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Crane flies - three families or one?

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Abstract. Arguments defending the "one family system" (i.e., Tipulidae comprising 3 subfamilies: Tipulinae, Limoniinae and Cylindrotominae) against the "three families system" (Tipulidae, Limoniidae, Cylindrotomidae) are given, mainly derived from the history of studies of Tipulomorpha.

Key words: crane flies, Tipulomorpha, Tipulidae, Limoniinae, Cylindrotominae.

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Some of my European colleagues have asked me why I group all crane flies into a single family (Tipulidae s.l.) instead of recognizing three separate families: Tipulidae s.s., Limoniidae and Cylindrotomidae. The most honest response would be "because that is what my teachers, J. Speed ROGERS and Charles P. ALEXANDER, did". Although long aware of this difference in taxonomic treatment, I never gave much thought to why it existed.

The three families of crane flies recognized by some taxonomists correspond exactly to the three subfamilies recognized by others. That is, the families, or subfamilies, are differentiated by the same respective sets of characters. Clearly, then, it is a matter of a difference in taxonomic opinion. My opinion has been influenced by the opinions of those whose studies of crane flies I turned to most often for answers relating to my own work. Accordingly, I think it could fairly be said that taxonomic opinion is largely a matter of historical precedent.

If that is so, a survey of the historical development of the concept of family, as applied to crane flies, could be instructive. LINNAEUS was not troubled with families. He did not deal with large numbers of species in his orders, and it sufficed for him simply to divide his orders into genera and their species. The idea that genera could be arranged in groups having similarities at a level below the order began to emerge late in the 18th century and early in the 19th. LATREILLE, for example, developed the concept of family-group in the early 1800's. He recognized a family Tipulariae in 1802, the name subsequently being

emended to Tipulidae and credited to LEACH (1817 or 1819). Under the present Code (ICZN, Art. 11-f; 1985), however, family Tipulidae is attributed to LATREILLE.

Early dipterists, such as MEIGEN, LOEW and BELING in Germany, WALKER in England, BELLARDI in Italy, BERGROTH in Finland, and OSTEN SACKEN chiefly in the United States, viewed the crane flies as a single family, although MACQUART classified them as Tipulidae longipalpes and Tipulidae brevipalpes as early as 1838.

Separation of the short-palped crane flies into a family Limnobiidae (based on *Limnobia* MEIGEN, 1818), later corrected to Limoniidae (based on *Limonia* MEIGEN, 1803), began in Europe about 1900. Families Tipulidae, Limoniidae (including *Trichocera*) and Cylindrotomidae were included, for example, in the Catalogus Dipterorum by KERTÉSZ, in 1902. Despite this ealier usage, SÉGUY, in the Traité de Zoologie (1951), credited North American entomologist MALLOCH with authorship of Limnobiidae (in a 1917 paper, in which MALLOCH also separated Bolitophilidae, Macroceridae and Platyuridae from Mycetophilidae). (That is, MALLOCH was something of a "splitter".)

In this classification of Diptera "based upon larval and pupal characters", MALLOCH did not reveal what characters he found reliable enough to constitute a family difference. In fact, he conceded that "It is difficult to separate the larvae and pupae of the two families". Recognition of two or three families of crane flies (as distinct from Tanyderidae and Ptychopteridae, sometimes called, respectively, the primitive and phantom crane flies) did not catch on in North America. Perhaps this was because only two years after MALLOCH's paper, ALEXANDER's first major work (i.e., Part I of The Crane-Flies of New York) appeared, with tipuline, limoniine and cylindrotomine crane flies all in Tipulidae.

North American entomologists, including all of those dipterists who worked on the taxonomy of crane flies prior to ALEXANDER's time, had consistently used the family name Tipulidae in the broad sense. This was true, for example, of OSTEN SACKEN (1887; and the dates indicated are only those of some major published work, not necessarily the first or last one by a named author), COMSTOCK (1895, with Tanyderidae included), COQUILLETT (1900), DOANE (1900), JOHANNSEN (1901), ALDRICH (1905), HOWARD (1905), WILLISTON (1908) and JOHNSON (1909). MALLOCH's (1917) paper just mentioned was, in fact, the one notable exception. By the mid-1920's, ALEXANDER's influence was surely being felt and can clearly be seen in such later works as CURRAN's (1934) The Families and Genera of North American Diptera.

Similarly, use of the three-family classification was never favored in England. This can be seen in the works of MIALL (1893) and EDWARDS (1914), prior to the ALEXANDER years, and in IMMS' famous textbook, from its first edition in 1921 to its tenth in 1977, and in such faunal papers on crane flies as those of KILLINGTON and HOBBY (1938) and COE (1950). I think this was due in large measure to the influence of F. W. EDWARDS (1914, and in many subsequent publications). EDWARDS dealt with the faunas of Asia, Africa and South America, in addition to Europe. (And here I would add parenthetically that I think studying a group world-wide can narrow or close taxonomic gaps perceived in a consideration of a more restricted or geographically limited fauna. This sort of world-view of Tipulidae, for an example, led ALEXANDER in 1929 to bring *Dicranomyia*, *Geranomyia*, *Rhipidia* and others together as subgenera in the genus *Limonia*.)

In Central Europe, the three-family concept was adopted by some dipterists but not others. LUNDSTRÖM (1907) in Finland, RIEDEL (1910) and ENDERLEIN (1912) in Germany and CZIŽEK (1911) in Moravia (Austria-Hungary) were four of the early crane-fly workers to use the three-family classification in major papers. RIEDEL in 1920 apparently switched to the one-family concept but later considered tipulines and limoniines separately. His 1920 paper was in a Swedish journal, and I suspect he was coerced by the editor.

I think it was a series of excellent taxonomic publications by P. LACKSCHEWITZ (in Latvia, 1925 to 1936, plus some posthumous papers) that strengthened the trend established by these four early students of crane flies and in turn greatly influenced subsequent workers in central and eastern Europe. LACKSCHEWITZ was soon followed by two more outstanding taxonomists of crane flies, E. N. SAVCHENKO in the U.S.S.R. (who in fact finished and published some of LACKSCHEWITZ's papers, as late as 1964, 28 years after the latter's death) and Bernhard MANNHEIMS in Germany. Both published extensively, SAVCHENKO's work being summarized in his volumes of the Fauna of the U.S.S.R. (1961-1973 on Tipulidae s.s., 1989 on Limoniidae) and Fauna of the Ukraine (1966-1987), and MANNHEIMS's in The Flies of the Palearctic Region (1950-1953).

Mention of two other highly productive students of crane flies, Brother Theowald (Theowald van LEEUWEN) and Pjotr OOSTERBROEK, both in Amsterdam, Netherlands, brings me more or less to the present. There are now a number of younger taxonomists of crane flies in the Netherlands and in central and eastern Europe, all using the three-family system. These include KRZEMIŃSKI, THEISCHINGER (who is now in Australia), ERHANDINCA, SLIPKA, STARÝ, MARTINOVSKY, MENDL, DUFOUR, VERMOOLEN, de JONG, TANGELDER and REUSCH.

In contrast, those twentieth-century Europeans favoring the broader understanding of Tipulidae, and working outside Britain, include PIERRE (1924, Fauna of France), SCHRÖDER (1925, Handbook of Entomology, in Germany), NIELSEN (1927, Denmark's Fauna), CRAMER (1968, in a faunal study, in Germany), and - most notably - Bo TJEDER, in Sweden, whose publications on crane flies span the years 1936 to 1979. STARÝ in Czechoslovakia, at first adopted the broader concept of Tipulidae (e.g., in his papers from 1968 to 1979), but his more recent publications use the three-family system. Similarly, MENDL, in Germany, initially used Tipulidae in the broad sense, 1971-1975, then switched to three families, 1976 to 1988.

What has been the attitude of dipterists outside Europe and North America? In seeking to answer this, I have concentrated on those who actually worked on the taxonomy of crane flies and, where possible, on those who published their views long enough ago not to have been strongly influenced by ALEXANDER. In Japan, these were MATSUMURA (1916) and ESAKI, HORI and YASUMATSU (1938). In India, BRUNETTI (1920); and in Indonesia, de MEIJERE (1911). In Australia, SKUSE (1889) and TILLYARD (1926, with *Trichocera* included in Tipulidae). In South America, there were REED (1888) and BRUCH (1939); and in Africa, WOOD (1952). Every one of these authors adopted the one-family concept of Tipulidae. Moreover, I was not able to find any author who did regard crane flies as belonging to three, or even two, families.

I would summarize this historical survey by pointing out that the three-family concept of the crane flies has pretty much been limited to central and eastern Europe. It has appealed mainly to taxonomists working with a geographically limited fauna (with the notable exception of SAVCHENKO, who dealt with both tipulines and limoniines of Asiatic U.S.S.R., as well as with those in Europe).

There seems also to be a relationship between the number of taxonomists specializing in such a restricted group and the taxonomic rank accorded the subject of their studies. (This may be seen most clearly in the classifications of vertebrates.) That is, the more one concentrates one's attention on a particular group of organisms, the more important that group seems to become. And if it is more important, one naturally emphasizes this by elevating it in taxonomic, or categorical, rank.

Another factor, I think, is that C. P. ALEXANDER, aware of the relatively numerous specialists on the crane flies in Europe, chose not to work on the European or West-Palearctic fauna. Accordingly, his influence, so profundly felt throughout the rest of the world, was less in Europe.

What kinds of arguments have been and can be advanced in support of one of these points of view or the other? As I mentioned ealier, in general the same sets of characteristics are used to separate respectively the subfamilies or families. Lists of supposedly differentiating characters are full of indecisive terms, such as "usually", "sometimes" and "frequently". The truly differentiating characters are few; and these give no clue to whether the separated taxa should be subfamilies or families.

In 1949, geneticist M. J. D. WHITE found what appeared to be a significant difference between tipuline and limoniine crane flies, in what he called their "genetic system". In his "group 1" of Nematocera, characterized by distance pairing of sex chromosomes in meiosis, he placed the Tipuloidea - that is, the Tipulidae s.s., the Cylindrotomidae and the Trichoceridae, but "with the exception of the Limoniidae, which cytological evidence suggests are best regarded as a distinct family outside the limits of group 1". He placed the limoniids provisionally in his "group 2", which included also Psychodidae, Simuliidae, Culicidae and Chironomidae, families in which sex chromosomes are not evident. WHITE did concede that the small sex chromosomes might have become attached to the ends of autosomes, as happens in some species of *Drosophila*. One might also argue that he based his conclusions on an inadequate sample. Group 1 was based on one European species of *Tipula* and one of *Ctenophora*, but includes some 4000 species in many genera. And group 2 was based on one European species of *Limonia (Dicranomyia)* and one of *Thaumastoptera*, as far as the Limoniidae were concerned, but that group includes over 11000 species in a huge number of genera. The point here is that very few species of Tipulidae s.l. have been examined cytologically.

Much more recently, WOOD and BORKENT, in the third volume of the Manual of Nearctic Diptera (1989: 1342-1344), have criticized the three-family view of crane flies adopted by HENNIG, but more particularly HENNIG's inclusion of Trichoceridae with those three in Infraorder Tipulomorpha. They found the nine character states that HENNIG regarded as synapomorphies of trichocerids and crane flies to be either symplesiomorphies or misinterpretations based on doubtful homologies, and the like. They proposed instead

that the Infraorder Tipulomorpha includes only the family Tipulidae, with its three subfamilies united by two larval synapomorphies: (1) "posterior margin of head capsule desclerotized and shallowly to deeply notched", and (2) "head capsule capable of complete withdrawal into thorax". While I agree with this aspect of their cladogram of Diptera, I have to disagree with their first character used to separate Tipulomorpha from all other flies. This is "mandible with prostheca on articulated lobe ('lacinia mobilis' of PILGRIM 1972) (plesiomorphic)" and thus to be expected in the Tipulidae, versus "prostheca arising directly from median surface of mandible (apomorphic)". In the genera of crane flies known to me, the prostheca, or brustia as it is sometimes called, is not on an articulated lobe; and in a search of the literature I was unable to find any species in which such articulation was clearly the case.

I think that the dipterists holding to the three-family understanding of crane flies and those who put them all into one family would agree that tipulines, limoniines and cylindrotomines are all more closely related to each other than any one of them is to any family outside the Tipulomorpha, as defined by WOOD and BORKENT. This is what we would expect if they had a common phylogenetic origin. It is likely that the opposing views can continue to co-exist peacefully. But I prefer Tipulidae in the broader sense because I think that systematic biology is more concerned with similarity than with uniqueness or difference. And considering the three taxa of crane flies as families draws attention to their few differences and at least to some extent overlooks their many similarities.