



## A new species of the genus *Mesosmittia* Brundin, 1956 (Diptera: Chironomidae) from the Neotropics with a cladistic analysis of the genus using quantitative characters

MARIANO DONATO

Laboratorio de Sistemática y Biología Evolutiva (LASBE), Museo de La Plata, Paseo del Bosque s/n (1900), La Plata, Argentina.  
E-mail: mdonato@fcnym.unlp.edu.ar

### Abstract

The new species *Mesosmittia museophila* from the Neotropics is described and illustrated based on male imagines. A cladistic analysis was conducted in order to assess its possible relationships with the remaining species in the genus, and it was found that *M. museophila* is the sister group of *M. mina* Sæther and these two species are closely related to *M. prolixa* Sæther. This analysis suggests that standardization is preferable to use of raw data and the latter are preferable to any statistical descriptor.

**Key words:** Diptera, Chironomidae, Orthoclaadiinae, *Mesosmittia*, continuous characters, parsimony, phylogeny, new species, South America

### Introduction

The orthoclad genus *Mesosmittia* Brundin belongs to the *Pseudosmittia* group (Brundin 1956, Sæther 1977). This genus was erected by Brundin (1956) for *Spaniotoma* (*Orthocladius*) *flexuella* Edwards and placed in different genera and subgenera until reaching its actual position. For a complete nomenclatorial history see Spies (2006). The first revision of the genus was made by Sæther (1985) who described one new species for the Neotropical region, six new species for the Nearctic region, and redescribed the Palearctic species *Mesosmittia flexuella*. Later, Sæther (1996) described a new species from the Afrotropical region and established the new combination *Mesosmittia nigerrima* (Kieffer, 1918). In the same paper, Sæther established the previously two new species described by Wang and Zheng (1990) as synonyms of *Mesosmittia patrihortae*. Andersen and Mendes (2002) described four new species and recorded several Nearctic species in the Neotropics. Finally, Sæther (2006) transferred *Mesosmittia jintuoctava* Sasa to the genus *Pseudosmittia*. The genus *Mesosmittia* occurs in the Afrotropical, Palearctic, Nearctic and Neotropical regions, with the latter being the region with highest diversity.

Data on the ecological requirements of *Mesosmittia* immature stages is scarce. The larva of *Mesosmittia flexuella* was described by Strenze (1950) and he stated that the immature stages were terrestrial. Cranston *et al.* (1989) reported adults of this species caught in emergence traps in fast flowing streams, suggesting an aquatic condition for the immature stages. Andersen and Mendes (2002) considered the records of the species described by Sæther (1985) as evidence suggesting semiaquatic habitat preferences.

In a cladistic analysis the most useful and non-controversial characters are those whose states are exclusive, but other features are also useful in systematics, such as meristic and continuous data. A problem of quantitative characters is how to treat the measured data. Pimentel and Riggins (1987) stated that descriptive statistics (e.g. mean, median, standard deviation, etc.) are sample estimates and have no phylogenetic signal. Moreover, they questioned the cladistic properties of means, standard deviations, or tests of significance that would allow them to be used in such a way. However, the authors recognized their lack of a theoretical basis to answer these questions.

Quantitative characters have rarely been included in cladistic analyses of morphological data, because the justification often given for excluding continuous characters is the difficulty in objectively assigning character states

(Pimentel & Riggins 1987, Cranston & Humphries 1988) although many so-called qualitative characters in fact conceal quantitative characters (Stevens 1991). Quantitative characters have also been criticized because they do not measure homology, but several studies (e.g. Rae 1998, Wiens 2001) have documented the usefulness of continuous characters in phylogenetic studies.

Several methods have been proposed to solve the codification of continuous characters (Mickevich & Johnson 1976, Colless 1980, Almeida & Bisby 1984, Thorpe 1984, Archie 1985, Chappill 1989, Thiele 1993, Strait *et al.* 1996, Wiens 2001). These methods have the common problem of assigning different states to terminals that do not differ significantly or the same state to terminals that are significantly different (Farris 1990). In addition, coding quantitative variation as continuous quantitative characters may be preferable to qualitative coding because it can potentially solve common problems in morphological phylogenetics such as vague character definitions and arbitrary character state delimitation (Wiens 2001). Goloboff *et al.* (2006) proposed the analysis of continuous characters as such by assigning to each terminal a range that goes from the mean minus one standard deviation to the mean plus one standard deviation, given normal distributions. As continuous or meristic characters are best treated as additive, TNT implemented the Farris (1970) and Goloboff (1993a) algorithms for optimization. These algorithms work with the differences in the numerical values of the variables being optimized, allowing for values between 0 and 65 and up to three decimals (for more details see Farris 1970 and Goloboff *et al.* 2006).

An issue that concerns quantitative characters is that of the benefits and disadvantages of standardization. Character standardization was proposed to ensure equal character contribution and to prevent characters with extremely large numbers from exerting more influence than those with smaller values. The standard score of an observation is the number of standard deviation units it is above or below the mean and is calculated by subtracting the mean from the observation, then dividing by the standard deviation (Sokal 1961). The standardization of character states makes all character means equal to zero, all character variances equal to unity, and ensures a normal distribution. The logic behind standardization has not been thoroughly investigated. Rohlf & Sokal (1965) analyzed the effects of character standardization in correlation and distance indices in numerical taxonomy, finding a greater degree of influence on the results of the former indices and a slight effect on the latter. As it was mentioned above, continuous characters were often dismissed in favour of discrete characters and therefore few papers have dealt with standardization in the field of Cladistics. Farris (1971) stated that standardization should act to reduce the apparent heterogeneity of evolutionary rate in different characters. Nonetheless, standardization can certainly yield scaled characters with differing ranges (Mickevich & Farris 1981).

The main goal of this study is to describe a new species of the genus *Mesosmittia* from the Neotropics and to assess its possible relationships with the other species in the genus using a combined data set of continuous and discrete characters. Additionally, problems related to continuous characters such as character standardization versus use of raw measurements, and use of ranges versus computation of statistic descriptors for them, are explored.

## Material and methods

The specimens were collected with a sweep net. Microscope slides were prepared by clearing with 10% KOH; neutralization with glacial acetic acid; dehydration in 80%, 96% and 100% ethanol and mounting in Canada balsam. Morphological measurements follow Sæther (1980) and unless otherwise stated are in  $\mu\text{m}$  rounded to the nearest 5. Measurements are given as ranges followed by the median, followed by the measurements of the holotype in square brackets. Photographs were taken with a Nikon Eclipse E200 compound microscope fitted with a Micrometrics SE Premium digital camera and connected to a personal computer. The comparison of the new species with the holotype of *Mesosmittia mina* was made by Professor Ole A. Sæther. The holotype and seven paratypes are housed in La Plata Museum (MLP) and two paratypes are deposited in Natural History Collections (ZMBN), Bergen Museum, University of Bergen, Norway.

In order to assess the relationships of the new species here described, a cladistic analysis was performed applying maximum parsimony and implied weights as optimality criteria. The taxa chosen to perform this analysis are the 13 well-described species of the genus *Mesosmittia* (Sæther 1985, 1996; Andersen & Mendes 2002) plus the new species. As the description of the species *M. nigerrima* is incomplete (Kieffer 1918) it was not included in the analysis. The assessment and coding of characters and character states was based on the literature.

This analysis comprised 30 continuous and 6 discrete characters. The characters and character states are self-explanatory and are listed in Appendix 1. Two issues related to continuous characters are explored: 1, character standardization versus use of the raw measurements, and 2, the use of measurement ranges versus computation of some statistic descriptor of them. The selected statistic descriptor was the median since it has the advantage that is little affected by few high values in the frequencies analyzed. The median is also preferable when it is impossible to obtain the measurements of all the items in a sample (Sokal & Rohlf 1969).

Four data sets were analyzed: 1) all characters expressed as ranges (except for those species whose description was based on one specimen, this is applicable for the rest of the data sets), 2) all characters expressed as the median of each range, 3) all characters standardized and expressed as ranges and 4) all characters standardized and expressed as the median of each range. Because of standardization, some characters (those below the mean) acquire negative values and therefore cannot be analyzed. To prevent this problem, the standardized matrix was transformed through the addition of a constant value of 3 to ensure positive values for all characters. Discrete characters were coded as non-additive and quantitative characters were analyzed as additive given that TNT allows treating this kind of characters. Data matrices are available from the author.

The data matrices were analyzed with TNT version 1.1 (Goloboff *et al.* 2008a) under maximum parsimony using equal and implied weights (Goloboff 1993b). Analyses with implied weighting were conducted by means of values for the concavity constant  $k=5-16$ , as suggested by Goloboff *et al.* (2008b).

All tree searches were performed using a Wagner tree as starting tree and 1000 random addition sequences plus TBR with 10 trees to save per replication, followed by TBR branch swapping.

The congruence among data sets and fundamental cladograms provide evidence of phylogenetic accuracy. As consensus methods summarize agreement (or disagreement) or congruence (or incongruence) between cladograms, they could be considered as an indirect measurement to evaluate the information content of a particular data set. For this purpose, strict consensus and agreement subtrees were calculated from the trees obtained with each matrix in order to assess the performance and congruence between each kind of data and thus choose between the different data sets.

Character support measurements were applied to the data set selected using the criterion explained above. Absolute and relative Bremer support values were calculated saving up to 6 steps longer suboptimal trees obtained with branch swapping. As the presence of characters with weights or costs can lead to wrong conclusions with regard to support using Bootstrap and Jackknife (Goloboff *et al.* 2003), the resampling methods chosen were absolute and GC (Group present/Contradicted) frequencies. They were estimated with 1000 replicates of Jackknife symmetrical resampling (Jackknife symmetric resampling is not affected by weighted characters) and the tree search strategy for each replicate was 10 random addition sequences plus TBR and saving 10 trees per replicate.

To root and polarize the trees, the Neotropical species *Allocladius bilobulatus* (Edwards), *A. neobilobulatus* (Paggi), *Pseudosmittia digitata* Sæther and *P. forcipata* (Goetghebuer) were selected as outgroups and their characters were taken from the literature.

## Systematics

### *Mesosmittia museophila* n. sp.

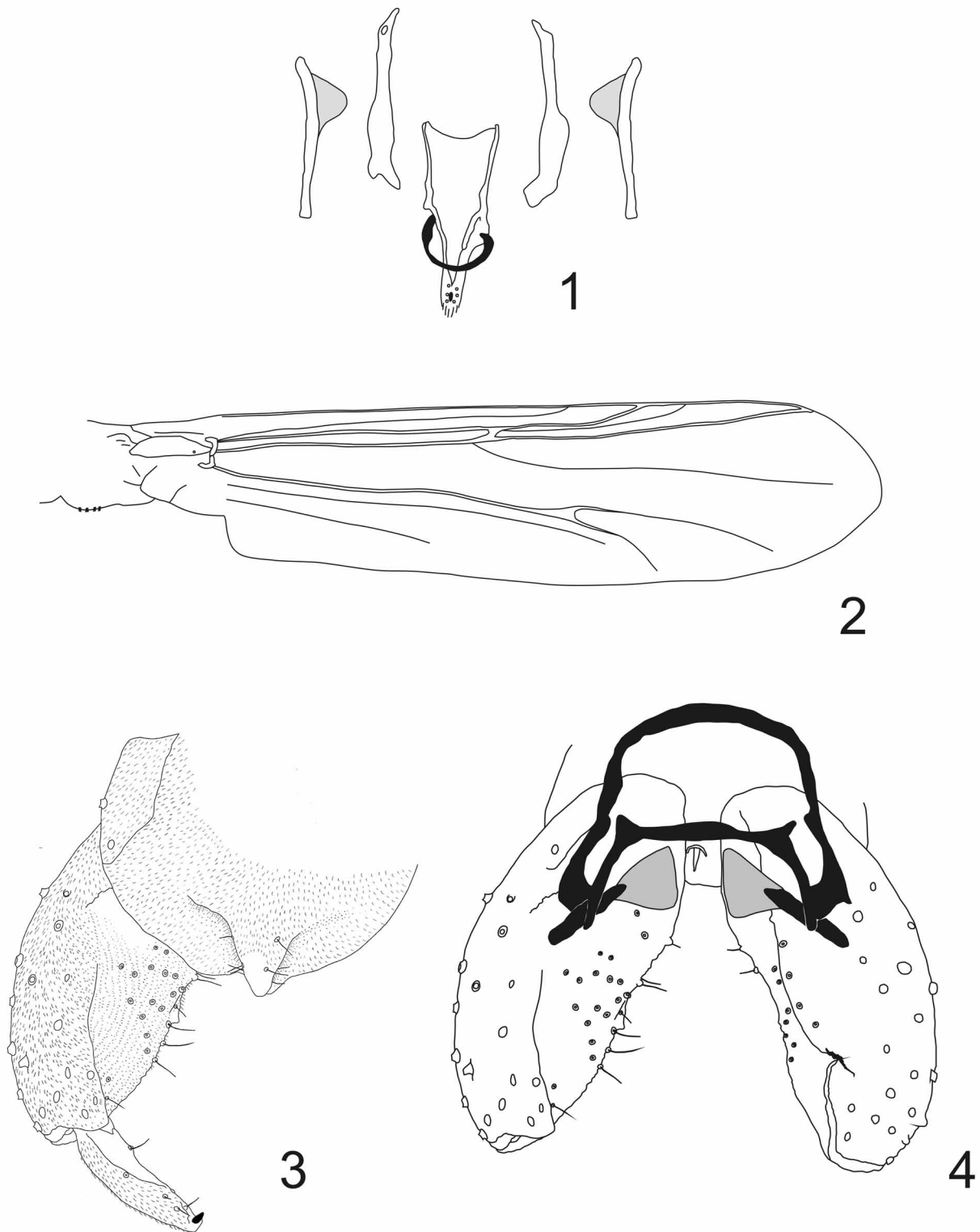
**Material examined.** Holotype male, MLP number 5307/1, ARGENTINA, Buenos Aires, La Plata, 34° 54' 30.9''S– 57° 56' 21.8''W, 8–IV–2005, sweep net, M. Donato; paratypes: 7 males, MLP numbers 5307/2–6 and 2 males in ZMBN, same data as holotype.

**Other material examined.** *Mesosmittia mina* Sæther, holotype male, U.S.A., Georgia, Clarke Co., Athens, Oconee River (ZMBN). Examined by Professor Ole A. Sæther.

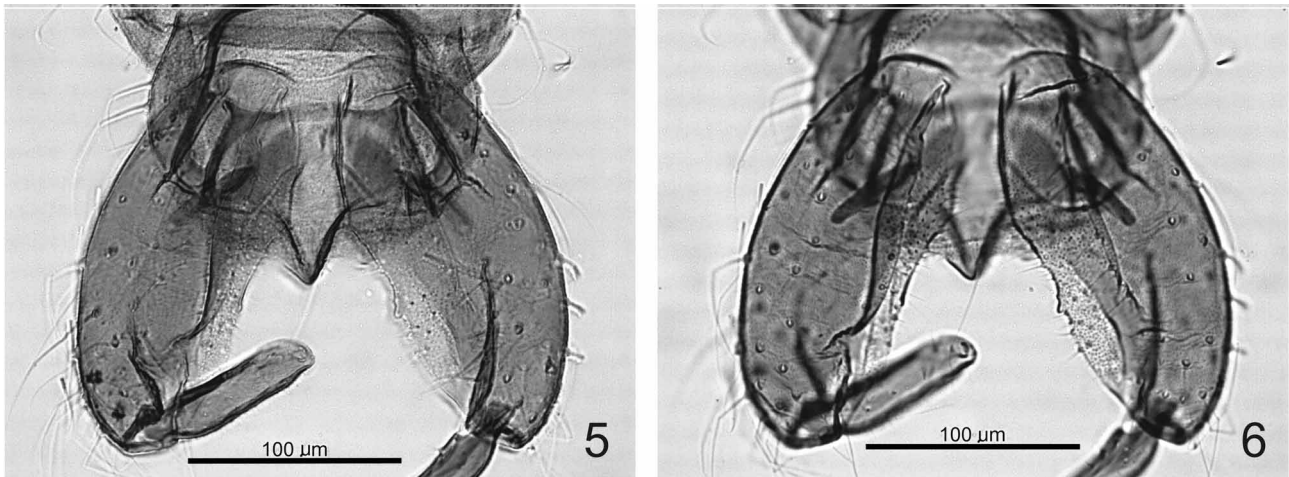
**Etymology.** Referring to the species swarming in the forest surrounding the La Plata Museum, using the Greek *philus* = friend as a suffix.

**Diagnosis.** distinguished from all other species of the genus by the presence of a notch on the ventral margin of the gonocoxite, except for *Mesosmittia mina*. *M. museophila* is separable from this species by the shorter and blunter preapical projection of the gonocoxite instead of the preapical projection sharply pointed and triangular in *M. mina*.

**Male imago** ( $n = 8-10$ )



**FIGURES 1–4.** *Mesosmittia museophila* sp. n. Male adult. (1) Tentorium, stipes and cibarial pump. (2) Wing. (3) Hypopygium dorsal view. (4) Hypopygium with tergite IX removed, right ventral view, left dorsal view.



FIGURES 5–6. *Mesosmittia museophila* sp. n. Male adult. Hypopygium general view. (5) dorsal view. (6) ventral view.

Total length 1.96–2.43, 2.13 [2.36] mm. Wing length 1–1.13, 1.08 [1.11] mm. Total length/wing length 1.81–2.23, 2.00 [2.13]. Wing length/length of profemur 2.29–2.76, 2.51 [2.47]. Coloration uniformly dark brown with legs light brown.

Head. Antennae with 13 flagellomeres, AR 1.17–1.48, 1.34 [1.43], ultimate flagellomere length 350–430, 400 [430]. Temporal setae 6–9, 7 [6], divided in 1–3, 2 [1] inner verticals and 4–6, 5 [5] outer verticals. Clypeus with 4–9, 8 [6] setae. Cibarial pump, tentorium and stipes as in Figure 1. Tentorium 123–152, 137 [152] long and 17–27, 24 [25] wide. Stipes 100–118, 110 [118] long and 7–12, 7 [7] wide. Palpomere lengths: 24–29, 27 (9) [27]; 39–56, 49 [56]; 69–86, 78 [78]; 64–83, 69 [78]; 93–113, 100 [100].

Thorax. Anteprepronotum with 0–2, 1 [0] lateral setae. Dorsocentrals 6–9, 7 [8]; acrostichals 8–12, 10 [10]; prealars 3–5, 4 [3]; supraalars 1; scutellars 5–8, 5 [6].

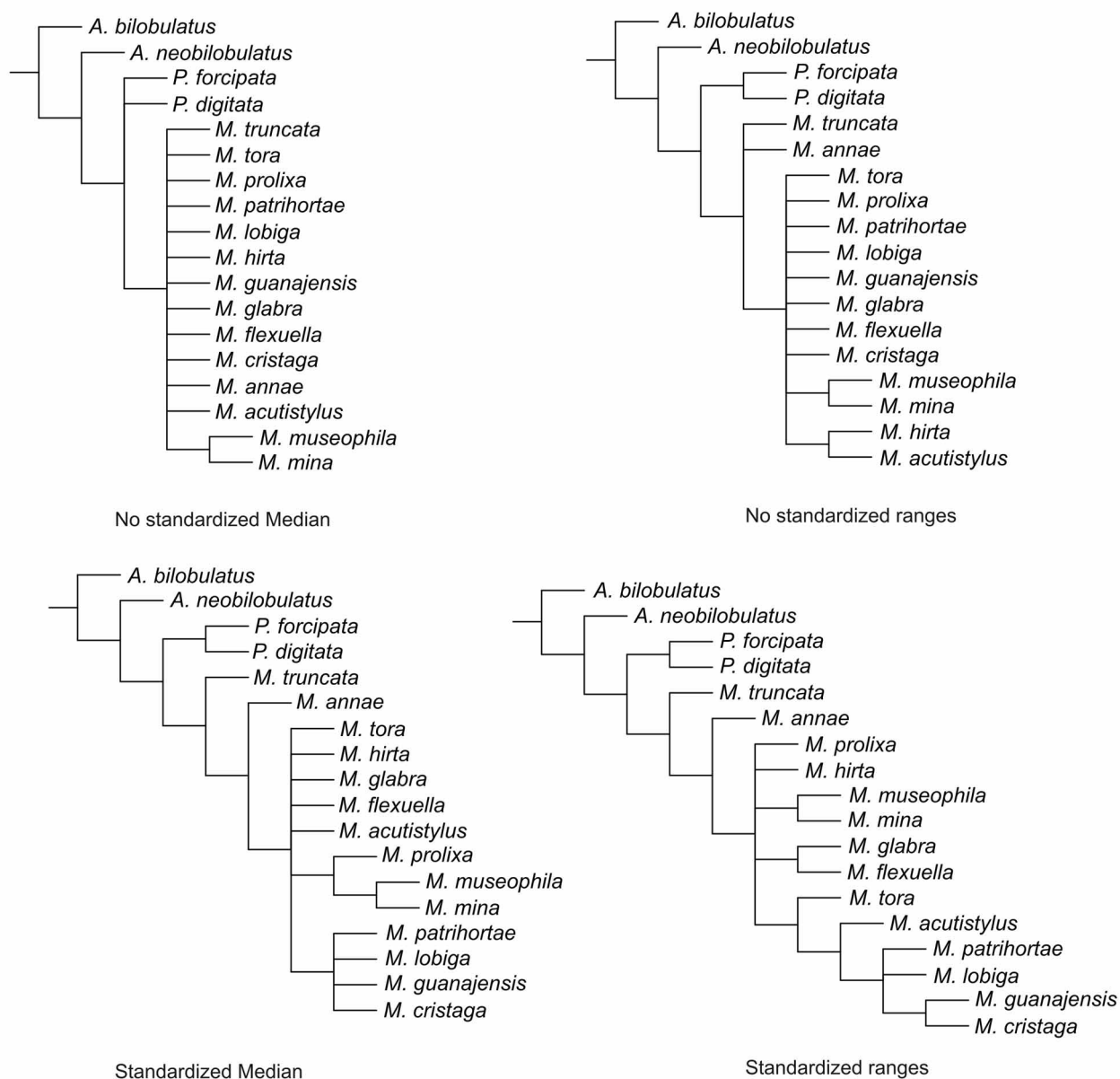
Wing (Fig. 2). VR 1.26–1.45, 1.39 [1.43]. C extension 12–24, 20 [22] long. Brachiolum with 1 seta; R with 0–2, 1 [0]; R1 with 0–1, 0 [0]; R4+5 with 0–1, 0 [0]; squama with 2–7, 4 [4] setae.

Legs. Spur of fore tibia 32–44, 39 [32] long (9); spurs of mid tibia: 15–17, 17 [17] and 17–24, 20 [24]; of hind tibia: 12–17, 16 [15] and 29–42, 37 [39] long. Width at apex of fore tibia 24–32, 29 [27]; of mid tibia 24–37, 29 [29]; of hind tibia 32–47, 38 [39]. Comb with 9–12, 9 [9] setae. Lengths (in mm) and proportions of legs in Table 1.

TABLE 1. Lengths (in µm) and proportions of legs of *Mesosmittia museophila* sp. n. (male) ( $n = 8–10$ ).

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>
p <sub>1</sub>	380–450, 435 [420]	520–630, 575 [530]	240–290, 260 [260]	140–170, 155 [150]
p <sub>2</sub>	430–500, 470 [460]	470–550, 495 [490]	200–220, 210 [200]	100–120, 110 [120]
p <sub>3</sub>	450–540, 490 [490]	540–630, 580 [570]	300–320, 310 [300]	150–170, 170 [160]
	ta <sub>3</sub>	ta <sub>4</sub>	ta <sub>5</sub>	LR
p <sub>1</sub>	100–120, 115 [110]	70–90, 80 [70]	60–70, 70 [70]	0.43–0.49, 0.46 [0.49]
p <sub>2</sub>	80–100, 85 [90]	50–70, 60	50–70, 60	0.38–0.43, 0.41 [0.41]
p <sub>3</sub>	130–150, 140 [130]	70–80, 75 [80]	60–70, 70 [70]	0.49–0.58, 0.53 [0.53]
	BV	SV		
p <sub>1</sub>	2.90–3.16, 3.05 [3.03]	3.65–4.00, 3.76 [3.65]		
p <sub>2</sub>	3.55–3.94, 3.81	4.57–5.00, 4.75 [4.75]		
p <sub>3</sub>	2.93–3.27, 3.11 [3.09]	3.19–3.77, 3.51 [3.53]		

Hypopygium (Figs. 3–6). Without microtrichia on apex of “anal point”. Setae on tergite IX 9–15, 11 [9], laterosternite IX with 4–7, 5 [5] setae. Phallapodeme 37–54, 46 [54] long; transverse sternapodeme 74–103, 92 [96] long. Virga 27–42, 29 [29] long. Gonocoxite 169–203, 195 [196] long; length of gonocoxite to apex of inferior volsella/ length of gonocoxite 0.16–0.24, 0.22 [0.22], distance along inner margin from gonocoxite to apex of inferior volsella 71–91, 86 [91]. Ventral margin of gonocoxite with a notch. Gonostylus 83–105, 91 [91] long; crista dorsalis low, almost straight; megaseta 5–7, 5 [5] long. HR 1.86–2.23, 2.09 [2.15]; HV 2.07–2.61, 2.34 [2.59].

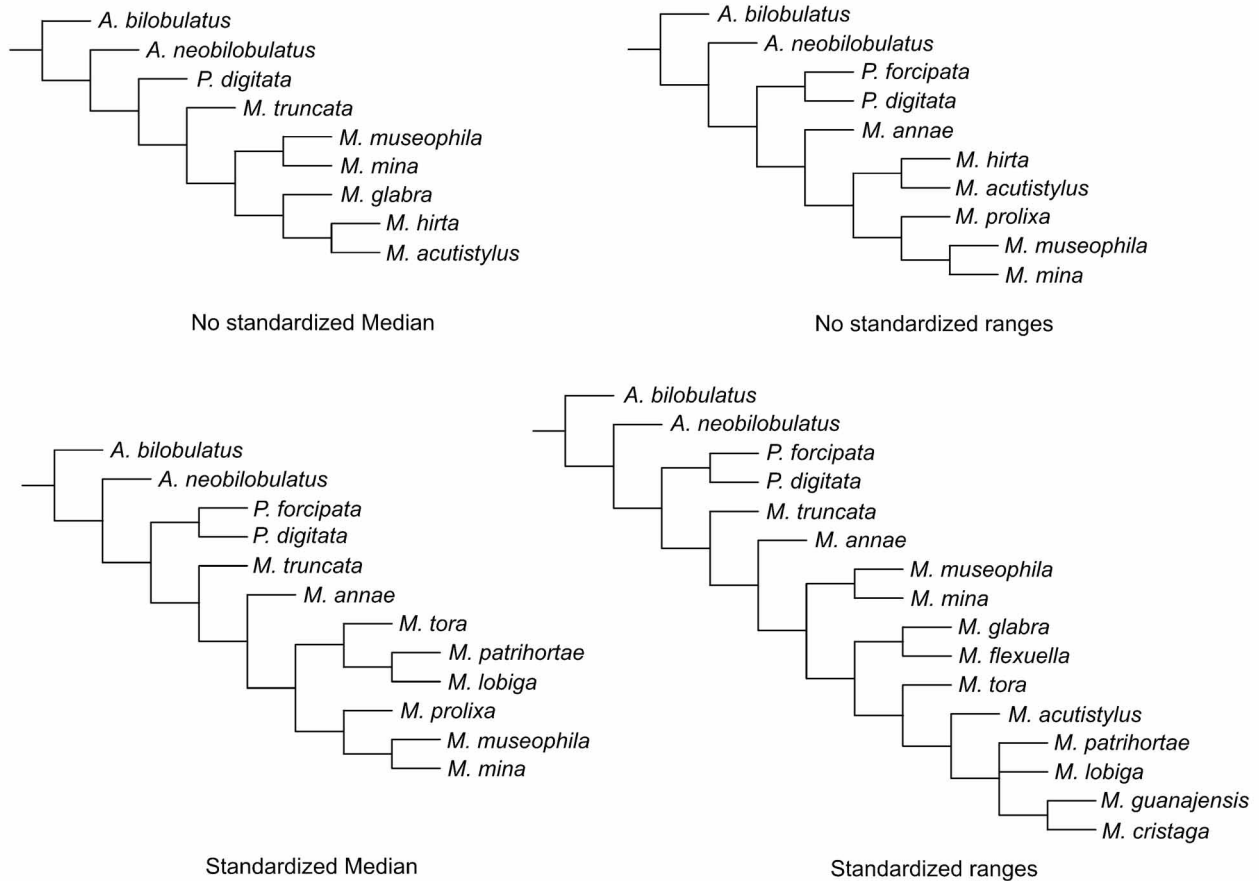


**FIGURE 7.** Strict consensus trees calculated for each set of trees obtained from each of the four data sets.

### Cladistic analysis

The analysis of each data set under different tree search strategies yielded several trees and are summarized in the strict consensus trees (Fig. 7) and the agreement subtrees (Fig. 8) respectively. The strict consensus and the agreement subtree obtained from the standardized ranges trees show the best resolution among the different data sets and

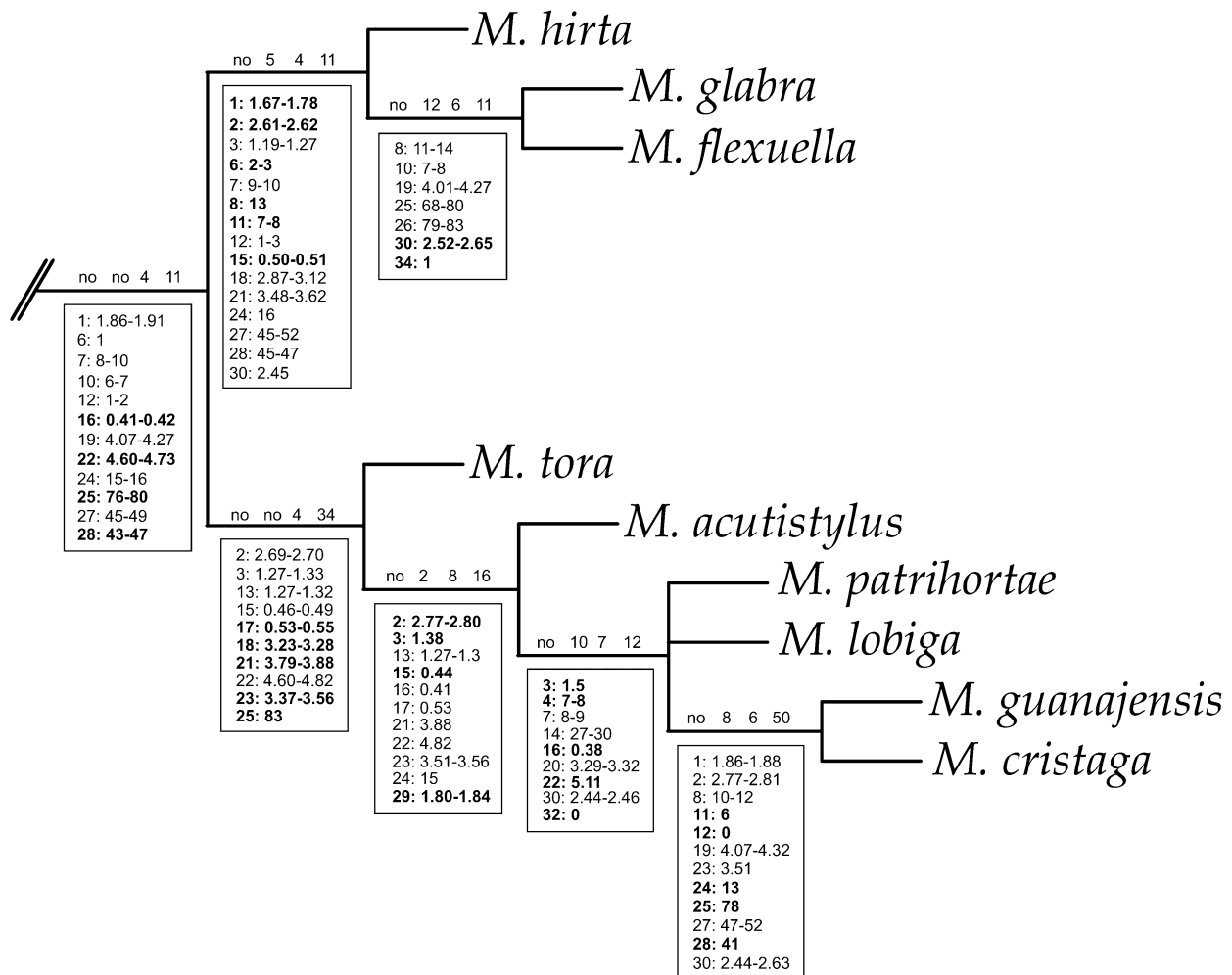
therefore is elected as the best hypothesis of relationships for the species of the genus *Mesosmittia*. The standardized ranges data set yielded two topologies and that with the best resolution (obtained under maximum parsimony and with implied weights K 10 to 16) is elected as the best hypothesis of relationships for the species of the genus *Mesosmittia* (Fig. 9).



**FIGURE 8.** Agreement subtrees calculated for each set of trees obtained from each of the four data sets.

This analysis suggests that the genus *Mesosmittia* is a monophyletic group supported by the character ‘total length/wing length’ of 1.86–1.94  $\mu\text{m}$  [character 1], ‘presence of 8 acrostichal setae’ [character 8], ‘presence of 4 prealar setae’ [character 9], presence of ‘4 setae on squama’ [character 11], character ‘C extension length’ of 30–41  $\mu\text{m}$  [character 14], character ‘Distance along inner margin from apex of gonocoxite to apex of inferior volsella’ of 39  $\mu\text{m}$  [character 28], ‘acrostichals starting just behind anteprepronotum’ [character 31], ‘parallel-sided medial longitudinal ridge’ [character 34] and ‘absence of anal point’ [character 35]. *Mesosmittia truncata* Sæther is the most basal species of the genus followed by *M. annae* Andersen & Mendes. The clade (*M. proluxa* Sæther (*M. museophila*, *M. mina* Sæther)) is the sister group of the remaining species. The species *M. hirta* Andersen & Mendes is the sister group of the species *M. flexuella* (Edwards) and *M. glabra* Andersen & Mendes and this clade is the sister group of the clade (*M. tora* Sæther, (*M. acutistylus* Sæther, (*M. lobiga* Sæther, *M. patrihortae* Sæther, (*M. guanajensis* Andersen & Mendes, *M. cristaga* Sæther))))). The characters and character states supporting the relationships here described are shown in Figure 9.

The new species *Mesosmittia museophila* is the sister group of *M. mina* and these two species are closely related to *M. proluxa*. The clade (*M. museophila*, *M. mina*) is supported by the synapomorphy ‘notch on the ventral margin of the gonocoxite’ present. The presence of this character in *M. mina* is not mentioned in the original description of this species and it was found by Professor Ole A. Sæther after the re-examination of the holotype. This clade is the sister group of *M. proluxa* sharing the synapomorphy ‘scarcely developed inferior volsella’ [character 33].



**FIGURE 9.** Cladogram obtained from the analysis of standardized ranges data set under equal weights (Length= 167.082; CI= 55.9; RI= 51.51; Fit= 22.3). Below nodes the characters and its optimized character states are shown, synapomorphies in bold. Continuous characters were transformed from the standardization to raw data for a better understanding. Above nodes from left to right: Absolute frequency, GC, Absolute Bremer support, Relative Bremer support.

## Discussion

In the revision of the genus *Mesosmittia*, Sæther (1985) proposed several hypotheses of relationships between the species belonging to this genus. *Mesosmittia prolixa* was proposed as the sister group of *M. mina* due to the shared presence of reduced inferior volsella and an apical projection of the gonocoxite. The species *M. tora*, *M. patrihortae* and *M. truncata* conformed another group defined by the similar form of their inferior volsella, the former species with a variable projection of the gonocoxite and the other two species having a more or less reduced inferior volsella. For this author, these species could be the sister group of the aforementioned group. Sæther considered the alternative hypothesis that these species could form a group, with the apical projection of the gonocoxite secondarily reduced in *M. patrihortae* and *M. truncata*. The species *M. acutistylus* was postulated tentatively as the sister species of *M. lobiga* plus *M. flexuella* and together forming the sister group of the other species, with no characters mentioned to support this proposal. The species *M. cristaga* is considered by Sæther (1996) as closely related to *M. patrihortae*, but the former species possesses a more strongly developed crista dorsalis, more numerous setae on squama, higher  $BV_3$  and presence of only 2 setae on the laterosternite.

The analysis performed in this study partially recovers some of the hypotheses of relationship proposed by Sæther (1985). The species *M. mina* is closely related to *M. prolixa* since the former is the sister species of *M.*



*museophila* and together form the sister group of *M. prolixa*. The character state “reduced inferior volsella” proposed by this author as supporting this relationship is corroborated, in addition to other character states as shown in Figure 9. The relationships of *M. acutistylus* proposed by Sæther are partially recovered since this species is the sister group of the clade that contains *M. lobiga* among others. Finally, though the species *M. cristaga* is not the sister group of *M. patrihortae*, both belong to the same clade, although the former is closely related to *M. guanajensis*. Besides, this analysis showed *M. truncata* as the basal species of the genus followed by *M. annae* and *M. flexuella* as the sister species of *M. glabra*.

Several authors agree that quantitative characters have phylogenetic signal and are therefore useful for cladistic analysis (Felsenstein 1988, Wiens 2001, MacLeod 2002, de Bivort *et al.* 2010 and literature cited therein). As the genus *Mesosmittia* is quite homogeneous (Sæther 1985), the use of this type of characters is justified since no other evidence is available to establish hypotheses of relationship. Similar patterns in the external morphology of the species in this genus lead to the problem of finding enough discrete characters to perform a cladistic analysis. The systematics of *Mesosmittia* is based mainly on characters derived from the male genitalia and some quantitative characters such as the number of setae on squama, and antennal ratio. As continuous characters are much more insidious to code adequately without excessively biasing the results (Farris 1990, Stevens 1991), the choice of analyzing quantitative characters as such instead of applying some kind of codification procedure was based on the fact that in this way no prior assumptions were made.

Goloboff *et al.* (2006) define scaling as one of the most pervasive problems in the analysis of continuous characters. These authors mentioned two problems related to this kind of character (costs of transformations in different characters and the problem of different scalings yielding different trees) with no obvious solutions. They proposed the use of implied weights as a possible solution for these problems of scaling. In this study this possible solution was tested empirically by analyzing four different data sets. In both cases, using the median or ranges, the standardized data sets yielded better results. Analyzing each non-standardized data set separately, the trees obtained under implied weights were better than those under equal weights, showing that implied weights is a good solution for these problems. This analysis suggests that standardization is preferable to raw data. As several authors have pointed out (Sneath & Sokal 1973, Goloboff *et al.* 2006) standardization is a very complex issue, a fact that is corroborated in this study. Undoubtedly this topic needs more study but, until future studies elucidate these problems, the use of standardization is desirable as opposed to the use of raw data.

Concerning the expression of data by means of the median versus the use of ranges, these results showed that the second option is better. The calculation of the median of each range for every species, as in the case of any statistic descriptor, tends to minimize the differences between them. Thus, the use of any statistic descriptor as expression of continuous measurements to perform a cladistic analysis entails the loss of character information. The use of raw data is preferable to any statistic descriptor but, as is the case of the standardization discussed above, more studies will corroborate or not this asseveration.

## Acknowledgements

I wish to thank Professor Ole A. Sæther for his kindness, predisposition and suggestions in the comparison of the holotype of *M. mina* with the new species here described. I also wish to acknowledge corrections and suggestions made by the anonymous reviewers and Dr. Wojciech Giłka. Free availability of the program TNT (<http://www.cladistics.org/tnt.html>) is made possible by funding from the Willi Hennig Society. This paper was supported by grants PIP N° 5535 (CONICET), PICT N° 26298 (Agencia Nacional de Promoción Científica y Tecnológica).

## References

- Almeida, M. & Bisby, F. (1984) A simple method for establishing taxonomic characters from measurement data. *Taxon*, 33, 405–409.
- Andersen, T. & Mendes, H. F. (2002) Neotropical and Mexican *Mesosmittia* Brundin, with the description of four new species (Insecta, Diptera, Chironomidae). *Spixiana*, 25, 141–155.
- Archie, J. W. (1985) Methods for coding variable morphological features for numerical taxonomic analysis. *Systematic Zoology*, 34, 326–345.
- Brundin, L. (1956) Zur Systematik der Orthoclaadiinae (Dipt. Chironomidae). *Report of the Institute of Freshwater Research*,

*Drottningholm*, 37, 5–185.

- Chappill, J. A. (1989) Quantitative characters in phylogenetic analysis. *Cladistics*, 5, 217–234.
- Colless, D. H. (1980) Congruence between morphometric and allozyme data for *Menidia* species. *Systematic Zoology*, 29, 288–299.
- Cranston, P. S. & Humphries, C. J. (1988) Cladistics and computers: a chironomid conundrum? *Cladistics*, 4, 2–92.
- Cranston, P. S., Oliver, D. R. & Sæther, O. A. (1989) The adult males of Orthocladiinae (Diptera: Chironomidae) of the Holarctic region - keys and diagnoses. *Entomologica scandinavica* Supplement, 34, 165–352.
- de Bivort, B. L., Clouse, R. M. & Giribet, G. (2010) A morphometrics-based phylogeny of the temperate Gondwanan mite harvestmen (Opiliones, Cyphophthalmi, Pettalidae). *Journal of Zoological Systematics & Evolutionary Research*, DOI: 10.1111/j.1439-0469.2009.00562.x.
- Farris, J. S. (1970) Methods for computing Wagner trees. *Systematic Zoology*, 19, 83–92.
- Farris, J. S. (1971) The hypothesis of nonspecificity and taxonomic congruence. *Annual Review of Ecology and Systematics*, 2, 277–302.
- Farris, J. S. (1990) Phenetics in camouflage. *Cladistics*, 6, 91–100.
- Felsenstein, J. (1988) Phylogenies and quantitative characters. *Annual Review of Ecology and Systematics*, 19, 445–471.
- Goloboff, P. A. (1993a) Character optimization and calculation of tree lengths. *Cladistics*, 9, 433–436.
- Goloboff, P. A. (1993b) Estimating character weights during tree search. *Cladistics*, 9, 83–91.
- Goloboff, P. A., Farris, J. S. & Nixon, K. C. (2008a) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 1–13.
- Goloboff, P. A., Mattoni, C. & Quinteros, A. S. (2006) Continuous characters analyzed as such. *Cladistics*, 22, 589–601.
- Goloboff, P. A., Carpenter, J. M., Arias, J. S. & Miranda Esquivel, D. R. (2008b) Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics*, 24, 758–773.
- Goloboff, P. A., Farris, J., Källersjö, M., Oxelmann, B., Ramirez, M. & Szumik, C. (2003) Improvements to resampling measures of group support. *Cladistics*, 19, 324–332.
- Kieffer, J. J. (1918) Chironomides d'Afrique et d'Asie conservé au Muséum National Hongrois de Budapest. *Annales historico-naturales Musei nationalis hungarici*, 16, 31–136.
- MacLeod, N. (2002) Phylogenetic signals in morphometric data. In MacLeod, N. & Forey, P. L. (Eds) *Morphology, Shape and Phylogeny*. CRC Press. pp. 100–138.
- Mickevich, M. F. & Johnson, M. S. (1976) Congruence between morphological and allozyme data in evolutionary inference and character evolution. *Systematic Zoology*, 30, 260–270.
- Mickevich, M. F. & Farris, J. S. (1981) The implications of congruence in *Menidia*. *Systematic Zoology*, 30, 351–370.
- Pimentel, R. A. & Riggins, R. (1987) The nature of cladistic data. *Cladistics*, 3, 201–209.
- Rae, T. C. (1998) The logical basis for the use of continuous characters in phylogenetic systematics. *Cladistics*, 14, 221–228.
- Rohlf, F. J. & Sokal, R. R. (1965) Coefficients of correlation and distance in numerical taxonomy. *The University of Kansas Science Bulletin*, 45, 3–27.
- Sæther, O. A. (1977) Female genitalia in Chironomidae and other Nematocera: morphology, phylogenies, keys. *Bulletin of the Fisheries Research board of Canada*, 197, 1–211.
- Sæther, O. A. (1980) Glossary of chironomid morphology terminology (Diptera: Chironomidae). *Entomologica scandinavica* Supplement, 14, 1–51.
- Sæther, O. A. (1985) The imagines of *Mesosmittia* Brundin, 1956, with description of seven new species (Diptera, Chironomidae). *Spixiana* Supplement, 11, 37–54.
- Sæther, O. A. (1996) Afrotropical records of the orthoclad genus *Mesosmittia* Brundin (Insecta, Diptera, Chironomidae). *Spixiana*, 19, 289–292.
- Sæther, O. A. (2006) Japanese *Pseudosmittia* Edwards (Diptera: Chironomidae). *Zootaxa*, 1198, 21–51.
- Sneath, P. H. A. & Sokal, R. R. (1973) *Numerical Taxonomy: the principles and practice of numerical classification*. San Francisco: Freeman. 573 pp.
- Sokal, R. R. (1961) Distance as a measure of taxonomic similarity. *Systematic Zoology*, 10, 70–79.
- Sokal, R. R. & Rohlf, F. J. (1969) *Introduction to Biostatistics*. New York: Dover Publications Inc. 363 pp.
- Spies, M. (2006) Case 3344 *Pseudorthocladus* Goetghebuer, 1943 and *Mesosmittia* Brundin, 1956 (Insecta, Diptera, Chironomidae): proposed conservation of the generic names. *Bulletin of Zoological Nomenclature*, 63.
- Stevens, P. F. (1991) Character States, Morphological Variation, and Phylogenetic Analysis: A Review. *Systematic Botany*, 16, 553–583.
- Strait, D. S., Moniz, M. A. & Strait, P. T. (1996) Finite Mixture Coding: A New Approach to Coding Continuous Characters. *Systematic Biology*, 45, 67–78.
- Strenzke, K. (1950) Systematik, Morphologie und Ökologie der terrestrischen Chironomiden. *Archiv für Hydrobiologie* Supplement 18, 207–414.
- Thiele, K. (1993) The Holy Grail of the Perfect Character: The Cladistic Treatment of Morphometric Data. *Cladistics*, 9, 275–304.
- Thorpe, R. S. (1984) Coding morphometric characters for constructing distance Wagner networks. *Evolution*, 38, 244–355.
- Wang, X. H. & Zeng, L. (1990) Two new species of *Mesosmittia* from China (Diptera: Chironomidae). *Acta Entomologica Sinica*, 33, 486–489.
- Wiens, J. J. (2001) Character analysis in morphological phylogenetics: problems and solutions. *Systematic Biology*, 50, 689–699.

**APPENDIX 1.** List of characters, character states and coding used in the cladistic analysis of the genus *Mesosmittia* Brundin. Quantitative characters were treated as standardized and no standardized ranges and standardized and no standardized Median (see text for further details).

---

Quantitative characters:

- 1- Total Length/Wing Length
- 2- Wing Length/Length of Profemur
- 3- Antennal ratio
- 4- Number of Temporal setae
- 5- Number of Clypeus setae
- 6- Number of Anteprenotal setae
- 7- Number of Dorsocentral setae
- 8- Number of Acrostichal setae
- 9- Number of Prealar setae
- 10- Number of Scutellar setae
- 11- Number of Squamal setae
- 12- Number of Radial setae
- 13- Venarum Ratio (VR)
- 14- C extension
- 15- Leg Ratio 1 (LR<sub>1</sub>)
- 16- Leg Ratio 2 (LR<sub>2</sub>)
- 17- Leg Ratio 3 (LR<sub>3</sub>)
- 18- Beinverhältnisse 1 (BV<sub>1</sub>)
- 19- Beinverhältnisse 2 (BV<sub>2</sub>)
- 20- Beinverhältnisse 3 (BV<sub>3</sub>)
- 21- Schenkel- Scheine- Verhältnis 1 (SV<sub>1</sub>)
- 22- Schenkel- Scheine- Verhältnis 2 (SV<sub>2</sub>)
- 23- Schenkel- Scheine- Verhältnis 3 (SV<sub>3</sub>)
- 24- Number of setae on Tergite IX
- 25- Phallapodeme Length
- 26- Sternapodeme Length
- 27- Virga Length
- 28- Distance along inner margin from apex of gonocoxite to apex of inferior volsella
- 29- Hypopygium ratio (HR)
- 30- Hypopygium value (HV)

Qualitative characters:

- 31- Acrostichal setae: 0 on mid scutum; 1 starting just behind anteprenotum
  - 32- Preapical projection of Gonocoxite: 0 absent; 1 weakly projected; 2 strongly projected
  - 33- Inferior volsella: 0 well developed; 1 scarcely developed
  - 34- Shape of medial longitudinal ridge: 0 absent; 1 parallel sided; 2 tapering to blunt apex
  - 35- Anal point: 0 present; 1 absent
  - 36- Notch on the ventral margin of the gonocoxite: 0 absent; 1 present
-