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Abolition of Alamirinae and ultimate rejection of Wasmann's theory of hermaphroditism in Termitoxeniinae (Diptera, Phoridae)

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Abstract. Alarmirinae females are the initial flying stages of the stenogastric stages of Termitoxeniinae, prior to the shedding of the wing membranes. This flying stage is described for *Termitophilomyia braunsi* (Wasmann, 1900), along with the male — the latter having been caught in copula. The subfamily Alamirinae is abolished. The genus *Alamira* Schmitz is retained for *A. termitoxenizans* Schmitz, 1951 and *A. mellea* Borgmeier, 1963. *Alamira peckorum* (Disney & Peterson, 1983) probably belongs to *Termitostroma* Reichensperger, 1931. At least some of the Afrotropical species of *Perissa* Borgmeier, 1967 probably belong to *Syntermitoxenia* Schmitz, 1936, but *P. tinglei* Disney, 1990 clearly belongs to a different genus. *Perittophora* Disney, 1990 appears to be a valid genus. The Oriental *Perissa orientalis* (Disney & Peterson, 1983) and *P. georgei* Disney, 1989 probably belong to *Odontoxenia* Schmitz, 1915. The type species, *P. pakistanensis* Borgmeier, 1967, is only known in the male sex, and so cannot yet be assigned to its correct genus of Termitoxeniinae. The description of the male of *T. braunsi* brings the number of Termitoxeniinae species now known in the male sex to seven. Wasmann's theory of protandrous hermaphroditism in the Termitoxeniinae is finally rejected.

Key words. Diptera, Phoridae, Termitoxeniinae, hermaphroditism.

Introduction

Until Schmitz (1951) erected the subfamily Alamirinae, for his new species *Alamira termitoxenizans*, the peculiar Termitoxeniinae were treated as a family quite distinct from the Phoridae. Schmitz, however, proposed the Alamirinae as the link between the two families, to the extant that he rejected his formerly strongly defended opinion (e. g. Schmitz 1929) that the two families were quite distinct. Indeed Rohdendorf (1964, 1974), having overlooked Schmitz's 1951 paper, not only treated the Termitoxeniinae as a distinct family but he placed them in a separate Infraorder — the Termitoxeniomorpha.

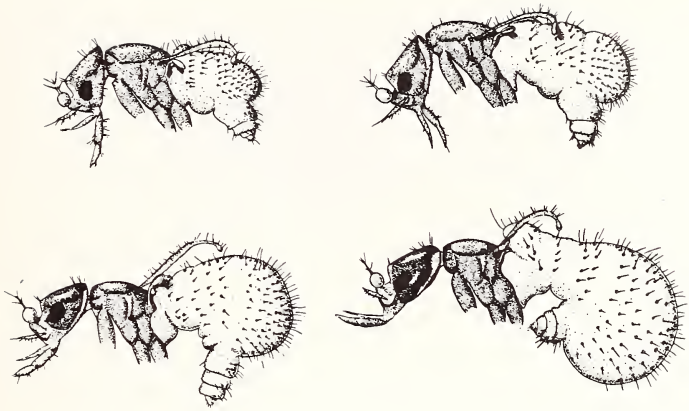
The Termitoxeniinae have been regarded as uniquely aberrant not so much for their morphological peculiarities as for a cluster of theories with regard to their development, as advanced by Wasmann (e. g. 1902, 1913). He originally proposed that these flies had dispensed with free-living larvae (his Ametabolism Theory), and suggested the stenogastric females (see below) hatched from the eggs. However, following the observations of Kemner (1922, 1926), who reported free-living (though short-lived) larvae emerging from the relatively enormous eggs after an incubation period in excess of three weeks, Wasmann eventually abandoned this theory. Unfortunately Rohdendorf (1964, 1974) ignored most of the West European literature on the Termitoxeniinae published after about 1920, and consequently misled Oldroyd (1964) and others.

Wasmann (1900) having initially treated the stenogastric forms as the males he modified this interpretation and proposed that the young, stenogastric adult undergoes a post-emergence development to the physogastric female. This development not only involves a differential expansion of the dorsal faces of some of the abdominal segments, with the result that the terminal segments are deflected forwards beneath the rest of the abdomen with the anus pointing anteriorly (Figs 1—2), but also changes in the musculature continue after emergence from the puparium (Wasmann 1902, Mergelsberg 1935). This development during the adult stage is an established fact, although much of the change in shape of the abdomen probably owes more to distension of the integument by the developing ovaries within than to any actual new growth of the integument itself.

Wasmann's most startling proposal was his theory of protandrous hermaphroditism, with the stenogastric stage being a functional male and the physogastric stage being a functional female. The evidence for this proposal was largely the complete failure of a number of field workers to obtain any males. In addition serial sections of the stenogastric stage showed a sperm-filled receptacle, at the end of a duct, while the ovaries still harboured immature eggs. By contrast the physogastric stage showed a well developed ovary with developing eggs. The sperm-filled sac and its duct were interpreted as a single testis and vas deferens (e. g. Wasmann 1913, Assmuth 1913). Others (e. g. Bugnion 1913, Silvestri 1920) interpreted the structure as a spermatheca. Controversy has ensued ever since. The majority has tended to accept Wasmann's interpretation, following the detailed studies by Mergelsberg (1935) in particular. The latter, however, failed to find any evidence of spermatogenesis in the so-called testis, and so postulated that this was completed in the pupal stage. He did, however, show that the so-called vas deferens had a cuticular intima. It has subsequently been pointed out (Disney 1989) that such a feature is compatible with it being a spermathecal duct but not with it being a vas deferens.

Like the Termitoxeniinae, the Alamirinae have only been known in the female sex, despite the description of several more species. However, it was recently proposed (Disney 1989) that the genus *Perissa* Borgmeier, 1967, only known in the male sex, were the missing males. This hypothesis proved to be correct (Disney 1990), and is established beyond doubt by the pairs caught in copula reported below.

The distinction between the Alamirinae and Termitoxeniinae, apart from speculations about the biology of the latter, has been based on two morphological features. First the terminal abdominal segments of the Termitoxeniinae are deflected ventrally, and during the post-emergence development of the adult they come to lie beneath the rest of the abdomen, with the anus pointing forwards (Figs 1—2). Second the wings are represented by wing "rudiments", such that the flies are flightless. That these appendages are wings was clearly demonstrated by Kemner (1937). However, Wasmann (e. g. 1902) did not even treat them as wing rudiments, but called them "die Appendices thoracales". This misled others (e. g. Séguy 1950) into treating these as wing rudiments, as opposed to wing stumps remaining after the shedding of the wing membranes. By contrast the terminal abdominal segments of the female Alamirinae are directed backwards, like other Phoridae, and the wings are fully developed. These distinctions feature in keys to families published when the Ter-



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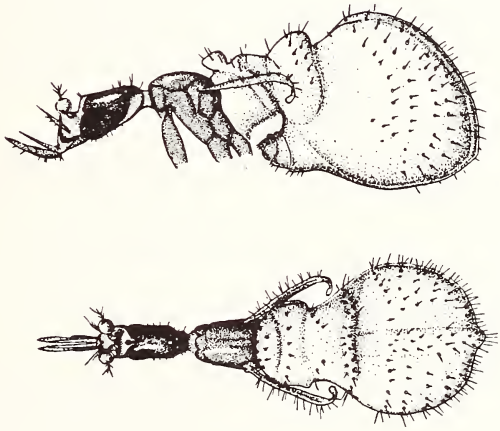

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Figs 1—2: *Termitophilomyia gracilis* (Reichensperger, 1931) female. 1, the development from the stenogastric to the physogastric stage; 2, mature physogastric stage in side and dorsal views. (from Mergelsberg 1935).

mitoxeniinae were still treated as a family (e. g. Brues et al. 1954). However, it is now known that female Alamirinae are prone to shedding their wing membranes, leaving stumps reminiscent of the wing "rudiments" of Termitoxeniinae (e. g. Disney & Peterson 1983). Indeed, critical examination of the wing rudiments of the latter in-

dicate that they too look like wing stumps rather than rudiments. However, ever since Wasmann (1900) it has been assumed that the Termitoxeniinae are flightless throughout their lives. Furthermore, when Schmitz (1951) proposed the subfamily Alamirinae he seems to have overlooked Kemner's (1932) report that in very young stenogastric females of *Javanoxenia punctiventris* (Schmitz, 1915) the terminal abdominal segments project rearwards. This oversight was despite its brief citation by Mergelsberg (1935).

It should be recalled that the classic interpretations of the Termitoxeniinae (e. g. Wasmann 1902, Mergelsberg 1935) were based on the laboratory study in Europe of material that had been preserved in the tropics by others. As reported by Mergelsberg (1935) sperm was most abundant in the preserved specimens of early stenogastrics examined by him. Because he was operating within the conceptual framework provided by Wasmann's theory of protandrous hermaphroditism, he appears not to have considered the simpler theory that the stenogastrics might have mated with males prior to shedding their wing membranes on taking up residence in the termite host's mound. The material examined by Wasmann, Mergelsberg and others had all been obtained by the excavation of termite mounds. This paper, however, presents evidence from specimens obtained while they were being observed (by M. S. C.) entering a termite mound or else they were caught outside the mound altogether. This fresh material has provided new data that directly challenge the Wasmann scenario. This is discussed below.

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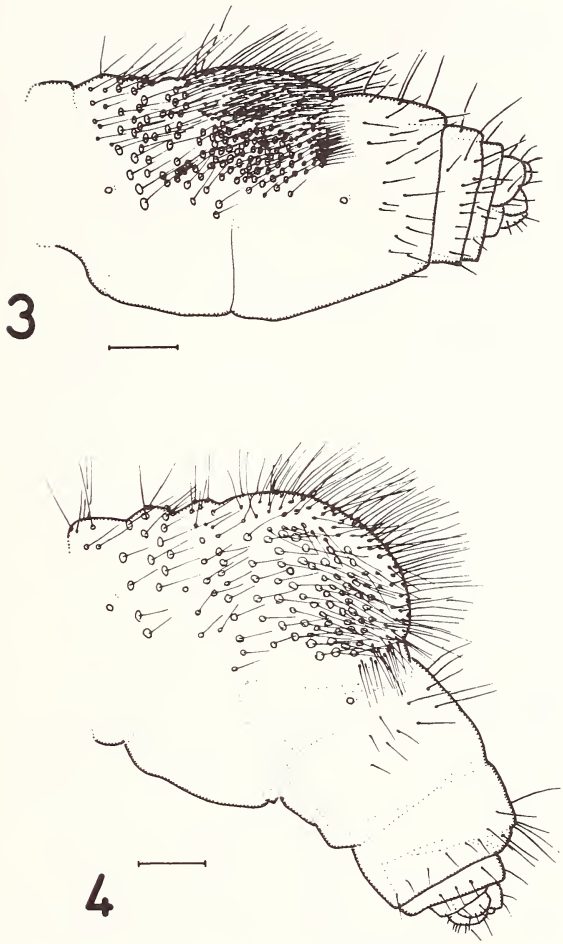
Termitophilomyia braunsi (Wasmann, 1900)

Termitoxenia braunsi Wasmann, 1900: 611. Holotype ♀, SOUTH AFRICA: Orange Free State (Natural History Museum, Maastricht) [not examined].

One of us (M. S. C.) has carried out extensive observations on this species arriving at the air vents of a mound of the termite *Odontotermes transvaalensis* (Sjostedt) in a garden in Harare, Zimbabwe. All these arrivals were in copula. They landed on the outer wall of the mound, up to 15 cm below the rim of an air vent. The males disengaged as the females immediately started ascending towards the vent. These females then entered the latter and, just below its rim, they shed their wing membranes. Detailed observations of the subsequent entry of the flies into the nest below, past the defending screen of termites, are being published elsewhere (Cumming in preparation). The arrival at the mound of the mating pairs took place in the morning only, between 0500 h and 1000h with the peak numbers typically between 0630 h and 0930 h.

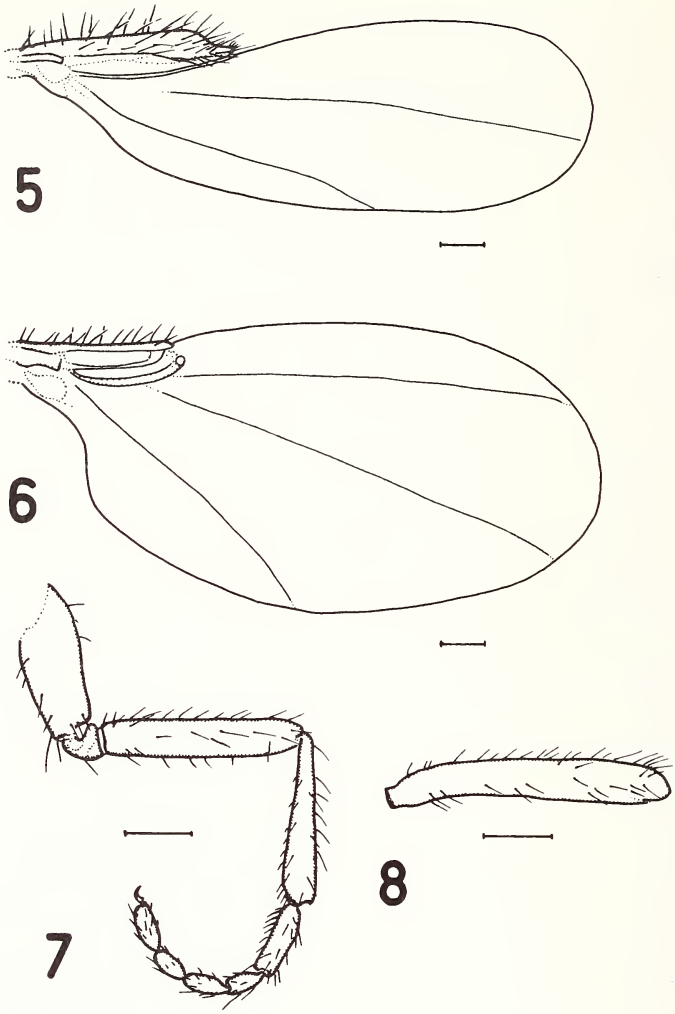
The females caught outside the termite mound were all early stenogastrics, with the anus directed rearwards (Fig. 3) and with the wing membranes still present (Fig. 5). Several males and a few females were also caught in water traps set near the mounds. These females tended to become distended by the uptake of water, leading to the deflection of the terminal abdominal segments (Fig. 4). We thus have specimens of the same species whose abdomens may be in the Alamirine or the Ter-



Figs 3—4: *Termitophilomyia braunsi* female, left faces of abdomen of fully-winged stenogastric stage. 3, a specimen caught at entrance to termite mound; 4, a specimen caught in a water trap, and distended by the uptake of water. (Scale bars — 0.1 mm).

mitoxeniine condition, and likewise the wings may be complete or represented by stumps only. The Alamirine-condition females will run to *Alamira peckorum* (Disney & Peterson, 1983) in the key to "Alamirinae" (Disney 1990). They differ in the relatively smaller apical portion of the costa, the presence of 1—3 bristles on the hypopleuron and the longer proboscis with more pointed labella. The male is described below for the first time.

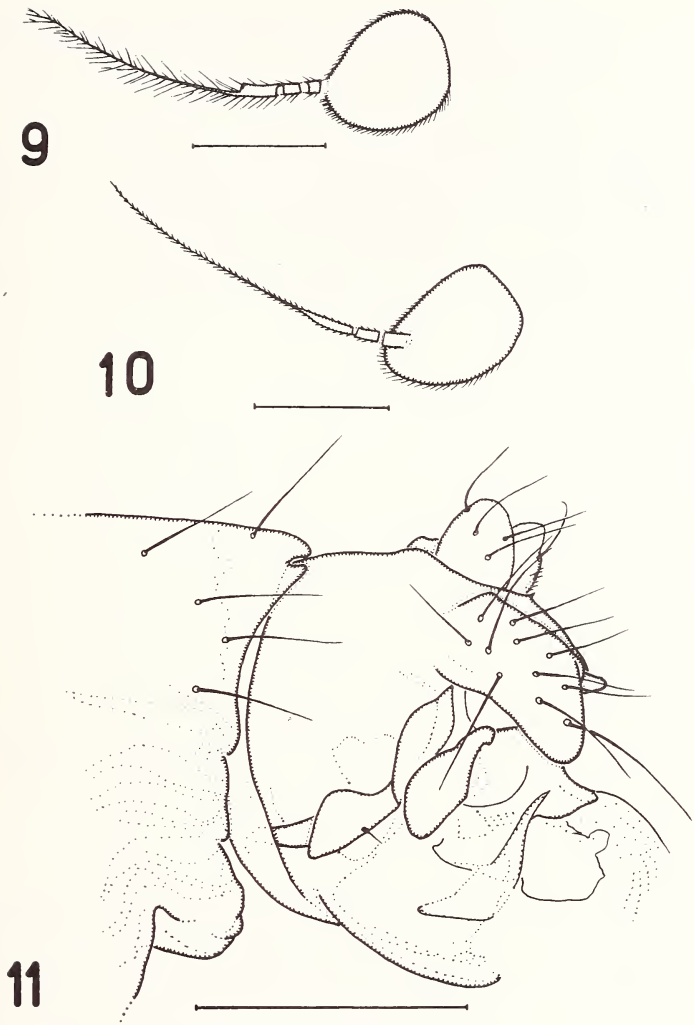
Male (Figs 6—8, 9, 11). Frons from pale brown to brown, being darker around ocelli, and with scattered hairs. Only those on vertex are distinctly differentiated.



Figs 5—8: *Termitophilomyia braunsi*. 5, right wing of stenogastric female; 6, right wing of male; 7, posterior face of male front leg; 8, anterior face of male hind femur. (Scale bars = 0.1 mm).

One or two fine bristles on each cheek and a single one on each jowl. The fusiform palps pale brown with fine bristles. Antennae brown and as Fig. 9. Proboscis relatively small, with pale labrum and paler labella which are rounded apically.

Thorax greyish brown, the scutellum and postnotum being darker. Scutum with irregular rows of fine dorso-central bristles and an irregular patch of notopleural plus pre-alar bristles. Scutellum with a posterior pair of fine bristles and an anterior pair of short hairs.



Figs 9—10: Males. 9, left antenna of *Termitophilomyia braunsi*; 10, left antenna of *"Perissa" tinglei*; 11, *T. braunsi* left face of hypopygium. (Scale bars = 0.1 mm).

Abdominal tergites brownish grey with hairs mainly restricted to posterior margins. Venter brownish grey and bare. Hypopygium as Fig. 11, and mainly greyish brown.

Legs brownish grey with darker mid coxae. Femora and tibiae slender. Hind femur as Fig. 8. Front leg as Fig. 7.

Wing as Fig. 6, with brownish grey veins and grey tinged membrane. Haltere mainly grey.

In the key to "Alamirinae" (Disney 1990) *T. braunsi* males run to couplet 15, *Perissa tinglei* Disney, 1990. However the latter has a shorter-haired arista with relatively long basal segments (Fig. 10) and a different hypopygium (Fig. 33 in Disney 1990).

Natural History: The specimens caught entering the mound of the termite *Odontotermes transvaalensis* confirm the association of this fly with this termite species (Wasmann 1900, Borgmeier 1964, Beyer 1965). It has also been reported with *O. latericius* (Haviland) in South Africa (Kistner 1982), and we report some with this species in Harare.

Material examined (by R. H. L. D.): numerous males and females, including three pairs caught in copula, ZIMBABWE, Harare, 19 Walmer Drive, Highlands, 17° 15' S, 31° 02' E, 26. VII. 1991, IX. 1991 (M. S. Cumming).

Discussion

It is clear that the female stenogastrics of *Termitophilomyia braunsi* caught outside the termite mound in Harare would be classified as Alamirinae in the existing literature. It is equally clear that these are merely the early, flying-stage, stenogastrics of a known Termitoxeniine species. It was recently concluded (Disney 1990) that the parallels between the Alamirinae and Termitoxeniinae "are so remarkable that they suggest the hypothesis that the Alamirinae is paraphyletic, by virtue of the exclusion of the Termitoxeniinae". We can now go further and abolish the Alamirinae altogether. The females are merely early-stage stenogastric Termitoxeniinae, prior to the shedding of the wing membranes and the deflection of the terminal abdominal segments. The males are the hitherto missing males of the Termitoxeniinae, which are evidently not resident in the termite host mounds, in contrast to the flightless-stenogastric stage and physogastric stage females. With the description of the male of *T. braunsi* above, the males of seven species are now known (Disney 1990). Wasmann's theory of protandrous hermaphroditism in the Termitoxeniinae is therefore finally rejected.

When the known "Alamirinae" species are treated as Termitoxeniinae, and are run through an annotated and modified (unpublished) version of Borgmeier's (1964) key to genera of Termitoxeniinae, then the following provisional conclusions are reached.

The genus *Alamira* is retained for *A. termitoxenizans* and *A. mellea* Borgmeier, 1963. *Alamira peckorum* probably belongs to *Termistroma* Reichensperger, 1931. At least some of the Afrotropical species of *Perissa* Borgmeier, 1967 probably belong to *Syntermitoxenia* Schmitz, 1936. However *P. tinglei*, especially in having palps which are not fusiform but which have bristles, is incompatible with any known Termitoxeniine genus. *Perittophora couturieri* Disney, 1990 also appears to be incompatible with any known Termitoxeniine genus. The Oriental *Perissa orientalis* (Disney & Peterson, 1983) and *P. georgei* Disney, 1989 probably belong to *Odontoxenia* Schmitz, 1915. The type species, *P. pakistanensis* Borgmeier, 1967, is only known in the male sex, and so cannot be assigned to its correct genus of Termitoxeniinae until its female is known. It is clear, however, that a complete revision of the Termitoxeniinae is now called for. One of us (R. H. L. D.) hopes to embark on this in the near future.

Our conclusion, that the "Alamirinae" represent the flying-stage stenogastric females plus the hitherto missing males of the Termitoxeniinae, is derived from the

observation of flies outside the host-termite's mound. It, perhaps, needs to be asked why they have been missed by previous workers interested in Termitoxeniinae.

It seems that Wasmann established a conceptual framework that militated against seeking the missing males outside the termite mounds. From the beginning he assumed the females were flightless at the time of their emergence, having implicitly interpreted the wing stumps as wing rudiments, and that they were exclusively resident in the termite mounds. The misinterpretation of the spermatheca as a testis seemed to be vindicated by Mergelsberg's (1935) report that young stenogastrics fixed (by Franssen) a few hours after emergence already had sperm in their so-called testes. Because of the assumption that Termitoxeniinae were always flightless, it seems possible that Franssen overlooked (or ignored) any flying stenogastrics and males of these tiny flies in his rearing containers. Furthermore if, as with *T. braunsi*, mating normally takes place early in the morning Franssen would have been more likely to have fixed the females after they had mated and shed their wing membranes. The few hours between emergence and fixation of the specimens were probably the critical few hours as far as the flying-stage stenogastric female and mating is concerned.

While Wasmann undoubtedly stimulated much research on Termitoxeniinae, a group he was the first to describe, his conceptual scheme also served to impede certain lines of investigation and so favour erroneous interpretations.

Zusammenfassung

Die Weibchen der Alamirinae sind Termitoxeniinae im flugfähigen frühen stenogastren Stadium, ehe sie beim Eindringen in den Termitenbau den Membranteil ihrer Flügel abwerfen. Dieses geflügelte Stadium wird für *Termitophilomyia braunsi* (Wasmann, 1900) beschrieben, ebenso das Männchen, das auf Grund von Kopulafängen der gleichen Art zugeordnet werden kann.

Die Subfamilie Alamirinae wird als Synonym der Termitoxeniinae eingezogen. *Alamira* Schmitz, 1951 wird als selbständige Gattung beibehalten und auf die Arten *A. termitoxenizans* Schmitz, 1951 und *A. mellea* Borgmeier, 1963 beschränkt. *A. peckorum* (Disney & Peterson, 1983) gehört wahrscheinlich zu *Termitostroma* Reichensperger, 1931. Wenigstens ein Teil der afrotropischen Arten von *Perissa* Borgmeier, 1967 gehört wahrscheinlich zu *Syntermitoxenia* Schmitz, 1936, aber *P. tinglei* Disney, 1990 gehört offenkundig einer anderen Gattung an. *Perittophora* Disney, 1900 scheint eine eigenständige Gattung zu sein. Die orientalischen Arten *Perissa orientalis* (Disney & Peterson, 1983) und *P. georgei* Disney, 1989 sind wahrscheinlich zu *Odontoxenia* Schmitz, 1915 zu stellen. Die Typusart, *P. pakistanensis* Borgmeier, 1967, ist nur im männlichen Geschlecht bekannt und kann deshalb noch keiner bestimmten Gattung der Termitoxeniinae zugeordnet werden.

Mit *Termitophilomyia braunsi* sind jetzt sieben Arten der Termitoxeniinae im männlichen Geschlecht bekannt. Die Theorie Wasmanns, die Termitoxeniinae seien protandrische Zwitter, wird endgültig verworfen.

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