A Fossil Thrips (Thysanoptera: Terebrantia) from a Cretaceous Deposit in Orapa[1]

Sandiso Mnguni[2,3,4], Shaw Badenhorst[3,4], and Marion Kathleen Bamford[3,4]

Evolutionary Studies Institute (ESI), School of Geosciences, University of the Witwatersrand, Johannesburg, Private Bag 3, Wits 2050, South Africa

J. Entomol. Sci. 60(3): 424–431 (July 2025)
DOI: 10.18474/JES24-50

Abstract A fossil thrips is described using a single compression fossil from an Upper Cretaceous deposit, the Orapa Diamond Mine in Botswana. It is the first record of a Cretaceous thrips from Africa. It is diagnosed by the following characteristics: general habitus; narrow, strap-like forewing and hindwing with fringe cilia; with forewing becoming progressively larger in distal third; and abdomen with dense transversal rows of microtrichia and terminal setae. The specimen is complete, except that the antennae are absent. At Orapa, the fossil thrips would have been possibly found feeding on leaves, stem or flower tissues of both gymnosperms and angiosperms in and around the crater lake. The fossil thrips adds to the taxonomic diversity of the Orapa fauna. Moreover, it broadens the knowledge of the diversity, geography and evolution of Mesozoic Thysanoptera.

Key Words epiclastic kimberlite, crater lake, Turonian, Africa, Southern Hemisphere

Thysanoptera are abundant in Cretaceous and Cenozoic amber deposits. As a member of the Superorder Paraneoptera dating back to the Triassic, Thysanoptera *sensu stricto* is a monophyletic group (Shmakov 2013) that is divided into two suborders, *viz.* Terebrantia and Tubulifera. There is still some dispute about their phylogenetic relationship, with some researchers advocating for an independent evolution from a common Psocoptera ancestor (Shmakov 2008). However, many researchers argue that Tubulifera evolved from Terebrantia, while some suspect that the latter is paraphyletic (Nel et al. 2011). Using molecular data, Buckman et al. (2013) recovered Tubulifera and the Terebrantia as sister clades. To date, the phylogeny of the Thysanoptera remains unresolved (Nel et al. 2011). Tubulifera only has 1 extant and 1 extinct family, while the remaining 8 extant and 4 extinct families belong to Terebrantia (Tong et al. 2019). Thysanoptera currently has 6,572 described species, with family Thripidae (primarily phytophagous) having the greatest contribution, with 2,263 species (Catalogue of Life, updated to 2024). They are small in size (ranging between 1–3 mm) and fragile in nature (similarly to Hemiptera lineages, such as aphids, psyllids and coccids). There are 180 fossil thrips described so far (Tong et al. 2019).

[1]Received 24 May 2024; accepted for publication 11 June 2024.
[2]Corresponding author (email: msandiso@gmail.com).
[3]ORCiD Numbers: 0000–0002–3077–2162 (Mnguni S.), 0000–0002–6651–9660 (Badenhorst S.) and 0000–0003–0667–130X (Bamford M.K.).
[4]Work (Institutional) Emails: Sandiso.Mnguni@wits.ac.za, Shaw.Badenhorst@wits.ac.za and Marion.Bamford@wits.ac.za.

Two fossil thrips described from Virginia and Kazakhstan, considered to be the oldest members of the family Triassothripidae Grimaldi & Shmakov (Grimaldi et al. 2004), are now formally known as the oldest thrips. These are *Triassothrips virginicus* Grimaldi & Fraser from the Late Triassic Cow Branch Formation of the United States of America and *Kazachothrips triassicus* Shmakov from the Late Triassic Tologoy Formation of Kazakhstan. Examples of Jurassic thrips include *Liassothrips crassipes* Martynov and *Karataothrips jurassicus* Sharov, both described from the Late Jurassic Karabastau Formation of Kazakhstan. Unfortunately, fossil thrips described from the Permian to the Tertiary periods have been lost during the Second World War (Ulitzka 2015), while many have been described and assigned without important diagnostic features. For example, *Rhipidothripoides involvus* Schliephake was described and named based on its hidden diagnostic features (Ulitzka and Mound 2017).

The Orapa Diamond Mine in Botswana is one of the major Cretaceous deposits in Africa. It has a large biota of compression and impression fossil plants and insects that have already been described by many researchers in the past (e.g., Bamford 1990, McKay 1990, Mnguni 2022, Waters 1990). It is one of 60 kimberlitic pipes in the area and is situated over a pair of adjoining diamondiferous epiclastic kimberlitic pipes measuring 1,600 m in length and 1,000 m in width (McKay and Rayner 1986, Rayner and McKay 1986). The kimberlitic eruptions of gas and steam resulted in a volcano that formed a large crater lake at the surface. In modern times, mining operations have removed the sediments, producing a large oval pit that is 80 m deep (Mnguni 2022). The crater lake at Orapa preserved both terrestrial and aquatic insects; including Coleoptera, Diptera, Hymenoptera, Blattodea, Orthoptera, Hemiptera, Thysanoptera, Neuroptera, Lepidoptera, and several other insect groups (see Brothers and Rasnitsyn 2003).

This work described the first fossil thrips from one of the major Cretaceous deposits in Africa. It is diagnosed as a thrips by its general habitus; distinct pronotum, mesonotum and metanotum; narrow, straplike forewing and hindwing with fringe cilia; forewing becoming progressively larger in distal third; and abdomen with dense transversal rows of microtrichia and terminal setae. The specimen adds onto the taxonomic diversity of the Orapa fauna. It also broadens the knowledge of the diversity, geography and evolution of Mesozoic Thysanoptera.

Materials and Methods

A single specimen of a damaged adult fossil preserved dorsally is described. The specimen was excavated at Orapa Diamond Mine (ODM) (21°18.465′S; 25°22.177′E) (Fig. 1), located in the northeast of Botswana, about 240 km due west of Francistown (McKay 1990, 1991). The deposit is approximately 824 km away from Johannesburg, South Africa. Based on the decay of 238 U in zircons in the kimberlite, the sediments are aged between 98.5 and 81.7 Ma, with a midpoint of 90.1 Ma (Haggerty et al. 1983) and 93.1 Ma (Davis 1977). Thus, the deposit is considered as Upper Cretaceous (Turonian, but possibly Cenomanian or Coniacian).

The fossil is a relatively well-preserved compression fossil, and only dorsal structures are visible. It was photographed in the Herbarium of the Evolutionary Studies Institute (ESI), at the University of the Witwatersrand, Johannesburg, South Africa. Observations and photography were done using an Olympus SZX7 binocular

Fig. 1. Top view of the Orapa Diamond Mine showing the open pit left after the removal of the crater lake facies and kimberlite (21°18.465′S; 25°22.177′E). Photo by I.J. McKay, June 2018.

microscope (with Olympus U-TV0.36XC camera). The specimen was examined under cross-polars to clarify the outlines, and non-polarized light was used at various angles to show relief. Polarizing filters were attached to swan-necked lights (the objective lens of the microscope), and were rotated to polarize the light and remove reflection. White paper was used to minimize light reflections and, subsequently, obtain better contrast on the photographs. Owing to the fragile nature and the oxidation of iron on the surfaces of the rocks, the fossil was studied without alcohol.

All the images were edited, adjusted and sharpened using Adobe Photoshop version 5.6.5.58 (Adobe Creative Cloud, University of the Witwatersrand, Johannesburg, South Africa). All the interpretations were observed using the microscope. All the measurements are scaled to 1 mm. This manuscript conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN).

Results

Systematic Palaeontology.

Class: Insecta Linnaeus, 1758
Order: Thysanoptera Haliday, 1836
Suborder: Terebrantia Haliday, 1836
Family: †Hemithripidae Bagnall, 1923
Genus: †*Hemithrips* Bagnall, 1923

Incertae sedis (Figs. 2A, B, 3A, B)

Diagnosis: General habitus; with distinct pronotum, mesonotum and metanotum; with narrow, strap-like, fringed wings bearing long hairs; forewing becoming progressively larger in its distal third; and abdomen with dense transversal rows of microtrichia and terminal setae. It is placed in extinct family Hemithripidae and

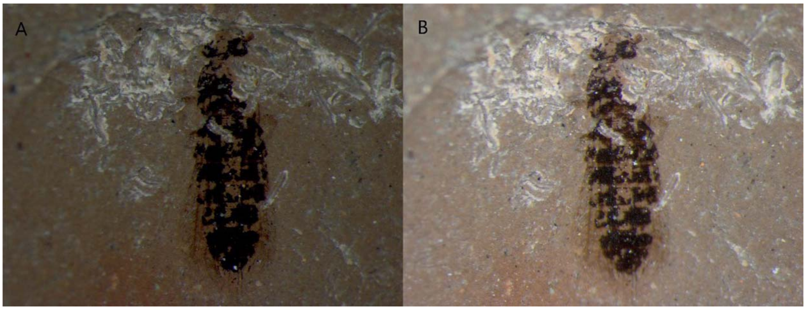

Fig. 2. Photograph of habitus, part, BP./2/25912, Orapa Diamond Mine, polarized light. (A) More contract, (B) more brightness. Scale bar = 1 mm.

genus *Hemithrips* due to an unusual shape of its head that largely resembles those of Hemiptera.

Type material studied: Alate adult, [specimen number BP/2/25912, Herbarium, Evolutionary Studies Institute (ESI), University of the Witwatersrand, Johannesburg, South Africa].

Type locality and horizon: Botswana, Orapa Diamond Mine, lacustrine deposit, Upper Cretaceous (Cenomanian–Campanian, possibly Turonian) (21°18.465′S; 25°22.177′E) (Davis 1977, Haggerty et al. 1983).

Description: Damaged specimen, missing antennae; with short, robust, cylindrical, lateral body shape, measuring 1.54 mm in length (from tip of vertex to tip of abdomen) and 0.46 mm in width (at the widest point of the abdomen). Head, thorax, and abdomen distinct.

Head slightly tilted, not retracted under pronotum, wider than long (0.18-mm long, 0.28-mm wide), narrowing anteriorly; widest at compound eyes; with curved gena and vertex. Compound eyes very large, semi-oval, protruding and completely occupying sides, distended ventrally. Antennae broken, with one visible thick barrel-shaped antennomere preserved in front of right eye. Mouthparts invisible, somewhat obscured by damage. Distinct neck wider than long (0.04-mm long, 0.24-mm wide), damaged on right side.

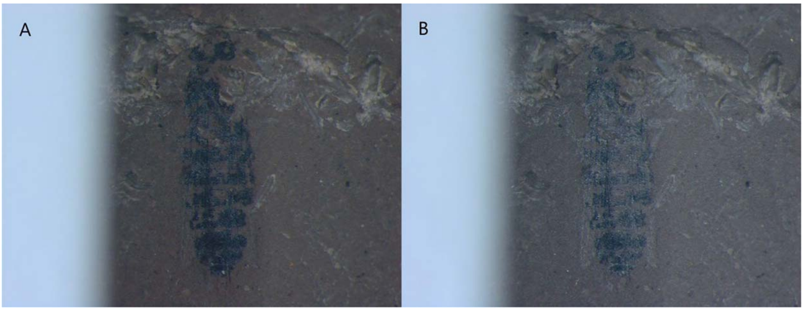

Fig. 3. Photograph of habitus, part, BP./2/25912, Orapa Diamond Mine, non-polarized light. (A) More contrast, (B) more brightness. Scale bar = 1 mm.

Thorax damaged on right side; slightly tilted, wider than long (0.34-mm long, 0.38-mm wide), slightly trapezoidal. Wings simple, narrow, straplike, folded, parallel-sided, becoming progressively larger in distal third, each with 1st and 2nd longitudinal veins lying close together, without cross veins, overlapping on abdomen, protruding over the end of the abdomen, each covered with microtrichia and clustered fringe cilia; preserved without forelegs, with midleg on left side, with hindleg on both left and right sides; all preserved legs angled, with thick femora, thin tibia.

Abdomen robust, almost symmetrical, longer than wide (1.06-mm long, 0.46-mm wide), with 7 visible abdominal segments; covered by wings bearing dense transversal rows of microtrichia; abdominal segment I damaged; abdominal segments I-IV lateral; abdominal segment VII tapering, with dense transversal rows of microtrichia and long terminal setae, without protruding tube.

Palaeoenvironment: The majority of extant thrips are phytophagous, while a few others are mycophagous or predaceous. Some of them damage crops and horticultural plants. A few are significant pollinators (Zhang et al. 2019). Notwithstanding that there would have been multiple switches in feeding habits during the evolution of thrips, leaf-feeding is considered to be a plesiomorphic character (ancestral), while flower-feeding is a derived state (Zhang et al. 2019). The thrips was preserved underneath Afriparosiphis *adamas* Mnguni, Badenhorst and Bamford, a species of an aphid described and informally named in another work. This suggests that aphids and thrips co-existed.

Remarks: Unfortunately, the specimen was damaged when the late Dr. I.J. McKay attempted to expose more of it. Initially, only the abdomen and a bit of the thorax were visible. Curiosity led to more exposure of the specimen. It turned out to be worth the effort; however, this exercise damaged the fossil in the end. Fortunately, it has enough characters to still warrant its description. We have decided not to name it because it lacks diagnostic characteristics.

Discussion

The work reports on a specimen belonging to Terebrantia. It shares morphological resemblance with *Cretothrips antiquus* Grimaldi (Grimaldi et al. 2004). Thrips are known to be one of the earliest gymnosperm pollen feeders and pollinators since the Late Permian (Peñalver et al. 2012). There are two species of *Gymnopollisthrips* Peñalver, Nel & Nel that have been reported to be early pollinators of Mesozoic gymnosperms. However, they became more prevalent in the Early Cretaceous. To support this notion, syninclusions of pollen have also been found in some specimens (Peñalver et al. 2012). Many living adult thrips can be found with one or more pollen grains on their bodies. However, pollination requires an experimental proof of pollen transfer. No study has been done on this. An accidental pollination remains possible, as is the case with many other insect pollinators.

Thrips have been recorded in many localities in the Early Tertiary, while few have been found in the Late Tertiary. Unfortunately, synapomorphies of the Thysanoptera, such as single mandible, tarsal segments being reduced to 1 or 2, and the pretarsus having claws reduced with a small eversible bladder (arolium) (Nel et al. 2010), are not visible on the specimen reported here. Nonetheless, it still offers more insights about the distribution of thrips. The specimen is rather an important find that shows that thrips have maintained their distinctive morphological characters for at least 100 million years. However, in modern days, thrips have become biologically diverse and inhabit various microhabitats (Nel et al. 2010, 2021).

According to Nel et al. (2007), apomorphies of extant taxa were possibly acquired in the Triassic. For example, thrips have unique mouthparts consisting of a labrum, labium, a pair of maxillary stipites, laciniae and left mandible; while lacking the right mandible (Grimaldi et al. 2004, Shmakov 2013). They use their mouthparts to probe and suck out fluid contents from plants. Another apomorphy involving the structure and function of forewings and mouthparts of thrips has caused researchers to infer that Thysanoptera are related to Hemiptera. While forewings and mouthparts suggest a close relationship between Thysanoptera and Hemiptera, fossils and molecular datasets suggests a much closer relationship between Thysanoptera and Psocodea (Buckman et al. 2013). In support of this, a pleiomorphic character of Thysanoptera includes having maxillary and labial palps that have been secondarily lost in Hemiptera.

Thysanoptera diversified and were widespread over the supercontinents of Gondwana and Laurasia in the Late Cretaceous (Ulitzka 2018). Their widespread distribution is confirmed by the presence of fossils in deposits that are far apart from each other. Extensive research has shown that extant genera have forewings and hindwings with straight fringe while fossil genera have wavy fringe (Tong et al. 2019). The wings (overlapping on the abdomen at rest to avoid an entanglement), together with setae, probably played a pivotal role in actively or passively trapping and transporting pollen, as most extant thrips are phytophagous (Shmakov 2013).

Researchers agree that the relationships of the suborders and families within Thysanoptera are well resolved. Zhang et al. (2019) recovered Thripidae as monophyletic, with 4 subfamilies within it, *viz.* Dendrothripinae, Sericothripinae, Panchaetothripinae, and Thripinae. Despite the monophyly of families and subfamilies described using morphological characters being largely validated by molecular data (Buckman et al. 2013), a much more robust phylogeny of Thripidae is still warranted. This is further highlighted by an increase in the descriptions of thrips. An increased taxonomic sampling has the potential to enhance our understanding of the evolution of thrips. Thrips are known to have a much higher diversity in tropical and subtropical regions than temperate regions (Zhang et al. 2019). Here, we attempt to contribute to an increased taxonomic sampling of the Thripidae, as the first step towards attaining the proposed task. Our contribution is interesting and important as the first fossil thrips from Africa. It probably flew in or was washed down into the crater lake at Orapa, was buried by mud, and subsequently became fossilized in the sediments. It presents valuable information pertaining the phylogeny, biogeography and evolution of modern Thysanoptera.

In conclusion, the phylogeny and evolution of Thysanoptera still needs to be explored more rigorously. Thysanoptera greatly diversified in the Late Cretaceous and were widespread over the supercontinents of Gondwana and Laurasia. The taxonomy and systematics of thrips is overly reliant on morphology. The new fossil thrips assigned to the Terebrantia is described using a single well-preserved specimen from Orapa Diamond Mine in Botswana. It is important as the first fossil record of Terebrantia from Africa, which provides important morphological information. It shows that the diversity and geographical distribution of thrips is greater than previously thought. In addition, this specimen adds to the taxonomic diversity of Orapa fauna. It also broadens our understanding of the diversity, geography, evolution and distribution of the Thysanoptera during the Cretaceous. The description of this fossil will hopefully help to elucidate relationships among extant taxa that diversified in the Late Cretaceous.

Acknowledgments

The authors thank The Office of the President of Botswana, Botswana National Museum (BNM) and De Beers Botswana Mining Company for the invitation and permission to collect and work on the fossil material from Orapa. The authors also acknowledge Mr. Jere Claase from Wirsam Scientific and Precision Equipment (Pty) Ltd. (Johannesburg, South Africa) for maintaining the Olympus microscope.

The support of GENUS: DSI–NRF Centre of Excellence in Palaeosciences [(DSI–NRF CoE–Pal) Grant UID 86073] toward this research is hereby acknowledged. Opinions expressed and conclusions arrived at in this publication are those of the authors and are not necessarily to be attributed to the sources of funding and support.

The authors declare that there are no potential conflict of interests; in a form of competing, financial, funding sources, owning of shares, and other payments.

SM dedicates this publication to his late supervisor, Dr. Ian James McKay (1963–2022) and his late former colleague, Ms. Lumka Anita Mdodana (1988–2023).

Contributions to this work by the authors are as follows: SM – Conceptualization; SM – Data curation; SM – Formal analysis; SM, MKB & SB – Funding acquisition; SM – Investigation; SM – Methodology; SM, SB & MKB – Project administration; SM – Resources; SM – Software; MKB & SB – Supervision; SB & MKB – Validation; SM – Visualization; SM – Roles/Writing - original draft; SM, SB & MKB – Writing - review and editing.

All the data sets related to this article will be shared with the audience upon request.

References Cited

Bamford, M.K. 1990. The angiosperm palaeoflora from the Orapa pipe, Botswana. Unpubl. PhD Thesis, Univ. Witwatersrand, Johannesburg, South Africa.

Brothers, D.J. and A.P. Rasnitsyn. 2003. Diversity of Hymenoptera and other insects in the Late Cretaceous (Turonian) deposits at Orapa, Botswana: a preliminary review. African Entomol. 11(2): 221–226. https://hdl.handle.net/10520/EJC32559.

Buckman, R.S., L.A. Mound and M.F. Whiting. 2013. Phylogeny of thrips (Insecta: Thysanoptera) based on five molecular loci. Syst. Entomol. 38(1): 123–133. https://doi.org/10.1111/j.1365-3113.2012.00650.x.

Davis, P.K. 1977. Effects of shock pressure on ^{40}Ar-^{39}Ar radiometric age determinations. Geochimica et Cosmochimica Acta 41(2): 195–205. https://doi.org/10.1016/0016-7037(77)90226-5.

Grimaldi, D., A. Shmakov and N. Fraser. 2004. Mesozoic thrips and early evolution of the order Thysanoptera (Insecta). J. Paleontol. 78(5): 941–952. https://doi.org/10.1666/0022-3360(2004)0782.0.CO;2.

Haggerty, S.E., E. Raber and C.W. Naeser. 1983. Fission track dating of kimberlitic zircons. Earth and Planetary Science Letters 63(1): 41–50. https://doi.org/10.1016/0012-821X(83)90020-1.

McKay, I.J. and R.J. Rayner. 1986. Cretaceous fossil insects from Orapa, Botswana. J. Entomol. Soc. Southern Africa 49: 7–17.

McKay, I.J. 1990. Cretaceous Carabidae (Coleoptera) from Orapa, Botswana. Unpubl. PhD Thesis, Univ. Witwatersrand, Johannesburg, South Africa.

McKay, I.J. 1991. Cretaceous Promecognathinae (Coleoptera: Carabidae): a new genus, phylogenetic reconstruction and zoogeography. Biol. J. Linnean Soc. 44(1): 1–12. https://doi.org/10.1111/j.1095-8312.1991.tb00603.x.

Mnguni, S. 2022. Upper Cretaceous Staphylinidae from Orapa Diamond Mine in Botswana. Unpubl. PhD Thesis, Univ. Witwatersrand, Johannesburg, South Africa.

Nel, P., D. Azar and A. Nel. 2007. A new 'primitive' family of thrips from Early Cretaceous Lebanese amber (Insecta: Thysanoptera). Cretaceous Res. 28(6): 1033–1038. https://doi.org/10.1016/j.cretres.2007.02.003.

Nel, P., E. Peñalver, D. Azar, G. Hodebert and A. Nel. 2010. Modern thrips families Thripidae and Phlaeothripidae in early Cretaceous amber (Insecta: Thysanoptera). Ann. Soc. Entomol. France. 46(1-2): 154–163. https://doi.org/10.1080/00379271.2010.10697651.

Nel, P., A.R. Schmidt, C. Bässler and A. Nel. 2011. Fossil thrips of the family Uzelothripidae suggest 53 million years of morphological and ecological stability. Acta Palaeontol. Polonica. 58(3), 609–614. https://doi.org/10.4202/app.2011.0016.

Nel, P., T. Schubnel, V. Perrichot and A. Nel. 2021. *Ankothrips*, the most ancient extant thrips genus (Thysanoptera: Melanthripidae). Papers in Palaeontol. 7(2): 825–837. https://doi.org/10.1002/spp2.1320.

Peñalver, E., C.C. Labandeira, E. Barrón, X. Delclòs, P. Nel, A. Nel, P. Tafforeau and C. Soriano. 2012. Thrips pollination of Mesozoic gymnosperms. Proc. National Acad. Sci. 109(22): 8623–8628. https://doi.org/10.1073/pnas.1120499109.

Rayner, R.J. and I.J. McKay. 1986. The treasure chest at Orapa Diamond Mine. Botswana Notes and Records 18: 55–61. https://journals.co.za/doi/pdf/10.10520/AJA052550590_803.

Shmakov, A.S. 2008. The Jurassic thrips *Liassothrips crassipes* (Martynov, 1927) and its taxonomic position in the order Thysanoptera (Insecta). Paleontol. J. 42: 47–52. https://doi.org/10.1007/s11492-008-1007-x.

Shmakov, A.S. 2013. Thrips (Insecta: Thysanoptera) from the Insect Limestone (Bembridge Marls, Late Eocene) of the Isle of Wight, UK. Earth and Environmental Science Trans. Royal Soc. Edinburgh 104(3-4): 317–325. https://doi.org/10.1017/S1755691014000097.

Tong, T., C. Shih and D. Ren. 2019. A new genus and species of Stenurothripidae (Insecta: Thysanoptera: Terebrantia) from mid-Cretaceous Myanmar amber. Cretaceous Res. 100: 184–191. https://doi.org/10.1016/j.cretres.2019.03.005.

Ulitzka, M.R. 2015. Two new species of Aeolothripidae from Baltic Tertiary amber (Insecta: Thysanoptera). Palaeodiversity 8: 89–94.

Ulitzka, M.R. and L. Mound. 2017. The fossil species *Merothrips dietrichi* (Schliephake) comb. n. redescribed and transferred from the genus *Heterothrips* (Thysanoptera). Zootaxa 4231(4): 573–576. https://doi.org/10.11646/zootaxa.4231.4.7.

Ulitzka, M.R. 2018. A first survey of Cretaceous thrips from Burmese amber including the establishment of a new family of Tubulifera (Insecta: Thysanoptera). Zootaxa 4486(4): 548–558. https://doi.org/10.11646/zootaxa.4486.4.8.

Waters, S.B. 1990. Cretaceous Diptera from Orapa, Botswana. Unpubl. PhD Thesis, Univ. Witwatersrand, Johannesburg, South Africa.

Zhang, S., L. Mound and J. Feng. 2019. Morphological phylogeny of Thripidae (Thysanoptera: Terebrantia). Invertebrate Systemat. 33(4): 671–696. https://doi.org/10.1071/IS19001.