in most Tipulidae that show this structure, a condition found in the species of *Savtshenkia* and in most species of *Mediotipula* (figs. 28-30). The posterior margin of sp2 is partly membranous in *brolemanni*, *cataloniensis*, and *galiciensis* (fig. 31, arrow).

15. – Sternite 8, posterior margin, U or V-shaped large membranous area: (0) absent; (1) present.

Figs. 3-12. – 3-6, *Tipula (Mediotipula) fulvogrisea*; 3, male terminalia, lateral view; 4, left inner gonostylus, lateral view; 5, sperm pump, dorsal view; 6, male right wing, dorsal view; 7, *T. (Savtshenkia) grisea*, male right wing, dorsal view; 8, 9, posterior part of right gonocoxite, aedeagal guide and appendages, ventral view (gonostyli omitted); 8, *T. (M.) mikiana*; 9, *T. (M.) sarajevensis*; 10, *T. (M.) mikiana*, ventral part of gonocoxite, lateral view; 11, 12, left inner gonostylus, lateral view; 11, *T. (M.) anatoliensis*; 12, *T. (M.) mikiana*.

Abbreviations: aed: aedeagus; aed gd: aedeagal guide; ant pt: anterior part of inner gonostylus; goncx: gonocoxite; i gonst: inner gonostylus; o gonst: outer gonostylus; post apod: posterior apodeme of sperm pump; post pt: posterior part of inner gonostylus; proj: projection on posterodorsal corner of gonocoxite; spm pmp: sperm pump; st7 etc.: sternite 7 etc.; sut x: suture x; tg7 etc.: tergite 7 etc.



Figs. 13-22, left inner gonostylus. – 13, *Tipula (Mediotipula) sarajevensis*, lateral view; 14, *T. (M.) nitidicollis*, lateral view; 15, *T. (M.) stigmatella*, lateral view; 16, 17, *T. (M.) caucasiensis*; 16, lateral view; 17, posterior view; 18, 19, *T. (M.) siebkei*; 18, lateral view; 19, posterior view; 20, 21, *T. (M.) galiciensis*; 20, lateral view; 21, posterior view; 22, *T. (M.) brolemanni*, lateral view.

The posterior margin of male sternite 8 is unmodified in the majority of species of the Tipulidae, being evenly convex and entirely sclerotized. This situation is present in the *Savtshenkia* species included in the analysis and in a few species of *Mediotipula* (fig. 32). Within *Mediotipula*, the posterior margin of sternite 8 is incised by a deep and broad U or V-shaped membranous area in *brolemanni*, *cataloniensis*, *caucasiensis*, *galiciensis*, *nitidicollis* (fig. 33), *siebkei*, and *stigmatella*.

16. – Tergite 9-10, narrow medial longitudinal suture: (0) absent; (1) present.

The medial part of the disk of tergite 9-10 is broadly membranous in *Savtshenkia alpha* and *ignobilis*, as is characteristic of the majority of species of *Savtshenkia*. In *hartigiana*, however, the medial part is entirely sclerotized. Within *Mediotipula*, the disk of tergite 9-10 is evenly sclerotized in *anatoliensis*, *fulvogrisea*, *mikiana*, and *nitidicollis* (fig. 34). In *sarajevensis* it is partly membranous as in certain species of *Savtshenkia*. The species *brolemanni*, *cataloniensis*, *caucasiensis*, *galiciensis*, *siebkei*, and *stigmatella* are distinguished by the presence of a narrow medial longitudinal suture on tergite 9-10 (fig. 35).

17. – Tergite 9-10, posterior margin, medial spinous extension: (0) absent; (1) present.

The majority of species of *Savtshenkia*, including the species added to the data set, carry a pair of spinous caudal extensions on the posterior margin of tergite 9-10. Within *Mediotipula*, a similar situation is found only in *anatoliensis* (fig. 36). The species *fulvogrisea* shows no distinct paired extensions, but has a widely emarginate posterior margin that is covered with black spines (fig. 37). The remainder of *Mediotipula* is distinguished by the presence of a medial spinous extension in between the lateral pair (figs. 34, 35, 38, 39, 40). See also next character.

18. – Tergite 9-10, posterior margin, medial spinous extension ventrally produced: (0) no; (1) yes.

The species of *Mediotipula* that carry a medial extension on the posterior margin of tergite 9-10 can be divided in those with a relatively small extension and those with a relatively large and anteroventrally produced extension. The first category includes *mikiana* (fig. 38), *sarajevensis*, and *stigmatella* (fig. 40), the second *brolemanni*, *cataloniensis*, *caucasiensis*, *galiciensis*, *nitidicollis* (fig. 39), and *siebkei*. In the species of the first category, the medial extension is of about the same size as the lateral ones, whereas it is much larger than the lateral extensions in the species of the second category. The latter condition is unique among the Tipulidae.

Female terminalia

19. – Cercus, almost straight and apex pointed: (0) no; (1) yes.

The majority of species of *Mediotipula* are characterized by the presence of a slightly downward curved female cercus that terminates in a rounded apex (fig. 41), a situation similar to that of the species of *Savtshenkia*, including those added to the data set. Within *Mediotipula*, *brolemanni*, *cataloniensis*, and *galiciensis* are distinguished by the presence of a straight and gradually narrowing cercus that terminates in an acute tip (fig. 42). Theowald (1978) used this character to separate his *brolemanni* group from the remainder of *Mediotipula*.

20. – Hypogynial valves, dorsal margin blackish sclerotized: (0) no; (1) yes.

All species of *Savtshenkia* are characterized by the blackish sclerotized dorsal margin of the hypogynial valves (De Jong 1994). Within *Mediotipula*, the hypogynial valves are moderately sclerotized throughout (fig. 45).

21. – Hypogynial valves, fused for some length: (0) no; (1) yes.

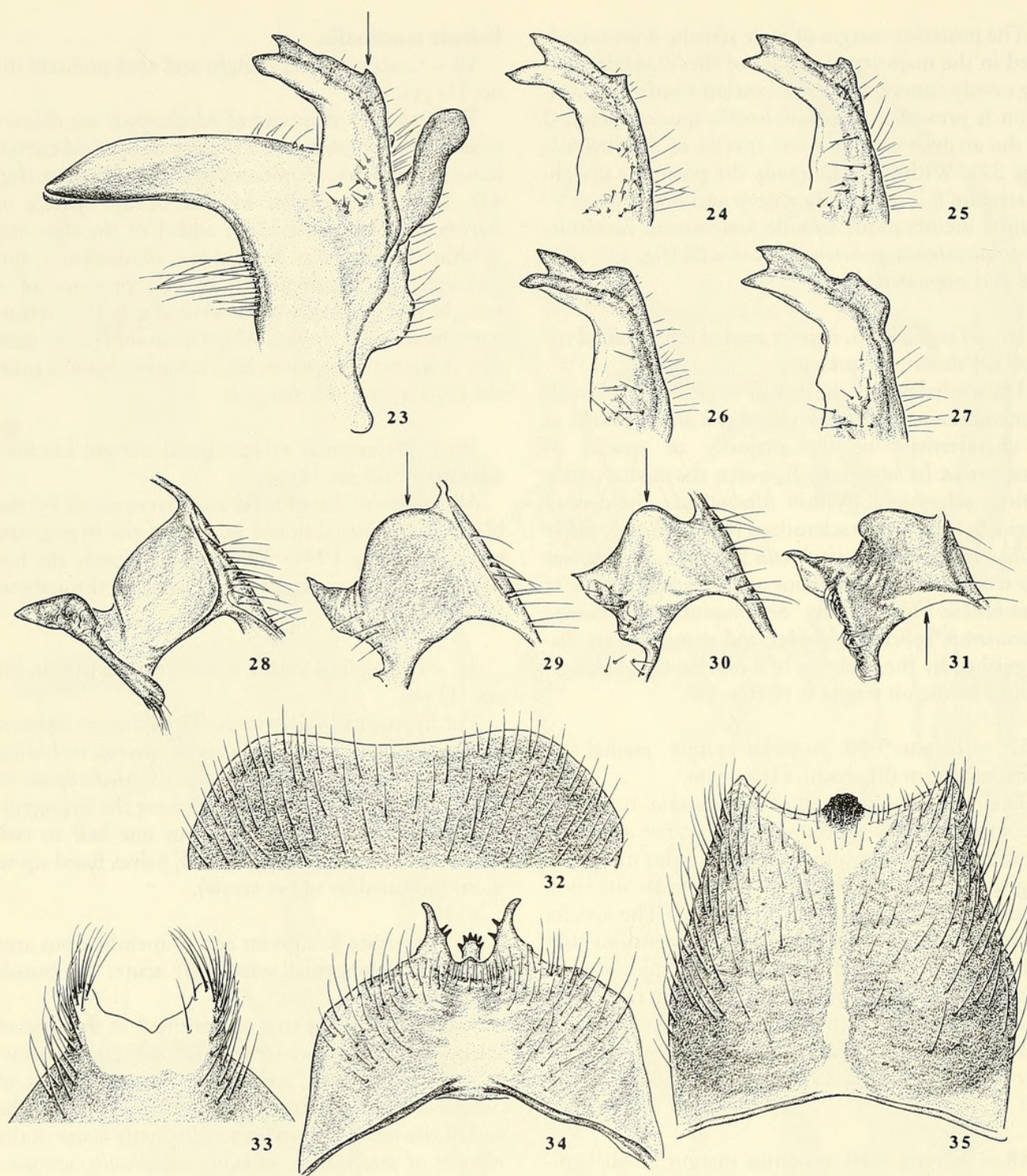
The hypogynial valves in the Tipulidae are separate up to their bases in the majority of species, including those of *Savtshenkia*. All species of *Mediotipula* of which I examined the female sex, have the hypogynial valves ventrally fused for about one half to two thirds of their length (figs. 43, 44, valves fused up to point indicated by upper arrow).

22. – Sternite 8, anterior end of membranous area at base of hypogynial valves: (0) acute; (1) broad, truncate.

The membranous area of sternite 8 at the base of the hypogynial valves narrows gradually and anteriorly terminates in an acute point in the species of *Savtshenkia* and in most species of *Mediotipula*. The end of the membranous area is distinctly acute in the females of *anatoliensis*, *mikiana*, *nitidicollis*, *sarajevensis*, and *stigmatella*. In the female paratype of *caucasiensis*, the only known female specimen of this species, it is less distinct (fig. 43, lower arrow). In the females of *brolemanni*, *cataloniensis*, *galiciensis*, and *siebkei*, the anterior end of this membrane is broad and truncate (fig. 44, lower arrow).

23. – Sternite 8, sclerotization at opening of gonopore: (0) absent; (1) present.

All females of *Mediotipula* studied are distinguished by the presence of a sclerotization of the ventral wall of the genital chamber near the opening of the gonopore. The sclerotization consists of a large and dorsally concave sclerite that is anterodorsally lo-



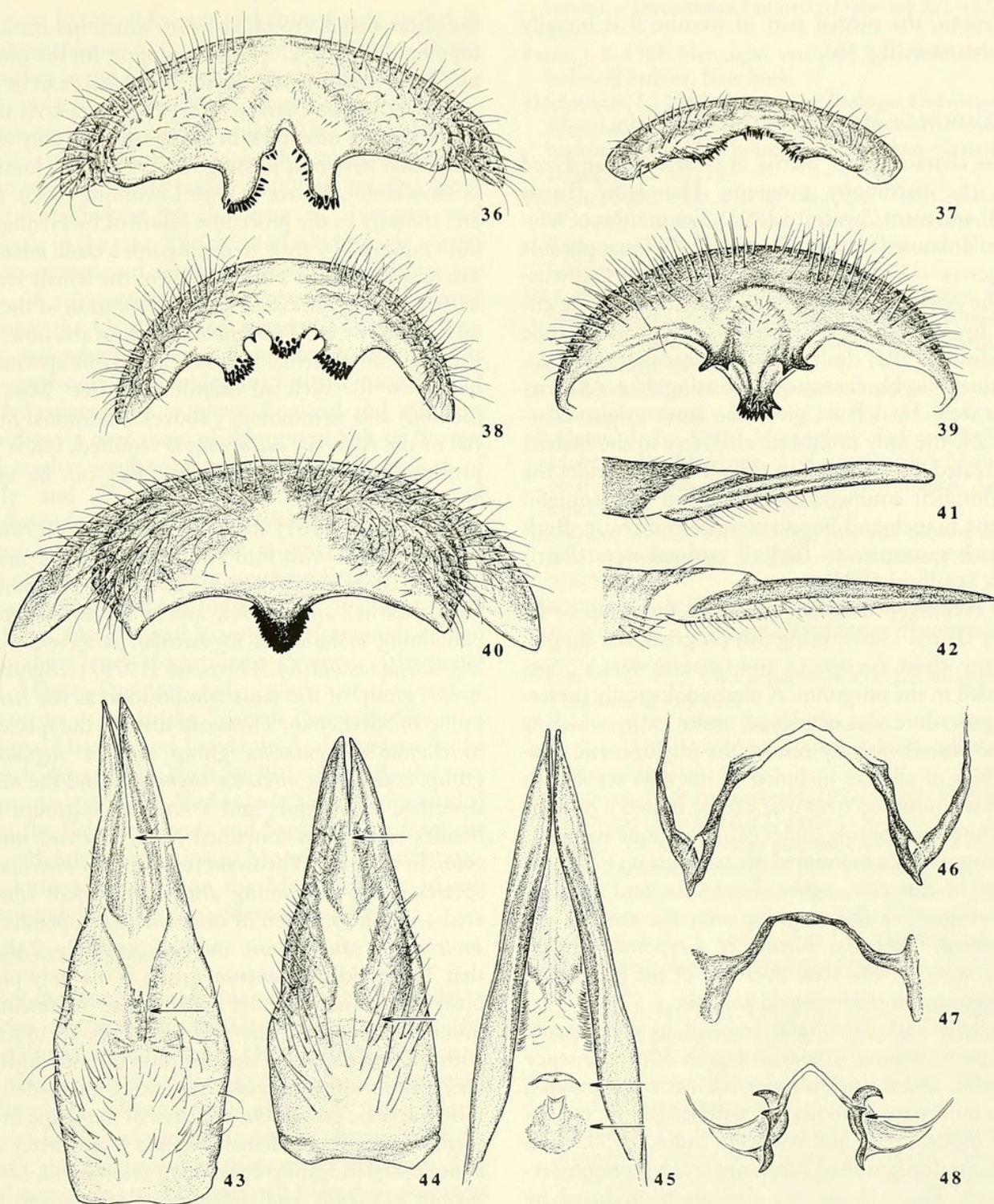
Figs. 23-35. – 23-27, *Tipula (Mediotipula) cataloniensis*, all Canillo, Andorra, 4-23 June 1979, 1500 m; 23, left inner gonostylus, lateral view; 24-27, posterior part of left inner gonostylus, lateral view; 28-31, right sp2, posterolateral view; 28, *T. (M.) nitidicollis*; 29, *T. (M.) caucasiensis*; 30, *T. (M.) siebkei*; 31, *T. (M.) galiciensis*; 32, 33, posterior margin of male sternite 8, ventral view; 32, *T. (M.) sarajevensis*; 33, *T. (M.) nitidicollis*; 34, 35, male tergite 9-10, dorsal view; 34, *T. (M.) nitidicollis*; 35, *T. (M.) stigmatella*.

cated, and a usually less distinct and smaller postero-ventral sclerite (fig. 45, arrows). This sclerotization is absent in the species of *Savtshenkia*.

24. – Sternite 9, medial part: (0) entirely sclero-

tized; (1) membranous over a narrow zone, lateral with sclerotized cavities; (2) membranous over a broad zone.

In most Tipulidae, the medial part of female sternite 9 is produced into a sclerotized elongate and



Figs. 36-48. — 36-40, male tergite 9-10, posterior view; 36, *Tipula (Mediotipula) anatoliensis*; 37, *T. (M.) fulvogrisea*; 38, *T. (M.) mikiana*; 39, *T. (M.) nitidicollis*; 40, *T. (M.) stigmatella*; 41, 42, female tergite 10 and left cercus, lateral view; 41, *T. (M.) siebkei*; 42, *T. (M.) galiciensis*; 43, 44, female sternite 8 and hypogynial valves, ventral view; 43, *T. (M.) caucasiensis*; 44, *T. (M.) siebkei*; 45, *T. (M.) anatoliensis*, female sternite 8 and hypogynial valves, dorsal view; 46-48, female sternite 9, ventral view; 46, *T. (M.) anatoliensis*; 47, *T. (M.) nitidicollis*; 48, *T. (M.) galiciensis*.

slender extension. Such an extension is present in the species of *Savtshenkia*. Within *Mediotipula*, none of the examined females shows an elongate and posteriorly produced medial section of sternite 9. The sternite is present as a slender and well-sclerotized struc-

ture in *caucasiensis*, *nitidicollis* (fig. 47), *siebkei*, and *stigmatella*. It is medially membranous over a relatively narrow zone and incorporates a pair of lateral sclerotized cavities in *brolemanni*, *cataloniensis*, and *galiciensis* (fig. 48, arrow). In *anatoliensis*, *mikiana*, and

sarajevensis the medial part of sternite 9 is broadly membranous (fig. 46).

DISCUSSION OF ADOPTED PHYLOGENY

The character state matrix of table 2 was analyzed with the parsimony programs Hennig86 (Farris 1988) and PAUP (Swofford 1993). For matters of reference, unknown characters are coded '?', inapplicable characters '-' in table 2. Platnick et al. (1991) discussed the potentially different treatment of missing entries by the programs Hennig86 and PAUP, while Maddison (1993) dealt with the consequences of coding inapplicable characters as missing data. All characters were, by default, given the same weight; character 24, the only multistate character in the matrix, was treated unordered. The matrix was run under the *ie**; (implicit enumeration) command of Hennig86 and the branch-and-bound algorithm of PAUP. Both methods guarantee to find all optimal trees (Farris 1988; Swofford 1993).

As Hennig86 does not allow the outgroup to be empty (Farris 1988), using this program, the supplementary *alpha*, *hartigiana*, and *ignobilis* were a priori included in the outgroup. A methodologically preferable procedure was employed under PAUP, which is able to simultaneously resolve the phylogenetic relationships of all taxa included in the data set and to compute unrooted trees that can be rooted a posteriori. Outgroup rooting under PAUP was done such that the outgroup is a monophyletic sister group of the ingroup. In this case, *alpha*, *hartigiana*, and *ignobilis* were assigned to the outgroup after the analysis was completed. Recently, Nixon & Carpenter (1993) gave a compact and clear overview of the proper use of outgroups in phylogenetic analysis.

Analysis with Hennig86 resulted in two equally most parsimonious trees with length 30, consistency index 82, and retention index 92; PAUP computed a single most parsimonious tree with length 30, consistency index 0.833, and retention index 0.930. Both programs distinguished *Mediotipula* as a monophyletic taxon. Fig. 2 shows the cladogram produced by PAUP when the outgroup is considered the monophyletic sister group of the ingroup. (Hennig86 declines to resolve the most basal node of a tree on account of implied polarities alone and places the three *Savtshenkia* species in a polytomy).

The solution for *Mediotipula* produced by PAUP is identical with one of the two alternative trees found by Hennig86. It is also identical with the strict consensus tree of the two equally most parsimonious trees computed by Hennig86. The second most parsimonious tree found by Hennig86 depicts *fulvogrisea* as the sister species of a clade *anatoliensis* to *cataloniensis*, within which *anatoliensis* is the sister species of

the clade *mikiana* to *cataloniensis* which has the same topology as in fig. 2. The only support for the monophyly of a clade *anatoliensis* to *cataloniensis* can be given by the female characters 21, 23, and 24. As these characters are unknown in *fulvogrisea* and only characters that have non-missing values affect the location of any taxon on a tree in PAUP (Swofford 1993), they are, contrary to the procedure followed by Hennig86, not employed by PAUP to distinguish a clade *anatoliensis* to *cataloniensis*. Future study of the female terminalia of *fulvogrisea* could lead to a solution of the basal trichotomy in *Mediotipula*. As things are, however, the few known female specimens of this species do not allow for such an examination (see 'Material, methods and terminology', above). Additional material of the Algerian *fulvogrisea* is required, but it will probably take some time before this can be safely amassed.

Savchenko (1961) divided the species of *Mediotipula* he dealt with into two groups, viz., a *siebkei* group containing *caucasiensis* (as *obtusiuscula* Lackschewitz) and *siebkei*, and a *stigmatella* group containing *mikiana* (as *stigmatella*), *sarajevensis*, and *stigmatella* (as *bidens*). Theowald (1978) recognized a *siebkei* group of the same composition as the *siebkei* group of Savchenko. Theowald divided the species of Savchenko's *stigmatella* group over a *stigmatella* group, containing *mikiana*, *stigmatella* and the newly described *anatoliensis*, and a *sarajevensis* group, that besides *sarajevensis* contained *fulvogrisea* and *nitidicollis*. In addition, Theowald recognized a *brolemanni* species group containing *aragoniensis* (here considered a junior synonym of *cataloniensis*; Appendix A), *brolemanni*, *cataloniensis*, and *galiciensis*. Fig. 2 shows that Theowald's *brolemanni* group is the only previously recognized species group that represents a monophyletic unit. The *brolemanni* group together with the species of the *siebkei* group of both authors, viz., *caucasiensis* and *siebkei*, constitute a well-defined monophyletic group. On the basis of the shape of the membranous area of female sternite 8 (character 22), a monophyletic group containing *brolemanni*, *cataloniensis*, *galiciensis*, and *siebkei* can be tentatively distinguished, but, as discussed under character 22, the expression of this character in the female paratype of *caucasiensis* leaves some doubts regarding the interpretation adopted here.

DISTRIBUTION

Mediotipula is primarily restricted to the Mediterranean subregion of the Palearctic (fig. 1). The species *anatoliensis* is known from its type locality in the Sultan Daglari mountains in the Turkish province Konya and from a locality in the western province Izmir. The species *fulvogrisea* is known from

the type locality Mascara and from Guelt es-Stel in northern Algeria only. The main distribution of *mi-kiana* lies in the Alps. Besides that, it is known from a few isolated localities in the Czech Republic, Germany, Poland, and Slovakia. The species *sarajevensis* is widely distributed in the central European mountains at levels under 1500 m, ranging from southern England in the west to Rumania and Bulgaria in the east. The range of *nitidicollis* is restricted to central and southern Spain. The distribution area of *stigmatella* extends over most of central Europe, the Caucasus and western Turkey. At present, *caucasiensis* is known from a few localities in the Caucasus only. The widespread distribution area of *siebkei* ranges from southern England and southern Scandinavia over most of the central belt of Europe and reaches southward to the north-eastern part of Sicily and Corsica. The remaining species of *Mediotipula*, viz., *galiciensis*, *brolemanni*, and *cataloniensis*, are confined to the mountainous northern part of Spain and adjacent southern France. The species *galiciensis* has been found in the Spanish provinces Lugo, Oviedo, and Vizcaya, *brolemanni* is known from the French departments Pyrénées Atlantiques and Hautes-Pyrénées only, while *cataloniensis* is known to occur in the Spanish Pyrenean provinces Gerona, Huesca, and Lerida, in Andorra, and in the French department Pyrénées-Orientales. At the moment, no species of *Mediotipula* have been recorded from the Balearic islands and Sardinia, nor from the Rif and Atlas mountains in Morocco. The only species known to occur on the Mediterranean islands Corsica and Sicily is the widespread *siebkei*.

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APPENDIX A

Synonymy

aragoniensis Theowald, 1978 = *cataloniensis*

Theowald, 1978 **syn. n.**

In his revision of *Mediotipula*, Theowald (1978) described three species from northern Spain as new and assigned them, together with *brolemanni*, to his *brolemanni* species group. In Theowald's concept, the *brolemanni* group contained the species *aragoniensis*, *brolemanni*, and *cataloniensis* from the Pyrenees and *galiciensis* from northern Spain. According to Theowald, a constant character separating *aragoniensis* and *cataloniensis* could be found in the structure of the posterior part of the inner gonostylus. Its tip should be more acute in *aragoniensis* and short and *brolemanni*-like in *cataloniensis*, whereas the dorsal crest of the posterior part ('Buckel' in Theowald 1978; character 7 in the present paper) should be placed somewhat laterally on the posterior part in *aragoniensis*, while it should have an acute dorsal angle in *cataloniensis*. The collection of ZMAN contains a series of 22 identical labelled males, giving Canillo in Andorra at 1500 m as locality and dates of capture 4 to 23 June 1979. Within this series, the posterior part of the inner gonostylus shows a range of forms intermediate between those considered typical of *aragoniensis* and *cataloniensis*. A number of these forms are shown in figs. 23-27. Considerable variation in the shape of the poste-

rior part is observed in other species of *Mediotipula* as well (see for instance Theowald 1978 on *sarajevensis*). I therefore conclude that both *aragoniensis* and *cataloniensis* are names that pertain to the same species. At the moment, the range of this species is known to extend in Spain from the north-eastern part of Aragón eastward to the Mediterranean coast of northern Cataluña. To the north it has been recorded from Andorra and the French department Pyrénées-Orientales. As the major part of its range seems to cover the Pyrenean northern portion of Cataluña, I prefer to denote this species *cataloniensis*. The species is most easily distinguished from the other species of *Mediotipula* by the medially curved corners on the posterior margin of male sternite 8 that are covered by medially directed strong setae.

APPENDIX B

Autapomorphies of the species of *Tipula* (*Mediotipula*)

anatoliensis: midventral area of gonocoxites present as a well-developed keel; inner gonostylus anterolaterally with a cluster of short setae (fig. 11, arrow).

brolemanni: anterior part of inner gonostylus relatively robust and short compared with that of close relatives (cf. fig. 22 with figs. 16, 18, 20, 23).

cataloniensis: posterior margin of male sternite 8 with medially directed tips, tips with long and strong medially directed setae; outer gonostylus with concentration of long setae at posterior margin.

fulvogrisea: male antenna extremely elongate.

galiciensis: no autapomorphy recognized.

mikiana: shape of posterior part of inner gonostylus (fig. 12).

nitidicollis: surface of thorax shining; branched gonapophysis; gonocoxite ring interrupted.

sarajevensis: shape of low posterior part of inner gonostylus (fig. 13).

siebkei: no autapomorphy recognized.

stigmatella: inner gonostylus about two times as high as inner gonostyli of other species of *Mediotipula* (fig. 15); sensory area on posterior part of inner gonostylus instead of dorsally on anterior part as in other species of *Mediotipula*; female sternite 8 bulbous.

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