Charles University

Faculty of Science

Study programme: Zoology

Branch of study: Zoology

Mgr. Michal Tkoč

Diversity, systematics, and phylogeny of families Opetiidae and Platypezidae (Diptera)

Diverzita, systematika a fylogeneze čeledí Opetiidae a Platypezidae (Insecta: Diptera)

DOCTORAL THESIS

Supervisor: doc. RNDr. Jakub Prokop, Ph.D.

Prague, 2021

ACKNOWLEDGEMENTS

I would like to thank to my supervisor, Jakub Prokop, for outstanding help and tolerance during my studies. I also thank very much to my wife Klárka Tkočová, daughter Emilka and son Eduard for their tolerance and support during my studies. My mother Ivana and father Karel are thanked for their financial and other support during my whole university studies, which began in 2005. My colleagues and friends, in alphabetical order, are thanked for their advice and other various help of many different aspects: Attila Balász, Csaba Balász, Petr Baňař, Miroslav Barták, Lukáš Blažej, Miroslav Čada, Albert F. Damaška, Martin Fikáček, Dale Greenwalt, Jiří Hadrava, Tereza Hadravová, Jiří Hájek, Christel Hoffeins, Hans-Werner Hoffeins, Peter J. Chandler, Pavel Chvojka, Josef Jelínek, Jan Ježek, David Kaspřák, Petr Kment, David Král, André Nel, Jan Macek, Lenka Macháčková, Igor Malenovský, Michal Mantič, Michael Mikát, Šárka Mikátová, Bohuslav Mocek, László Papp, Jiří Preisler, David Rédei, Jindřich Roháček, Rudolf Rozkošný, Toyohei Saigusa, Lukáš Sekerka, Anatole I. Shatalkin, Tomáš Sikora, Jeff Skevington, Jiří Skuhrovec, Zoltán Soltész, Gunilla Ståhls, Jaroslav Starý, Jan Ševčík, Petr Šípek, Jan Šumpich, Andrea Tóthová, Miloš Vála, Jaromír Vaňhara, Tomáš Vendl, Dominik Vondráček, Pavel Vonička, Tadeusz Zatwarnicki, David Zelený and many others. Special thanks go to the colleagues and friends who provided permission to use their photographs to this PhD thesis: R. Andrade, P. Bedell, P. Coin, D. Gavryushin, M. Hauser, S. Luk, J. Roháček, and K. Schulz.

AUTHOR STATEMENT

I declare that I have prepared this thesis independently and that I have provided all the information sources and literature used. My involvement in the research presented in this thesis is expressed through the authorship order of the included publications. This thesis has not been submitted for the purpose of obtaining of the same or another academic degree earlier or at another institution.

In Prague, 7th July 2021 Mgr. Michal Tkoč

TABLE OF CONTENTS

ABSTRACT

This doctoral thesis is focused on flat-footed fly families Opetiidae, Platypezidae and genus *Microsania* (Insecta: Diptera). The thesis consists of general introduction to the systematics, taxonomy, diversity, zoogeography, phylogeny, and biology of the flat-footed flies. Systematics and taxonomy are summarized based on historical as well as recent literature. Each important taxon is shortly introduced and information about its taxonomy, morphology, diversity, distribution, and biology is provided. The next two chapters deal with fossil species and research on species diversity. The following part is a summary and plan for future research. Final chapter consists of 9 published peer-reviewed articles (5 in impacted international journals and 4 in journals without impact factor).

The first article is a molecular phylogeny study of relationships between genera of flat-footed flies. The results show Platypezidae consisting of two well-supported clades, the first with the subfamilies Melanderomyiinae + Callomyiinae and the second formed by subfamily Platypezinae. Genus *Microsania* was resolved as a separate lineage distant from Platypezidae which clustered with Opetiidae as its sister group, both together forming a sister group to Platypezidae. The genus *Agathomyia* proved to be paraphyletic. Bifurcated setae on legs of adult Platypezidae were proposed as a new synapomorphy of the family, exclusive of *Microsania*. Outstretched wings and only a small overlap of their surfaces at resting position were considered as a new synapomorphy for the subfamily Platypezinae. Other phylogenetically important characters defining main clades were documented, and their relevance in phylogenetic studies is discussed. The current systematic concept of Platypezidae is discussed, and new phylogenetic hypotheses were proposed.

Second article is detailed description of the species *Callomyia triangulata* Tkoč, 2012 found in south China (Yunnan Province). The species is compared with the only other species of *Callomyia* known from the Oriental Region, *C. coei* from Nepal, from which it differs mainly by the thoracic and abdominal coloration. All relevant characters of the new species were illustrated and photographed. It is discussed, that both species are probably Palaearctic elements from the higher altitudes of the Oriental Region.

Third article is study of the biodiversity and faunistic of Romanian species of Opetiidae and Platypezidae, with 18 species recorded in this country. Three species are new records for Romania as *Agathomyia vernalis*, *Callomyia saibhira*, and *Lindneromyia hungarica*. The

male of *Callomyia saibhira* is diagnosed and redescribed. Information about distribution and biology of all 18 species is provided and figured.

Fourth article is thematically non-related to the main theme of this dissertation. It is a description of *Microphorites moravicus* (Dolichopodidae sensu lato) from rare Paleogene amber of Študlov locality (Moravia, Czech Republic).

Fifth article is a description of a new fossil species of Platypezidae, *Agathomyia eocenica*, from the middle Eocene of Kishenehn Formation (Montana, USA). It is the first known fossil species of *Agathomyia*. Diagnostic morphological characters were described and photographed in detail and compared with the recent species *A. antennata*.

Last four articles are biology, faunistic and biodiversity studies: (i) Records of *Polyporivora picta* from the Czech Republic and Greece, its larval biology and distribution in Europe; (ii+iii) Two articles with new records of Platypezidae from the Czech Republic, Bohemia and Slovakia; (iv) Biodiversity of Opetiidae and Platypezidae of the Jizerské hory Mts. and adjacent regions.

Key words

Opetiidae; Platypezidae; *Microsania*; flat-footed flies; smoke flies; systematics; diversity; zoogeography; distribution; phylogeny; biology

CZECH ABSTRACT

Tato disertační práce je zaměřena na stlačenkovité čeledi Opetiidae, Platypezidae a na rod *Microsania* (Insecta: Diptera). Práce obsahuje obecný úvod do systematiky, taxonomie, diverzity, zoogeografie, fylogeneze a biologie stlačenkovitých. Systematika a taxonomie jsou shrnuty na základě historické i současné literatury. Každý důležitý taxon je krátce představen a jsou poskytnuty informace o jeho taxonomii, morfologii, diverzitě, rozšíření a biologii. Další dvě kapitoly se věnují fosilním druhům a výzkumu druhové diverzity. Následuje shrnutí a plán budoucího výzkumu. Závěrečná kapitola se skládá z devíti publikovaných recenzovaných článků (5 v impaktovaných mezinárodních časopisech a 4 v časopisech bez impakt faktoru).

První článek je studie molekulární fylogeneze vztahů mezi rody stlačenkovitých. Ve výsledném stromu byla čeleď Platypezidae tvořena ze dvou dobře podpořených fylogenetických linií, první s podčeleděmi Melanderomyiinae + Callomyiinae a druhá tvořený podčeledí Platypezinae. Rod *Microsania* byl vyčleněn jako samostatná linie vzdálená od Platypezidae, která vykazovala příbuznost s čeledí Opetiidae jako sesterskou skupinou, přičemž obě skupiny společně tvořily sesterskou skupinu k čeledi Platypezidae. Rod *Agathomyia* byl vyhodnocen jako parafyletický. Rozvětvené sety na nohou dospělců Platypezidae jsou navrhovány jako nová synapomorfie čeledi, kromě rodu *Microsania*. Roztažená křídla a jen malé překrytí jejich povrchů v klidové poloze jsou považovány za novou synapomorfii podčeledi Platypezinae. Dále byly zdokumentovány další fylogeneticky důležité znaky definující hlavní fylogenetické větve a diskutuje se jejich význam ve fylogenetických studiích. Byla zde komentována současná systematická koncepce čeledi Platypezidae a byly navrženy nové fylogenetické hypotézy.

Druhý článek je podrobný popis druhu *Callomyia triangulata* Tkoč, 2012 z jižní Číny (provincie Yunnan). Tento druh byl srovnán s jediným dalším druhem *Callomyia* známým z orientální oblasti, *C. coei* z Nepálu, od kterého se liší hlavně zbarvením hrudi a zadečku. Všechny relevantní znaky nového druhu byly ilustrovány a vyfotografovány. V práci jsou považovány oba druhy za pravděpodobné palearktické prvky z vyšších nadmořských výšek v orientálním regionu.

Třetí článek je studie biodiverzity a faunistika rumunských druhů Opetiidae a Platypezidae s výsledkem 18 celkem zaznamenaných druhů. Tři druhy jsou pro Rumunsko novými záznamy: *Agathomyia vernalis*, *Callomyia saibhira* a *Lindneromyia hungarica*.

Samec *Callomyia saibhira* byl diagnostikován a redeskribován. Jsou zde poskytnuty informace o rozšíření a biologii všech 18 druhů a jejich fotografie.

Čtvrtý článek tematicky nesouvisí s hlavním tématem této disertační práce. Jedná se o popis druhu *Microphorites moravicus* (Dolichopodidae *sensu lato*) ze vzácného paleogenního jantaru z lokality Študlov (východní Morava, Česká republika).

Pátým článkem je popis nového fosilního druhu Platypezidae, *Agathomyia eocenica*, ze středního eocénu, formace Kishenehn (Montana, USA). Je to doposud první známý fosilní druh rodu *Agathomyia*. Diagnostické morfologické znaky byly podrobně popsány a porovnány s recentním druhem *A. antennata*.

Poslední čtyři články jsou biologické, faunistické a biodiverzitní studie: (i) Nálezy *Polyporivora picta* z České republiky a Řecka, jejich larvální biologie a rozšíření v Evropě; (ii + iii) Dvě studie s novými nálezy Platypezidae z České republiky, Čech a Slovenska; (iv) Biodiverzita čeledí Opetiidae a Platypezidae Jizerských hor a přilehlých oblastí.

Klíčová slova

Opetiidae; Platypezidae; *Microsania*; stlačenkovití; kouřomilkovití; systematika; diverzita; zoogeografie; rozšíření; fylogeneze; biologie

LIST OF INCLUDED PUBLICATIONS

This PhD thesis is based on the following articles published in renowned scientific journals:

1. Tkoč M., Tóthová A., Ståhls G., Chandler P. J. & Vaňhara J. 2017: Molecular phylogeny of flat-footed flies (Diptera: Platypezidae): Main clades supported by new morphological evidence. *Zoologica Scripta* **46**: 429–444.

2. Tkoč M. 2012: A new species of the flat-footed fly genus *Callomyia* (Diptera: Platypezidae) from South China. *Acta Entomologica Musei Nationalis Pragae* **52**: 289–296.

3. Tkoč M. & Roháček J. 2014: Diversity, distribution and biology of Romanian flat-footed flies (Diptera, Opetiidae and Platypezidae) with taxonomic notes on *Callomyia saibhira* Chandler. *Zookeys* **459**: 95–118.

4. Tkoč M., Nel A. & Prokop J. 2016: Discovery of a new species of the Cretaceous genus *Microphorites* Hennig, 1971 (Diptera: Dolichopodidae s. lat.) in Paleogene amber from eastern Moravia (Czech Republic). *Insect systematics & evolution* **47**: 181–193.

5. Greenwalt D. E., Bickel D. J., Kerr P. H., Curler G. R., Brown B. V., de Jong H., Fitzgerald S. J., Dikow T., **Tkoč M.**, Kehlmaier Ch. & Amorim D. S. 2019: Diptera of the middle Eocene Kishenehn Formation. I. Documentation of diversity at the family level. *Palaeontologia Electronica* **22.2.50A**: 1–56.

And on non-impacted peer-reviewed journals:

6. Tkoč M. 2011: New records of *Polyporivora picta* (Meigen, 1830) from the Czech Republic and Greece with notes on its larval biology and distribution in Europe (Diptera: Platypezidae). *Acta Musei Silesiae, Scientiae Naturales* **60**: 263–267.

7. Tkoč M., Mocek B. & Barták M. 2012: New records of the flat-footed flies (Diptera: Platypezidae) from the Czech Republic and Slovakia. *Klapalekiana* **48**: 269–274.

8. Tkoč M. 2016: New records of the flat-footed flies (Diptera: Platypezidae) from the Czech Republic and Bohemia. *Acta Musei Silesiae*, *Scientiae Naturales* **65**: 65–70.

9. Tkoč M., Roháček J., Preisler J. & Vonička P. 2020: Biodiversity of flat-footed flies (Diptera: Opetiidae and Platypezidae) of the Jizerské hory Mts, Frýdlant region, and Liberec environs (northern Bohemia, Czech Republic). *Sborník Severočeského Muzea*, *Přírodní Vědy* **38**: 27–54.

1. INTRODUCTION

Life and its diversity will always be of interest to scientists and biologists. Insects are the world's most diverse group of animals, making up more than 58 % of the known global biodiversity. They inhabit all habitat types, except the seas and oceans (with few exceptions) and play major roles in the function and stability of terrestrial and aquatic ecosystems. Globally, more than one million insect species are currently known and described (FOOTTIT & ADLER 2017).

Diptera are among the four most diverse insect orders (the other three are Coleoptera, Lepidoptera and Hymenoptera), current world number of extant species is more than 155,000 (STORK 2018, PAPE et al. 2011). This diversity is result of long evolutionary history. The current phylogeny of the group is summarized on Fig. 1. Traditionally, there are two major groups of Diptera: Nematocera and Brachycera. While Brachycera are monophyletic, Nematocera are a paraphyletic group. From a morphological and pedagogical point of view, this division is still used and justified. From a phylogenetical point of view, a different division is already used, and this is also reflected in the current taxonomy of the whole group. There are three major episodes of rapid radiation in the evolution of Diptera reflecting the following groups: lower Diptera (220 Ma), lower Brachycera (180 Ma), and Schizophora (65 Ma) (WIEGMANN et al. 2011).

Within Brachycera, four major monophyletic groups are recognized: Eremoneura (flies with three larval instars), Cyclorrhapha (flies that pupate in a puparium, the hardened skin of the last larval instar), Schizophora (flies that escape from their puparium using an evertable frontal pouch, the ptilinal sac) and Calyptratae (larger flies with wings that have an enlarged basal lobe, the calypter). Within Cyclorrhapha, the earliest branched group is the Phoroidea (named Platypezoidea according to some authors). Superfamily Phoroidea or Platypezoidea consists of 5 extant fly families: Lonchopteridae, Opetiidae, Platypezidae, Ironomyiidae, and Phoridae (Fig. 1).

The Platypezidae, flat-footed flies, are a small family of brachycerous flies comprising more than 250 species in 19 extant genera of worldwide distribution. The highest number of known genera occurs in the Nearctic and Palaearctic regions, 15 and 13, respectively (Table 5), and the platypezid fauna is best explored in these two zoogeographical regions. The adults live mostly in forested habitats and can be usually observed sitting or running rapidly on broad leaves or hovering above them. The adults of *Microsania* Zetterstedt, 1837 exhibit a special type of behaviour - both sexes are attracted to smoke of bonfires, sometimes

forming swarms in the smoke, where they have been reported to mate (SNODDY & TIPPINS 1968; CHANDLER 1978; MILBERG et al. 2015). All known larvae are mycophagous, feeding on fruiting bodies or fungal mycelia of a diverse array of fungal hosts (CHANDLER 2001; STÅHLS et al. 2014, 2015; ŠEVČÍK 2004, 2010). Although several cases of polyphagy are known, most of the species are monophagous or oligophagous. Larval morphology and biology of species from the following genera are unknown: *Opetia* Meigen, 1804; *Microsania*; *Grossoseta* Kessel and Kirby, 1968; *Platypezina* Wahlgren, 1910; *Metaclythia* Kessel, 1952 and *Pamelamyia* Kessel & Clopton, 1970.

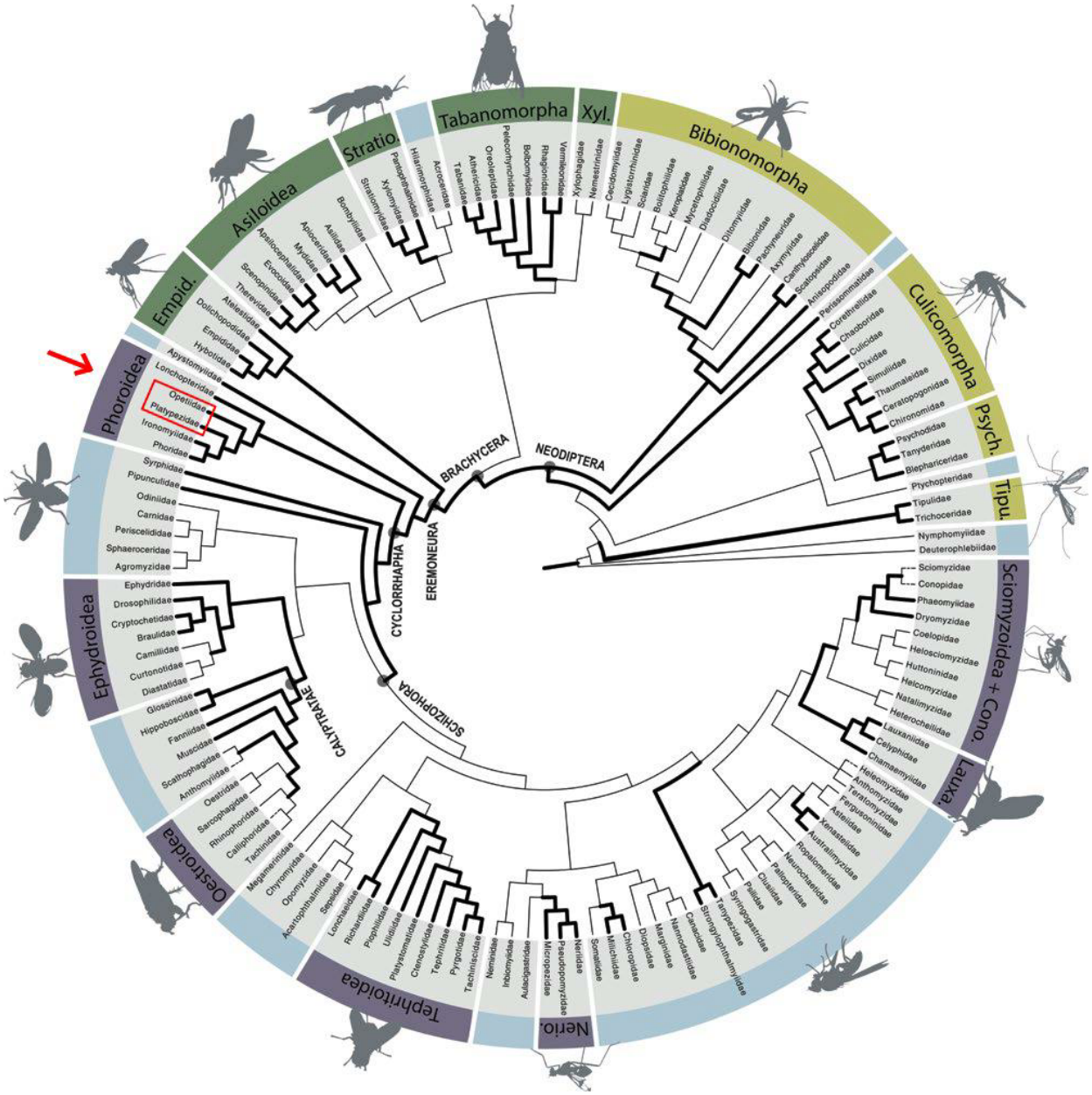

Figure 1. The Diptera tree of life with highlighted position of Opetiidae and Platypezidae. Tree adopted from WIEGMANN & YEATES (2017).

The aim of this thesis is to provide information about the diversity, systematics, and phylogeny of flat-footed families. The thesis is mainly based on molecular phylogenetic study (TKOČ et al. 2017 - **PUBLICATION 1**), supplemented with several taxonomical, biodiversity and faunistic studies. A special chapter is devoted to fossil species of Opetiidae and Platypezidae. The paper with description of fossil species, *Microphorites moravicus* Tkoč, Nel & Prokop, 2016 (Diptera: Dolichopodidae) is also included as one of the included publications (TKOČ et al. 2016 - **PUBLICATION 4**). It was found in rare Palaeogene Moravian amber (Študlov amber), unfortunately no Opetiidae or Platypezidae was found in this amber so far. It was included in this thesis to show the ability of the author to work with fossil species, even it belongs to another group of flies.

2. SYSTEMATICS, TAXONOMY, AND DIVERSITY

The first European monograph (CZERNY 1930) deals with 41 species (one species described as new) belonging to 6 genera. A key was created for all species, the key for genera was processed separately. There are 26 figure plates in the text, important for determination. A morphological description with drawings was created for each species, and distribution data were given. The work contains descriptions of larval stages and puparia of three species, including figures.

TANASIJTSHUK (1970) published the key to the European part of the former USSR (25 species, 6 genera). The first key in the current taxonomical concept was published by CHANDLER (1973) for the British Isles (25 species, 11 genera, 3 subfamilies). The work also contains a description of the generalized wing. A year later, CHANDLER (1974) extended this key (31 species, 12 genera) and revised the Palaearctic species of the genus *Callomyia*.

SHATALKIN (1985) published the key to the fauna of both families of the former USSR. There is a key of all 13 currently valid genera and for each genus there is also a key of individual species. Most descriptions of a total of 81 species are supplemented by schematic drawings. Further information on the distribution, findings, biology and phylogeny are in the accompanying text.

In the Catalog of Palaearctic Diptera (CHANDLER 1991), the replacement of the genus *Opetia* into a separate family Opetiidae (three species, two of which from Japan) was accepted for the first time. For the family Platypezidae there are three subfamilies, the subfamily Microsaniinae included the genus *Microsania* with 6 species, the subfamily Callomyiinae with three genera (*Platypezina*, *Agathomyia* and *Callomyia*) and a total of 35 species. The third subfamily Platypezinae included 8 genera (*Protoclythia*, *Seri*, *Bolopus*,

Polyporivora, *Kesselimyia*, *Platypeza*, *Paraplatypeza*, and *Linderomyia*) with a total of 29 species. Thus, according to the catalog, the fauna of the Palaearctic Region counts of 70 species from the Platypezidae family (CHANDLER 1991).

The Manual of Palaearctic Diptera summarized the findings and descriptions of both families (CHANDLER 1998, CHANDLER & SHATALKIN 1998). An important part is also the key of genera for adults and the key of larval stages and puparia. The taxonomy and classification are the same as in the monograph below commented.

The current systematics, presented in the European monograph of flat-footed flies (CHANDLER 2001), includes two families, the family Opetiidae with one species and the family Platypezidae with the subfamilies Melanderomyinae, Microsaniinae, Callomyiinae and Platypezinae comprising 12 genera with a total of 43 species. The current taxonomy of families follows the system presented in this work. The phylogenetic part is processed based on 52 morphological features. The taxonomic part includes morphological descriptions of adults of all species with emphasis on identification characters, morphological descriptions of known larval stages and puparia with a key as well as keys of adults to all genera. For each species, information on biology, its distribution and on the type material is given. Furthermore, in the work we can find a historical overview of the study of families, an overview of fossil finds and general morphological diagnoses of higher taxa (family, genus).

2.1 FAMILY OPETIIDAE

GRIFFITHS (1972) was the first to note the numerous differences of *Opetia* (Fig. 3a) from other platypezids, and HENNIG (1976) also commented on its distinctness from other Muscomorpha based on the male genitalia and antennal structure. CHVÁLA (1981) accepted these findings and proposed the monotypic family Opetiidae of which a detailed diagnosis was published later (CHVÁLA 1983). However, DISNEY (1987) considered *Opetia* not to belong to Cyclorrhapha based on presence of two-jointed arista and very short ejaculatory duct, which does not allow the circumversion[1] of the genitalia. CUMMING et al. (1995), proved this observation (DISNEY 1987) incorrect by finding in *Opetia* a short vasa deferentia but a long ejaculatory duct, thus demonstrating that the circumversion[1] of the genitalia is also present in *Opetia*.

Since the description of *Opetia nigra* Meigen, 1830, the family Opetiidae was known only as the Palaearctic group. Later AMORIM et al. (2018) described the first known opetiid known from Southern Hemisphere – *Puyehuemyia chandleri*. The description is based on a female

[1] Hypopygial circumversion, a term first proposed by FEUERBORN (1922) for the characteristic 360° clockwise rotation of terminalia of Cyclorrhapha. For more details see SINCLAIR et al. (2013) and GALINSKAYA et al. (2019).

specimen (Fig. 3b) collected in Valdivian Forest[2] in the Province of Osorno (Fig. 3e), south Chile. The three-articled condition of the stylus-like arista in *Puyehuemyia* (Figs 3c, 3d) corroborates the hypothesis that the two-articled condition in *Opetia* is independently derived, as it is in the Empidoidea and many schizophorans. *Puyehuemyia chandleri* has female terminalia typical of parasitoid groups, as does *Opetia*, although life history of both species is not known (according to AMORIM et al. 2018).

There are 5 species in two genera currently known in the world (Tab. 1). Species of the genus *Opetia* are members of the Palaearctic fauna (*Opetia nigra* in the western Palaearctic and three other *Opetia* species in the eastern Palaearctic, see Fig. 2).

Table 1. Family Opetiidae. Overview of all currently known extant species.

Genus	Species	Zoogeography	Author
Opetia	*nigra*	PA	Meigen, 1830
Opetia	*anomalipennis*	PA	Saigusa, 1963
Opetia	*alticola*	PA	Saigusa, 1963
Opetia	*ussuriensis*	PA	Shatalkin, 1985
Puyehuemyia	*chandleri*	NT	Amorim, Silva & Brown, 2018

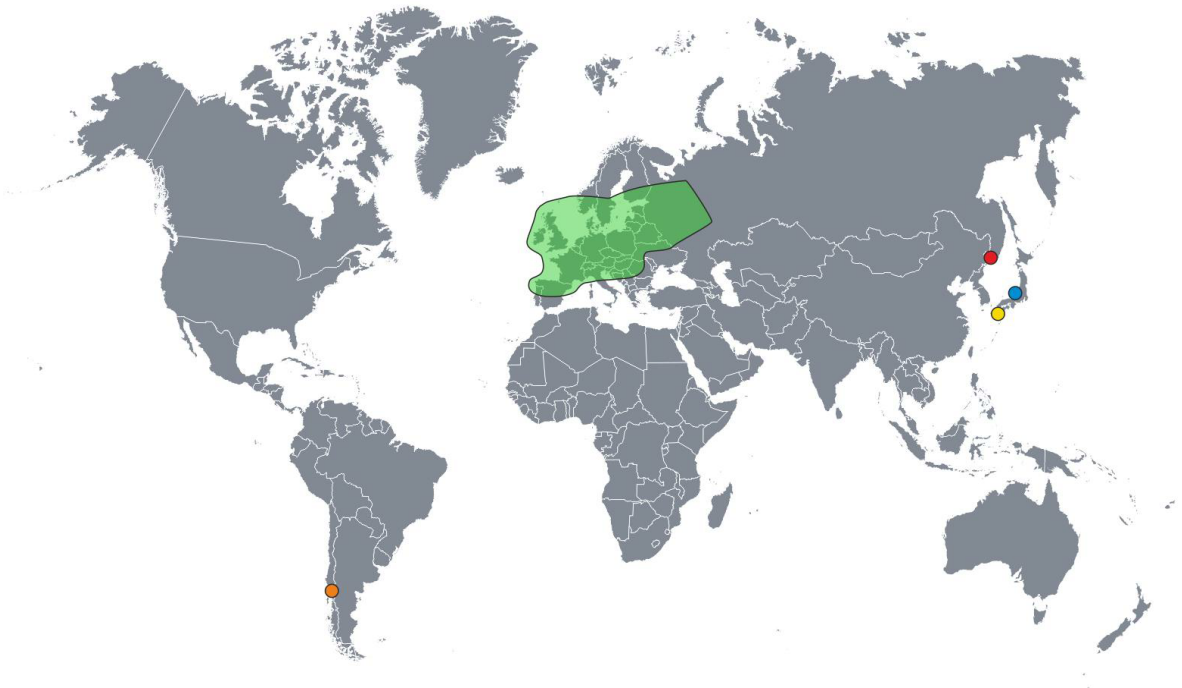

Figure 2. Distribution of family Opetiidae. ●: *Opetia nigra*; ●: *Opetia anomalipennis*; ●: *Opetia alticola*; ●: *Opetia ussuriensis*; ●: *Puyehuemyia chandleri*.

[2] The Valdivian temperate forest is an ecoregion on the west coast of southern South America, in Chile and extending into Argentina. The forests are named after the city of Valdivia.

Figure 3. Family Opetiidae and genus *Microsania*: a – *Opetia nigra*, male; b – *Puyehuemyia chandleri*, female; c – *P. chandleri*, female head with antenna sublaterally; d – *P. chandleri*, female head dorsally; e – habitat of *P. chandleri*; f – M. Tkoč showing technique of collecting *Microsania* sp.; g – *Microsania pectipennis*, female; h – *M. meridionalis*, male with mites under the abdomen. Photos b-e from AMORIM et al. (2018). Photos a, f, g by J. Roháček; photo h by R. Andrade.

2.2 GENUS *MICROSANIA* Zetterstedt, 1837

The world fauna of *Microsania* is represented by 22 species (Tab. 2). Its distribution has an interesting pattern. It is not limited to one or two zoogeographical regions as other platypezid genera; it is distributed in all six main zoogeographical regions. Both sexes of the genus have entirely dark body coloration. Larval biology is still unknown, but adults are usually attracted to smoke in which the males form aerial swarms (CHANDLER 2001). The females (Fig. 3g) are also occasionally attracted to smoke and both sexes can be collected by sweeping around or in smoke (Fig. 3f).

This genus is also present in the Neotropical Region (Brazil) and mainland south-east Asia (Thailand) (both M. Tkoč, unpublished data). There is one published record from Panama without further details (MELANDER 1922), and some undescribed species are known from Panama, Dominica, and Costa Rica (CHANDLER 2010).

Species of *Microsania* commonly have clusters of phoretic mites on the abdomen (Fig. 3h), unrecorded in other Platypezidae. CHANDLER (2001) and TKOČ et al. (2017) summarized all such observations. These mites are often occurring on fungi, compost, soil, manure, mammal, and bird nests. This might indicate possible terrestrial habitat of *Microsania* spp.

Table 2. Genus *Microsania*. Overview of all currently known extant species.

Species	Zoogeography	Distribution	Author
Microsania albani	OR	Philippines	Chandler, 1994
M. alticola	AF	Dem. Rep. of the Congo	Collart, 1955
M. arthuri	AUS	S. Australia, Tasmania	Chandler, 1994
M. australis	AUS	S. Australia	Collart, 1938
M. boycei	AUS	S. Australia	Chandler, 1994
M. capnophila	PA	N. Europe, Russia	Shatalkin, 1985
M. collarti	PA	Europe, European Russia	Chandler, 2001
M. fijiensis	AUS/OCE	Fiji	Sinclair & Chandler, 2007
M. fumida	PA	Russia	Shatalkin, 1985
M. ghesquierei	AF	Dem. Rep. of the Congo	Collart, 1936
M. hebridensis	AUS	Vanuatu	Chandler, 1994
M. imperfecta	NE	USA, Canada	(Loew, 1866)
M. lanka	OR	Sri Lanka	Chandler, 1994
M. meridionalis	PA	Europe	Collart, 1960
M. nigralula	AUS/OR	Australia, Papua New Guinea	Chandler, 1994
M. occidentalis	NE	USA, Canada	Malloch, 1935
M. pallipes	PA	Europe	(Meigen, 1830)
M. pectipennis	PA	Europe, Eur. Russia, Far E. of Russia	(Meigen, 1830)
M. straeleni	PA	Europe	Collart, 1954
M. tonnoiri	AUS	New Zealand	Collart, 1934
M. unicornuta	AUS/OR	Papua New Guinea	Chandler, 1994
M. vrydaghi	PA	Europe	Collart, 1954

2.3 FAMILY PLATYPEZIDAE

The family Platypezidae is basal cyclorrhaphous family of Diptera, belonging to the superfamily Phoroidea (= Platypezoidea). They are small brachycerous flies ranging from 1.4 to 10.0 mm in wing length. Their coloration is often black (males) or composed of black, orange, and grey (females), and some species have silvery grey reflective patterns. Males have holoptic eyes, the female eyes are dichoptic. The larvae could be flat or cylindrical. All known larvae are mycophagous and live burrowed in the fungus fruiting bodies tissue or under bark of dead trees on fungal mycelia; one species is gall-forming on sporocarps of a polypore – *Agathomyia wankowiczii* (Schnabl, 1884). Adults can be spotted on broad leaves in forested habitats, during fast erratic movements, females can be observed during oviposition on host fungi. Swarming behaviour is also recorded in some species.

The European flat-footed flies were treated by CHANDLER (2001), and some other recent studies of the world fauna (ROTHERAY et al. 2004; KRIVOSHEINA 2008a,b; TKOČ & VAŇHARA 2008a; CHANDLER 2010; CUMMING & CUMMING 2011; TKOČ 2012; STÅHLS et al. 2014, 2015; CUMMING & WHEELER 2016; REEMER & DE JONG 2016; TKOČ et al. 2017) have resulted in relatively detailed assessment of the morphology of adults and immature stages, including data on their biology, behaviour, phenology and distribution. ROTHERAY et al. (2004) provided generic descriptions of immature stages of 11 Holarctic genera. KRIVOSHEINA (2008a,b) reviewed the biology and provided detailed descriptions of the immature stages of Palaearctic species of *Callomyia* Meigen, 1804, *Polyporivora* Kessel and Maggioncalda, 1968, *Seri* Kessel and Kessel, 1966 and *Bolopus* Enderlein, 1932. Platypezidae belong to the group of cyclorrhaphous families without ptilinal fissure (together with Lonchopteridae, Opetiidae, Ironomyiidae and Phoridae) formerly named Aschiza, currently known as lower Cyclorrhapha (YEATES & WIEGMANN 1999). MCALPINE (1989) divided lower Cyclorrhapha into Platypezoidea (Lonchopteridae, Opetiidae, Platypezidae, Ironomyiidae, Phoridae, Sciadoceridae) and Syrphoidea (Syrphidae, Pipunculidae). Other authors classified lower cyclorrhaphan families differently, and thus, the concept of this group is not uniform (e. g., HENNIG 1948; GRIFFITHS 1972; DISNEY 1988). BROWN (1992) summarized previous concepts of taxon names Hypocera, Phoroidea and Phoridea and considered Phoroidea to include families Sciadoceridae and Phoridae. After detailed study of morphology (mainly the pleuron and wings), BROWN et al. (2015) changed the former family Sciadoceridae to Sciadocerinae, a subfamily of Phoridae. Relationships of lower cyclorrhaphan families and concepts of Platypezoidea/Platypezidae, Hypocera/Phoroidea/Phoridea and Syrphoidea/Syrphidae were

reviewed, analysed and debated by many authors (GRIFFITHS 1972; MCALPINE 1989; BROWN 1992, 1995; DISNEY 1994; CUMMING et al. 1995; ZATWARNICKI 1996; YEATES & WIEGMANN 1999; COLLINS & WIEGMANN 2002; ROTHERAY & GILBERT 2008; BROWN et al. 2015; LI & YEATES 2018) who suggested often different hypotheses of their relationships, resulting in inconsistent phylogenies among lower cyclorrhaphan families. In this dissertation thesis I follow the classification of lower Cyclorrhapha and Platypezoidea as presented by COLLINS & WIEGMANN (2002) and WIEGMANN et al. (2011). According to their analyses of molecular data matrices, the Platypezoidea are considered to represent a sister group to all other Cyclorrhapha, whilst Syrphidae are not sister to Pipunculidae. Platypezoidea are probably an old cyclorrhaphan lineage, formed and radiated in the Early Cretaceous (145–100 Mya), which took place much before the early Tertiary radiation of Schizophora (65–40 Mya) (WIEGMANN et al. 2011).

The world fauna of Platypezidae (including *Microsania* and fossil species) had 252 known species according to PAPE et al. (2011). Several new species have been described or resurrected from synonymy since the year 2011 (TKOČ 2012 – 1 new species; STÅHLS et al. 2015 – 4; HAN & YANG 2016 – 3; HAN & YANG 2017a – 4; HAN & YANG 2017b – 5), so the current species number is 269.

Modern systematic history of Platypezidae

KESSEL & MAGGIONCALDA (1968), in their first modern generic revision of Platypezidae, erected three new subfamilies based on morphological evidence: Opetiinae (containing *Opetia*, *Atelestus* Walker, *Microsania* Zetterstedt and *Melanderomyia* Kessel), Platypezininae (*Platypezina* Wahlgren, *Grossoseta* Kessel & Kirby, *Callomyia* Meigen and *Agathomyia* Verral) and Platypezinae (*Protoclythia* Kessel, *Platypeza* Meigen, *Paraplatypeza* Kessel & Maggioncalda, *Plesioclythia* Kessel & Maggioncalda, *Symmetricella* Kessel, *Grossovena* Kessel & Maggioncalda, *Penesymmetria* Kessel & Maggioncalda, *Polyporivora* Kessel & Maggioncalda, *Calotarsa* Townsend, *Seri* Kessel & Kessel, *Metaclythia* Kessel, and *Lindneromyia* Kessel).

The genus *Atelestus* was affiliated to the subfamily Hybotinae within Empididae by COLLIN (1961) in contrast to KESSEL (1960, as *Platycnema* Zetterstedt) and KESSEL & MAGGIONCALDA (1968) who placed it in Platypezidae. This view was not accepted by GRIFFITHS (1972) and consequently CHVÁLA (1981, 1983) erected a separate family Atelestidae within Empidoidea. Currently the Atelestidae is considered either a sister group to

remaining Empidoidea (COLLINS & WIEGMANN 2002; MOULTON & WIEGMANN 2004, 2007), or a sister group to the Hybotidae (SINCLAIR & CUMMING 2006).

SHATALKIN (1985) and CHANDLER & SHATALKIN (1998) reviewed the classification of Opetiidae and Platypezidae and subsequently CHANDLER (2001) developed the currently accepted classification of Platypezidae based on analysis of adult morphological characters. A review of all currently valid genera with their distribution in the main zoogeographical regions is provided in Tab. 3.

Table 3. Worldwide distribution of the genus *Microsania* and Platypezidae genera. Assembled according to SMITH (1980); KESSEL (1987); CHANDLER (1989, 1994, 2010); CHANDLER & SHATALKIN (1998) and TKOČ et al. (2017).

Subfamily	Genus	Author	Neotropical	Nearctic	Palaearctic	Oriental	Afro-tropical	Austral-asian
	Microsania	Zetterstedt, 1837	+	+	+	+	+	+
Melanderomyiinae	***Melanderomyia***	Kessel, 1960	-	+	-	-	-	-
Callomyiinae	***Grossoseta***	Kessel & Kirby, 1968	-	+	-	-	-	-
	Platypezina	Wahlgren, 1910	-	+	+	-	-	-
	Agathomyia	Verrall, 1901	+	+	+	+	-	+
	Bertamyia	Kessel, 1970	+	+	-	-	+	-
	Callomyia	Meigen, 1804	+	+	+	+	-	-
Platypezinae	***Calotarsa***	Townsend, 1894	+	+	-	-	-	-
	Protoclythia	Kessel, 1950	-	+	+	-	-	-
	Seri	Kessel & Kessel, 1966	-	+	+	-	-	-
	Bolopus	Enderlein, 1932	-	-	+	-	-	-
	Polyporivora	Kessel & Maggioncalda, 1968	-	+	+	+	-	-
	Kesselimyia	Vaňhara, 1981	-	-	+	-	-	-
	Platypeza	Meigen, 1803	+	+	+	+	-	-
	Pamelamyia	Kessel & Clopton, 1970	-	-	-	-	+	-
	Paraplatypeza	Kessel & Maggioncalda, 1968	-	+	+	+	-	-
	Lindneromyia	Kessel, 1965	+	+	+	+	+	+
	Metaclythia	Kessel, 1952	-	+	-	-	-	-

2.4 SUBFAMILY MELANDEROMYIINAE

Genus *Melanderomyia* Kessel, 1960

The monotypic genus *Melanderomyia* was described by Kessel, 1960 to include the species *M. kahli* from the Nearctic Region (KESSEL 1960). *M. kahli* is associated with *Phallus* sp. (Phallaceae) (KESSEL 1961c), from which no other Platypezidae species is known to develop, oviposit or has been reared (SMITH 1956, CHANDLER 2001). Both sexes are unicolorous, brown to black (Figs 5b, 5c). The females can be spotted ovipositing on *Phallus* sp. fruiting bodies and can be collected or trapped in such situations (Fig. 5a). The current distribution is restricted to Canada and USA (Fig. 4).

Molecular results of TKOČ et al. (2017) do not support sister group relationship of *Melanderomyia* and *Microsania* as was published by CHANDLER (2001). The morphological resemblance of these two genera is rather superficial, not supported by real synapomorphies (TKOČ et al. 2017).

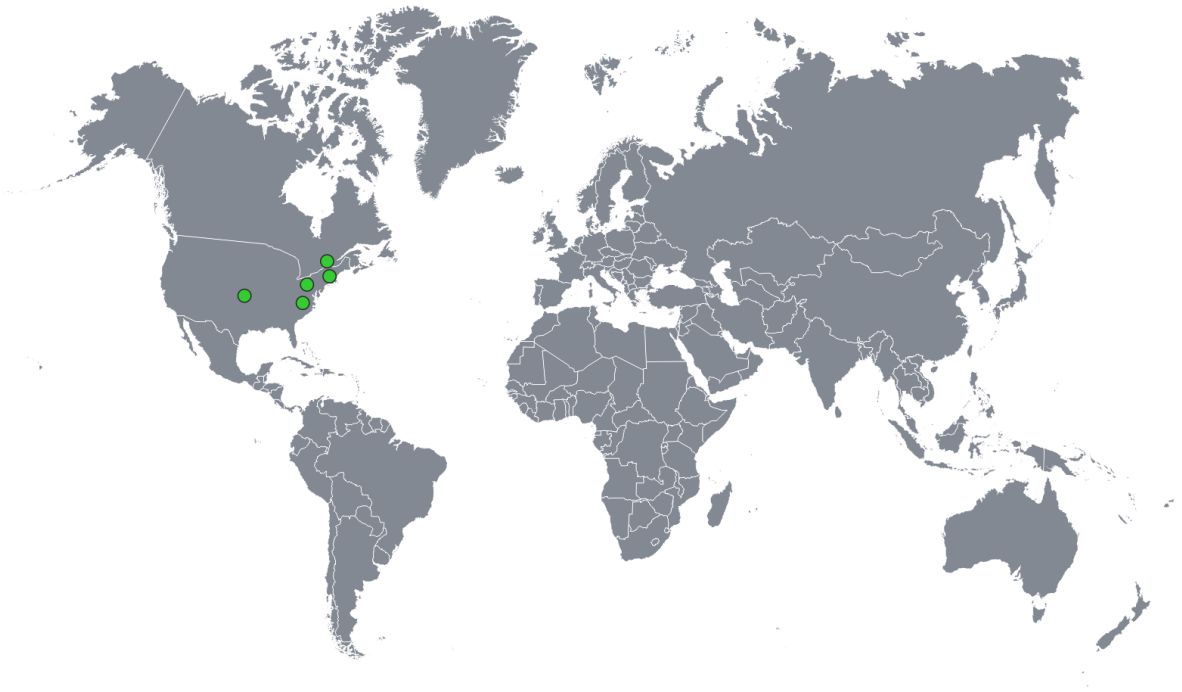

Fig. 4. Distribution of Melanderomyiinae. ●: *Melanderomyia kahli* Kessel, 1960.

2.5 SUBFAMILY CALLOMYIINAE

Subfamily Callomyiinae includes five genera (Tab. 3), the genus *Chydaeopeza* Shatalkin, 1992 was synonymized with *Agathomyia* Verrall, 1901 (TKOČ et al. 2017). Majority of the species are distributed in the Nearctic and Palaearctic regions, but some species from *Agathomyia*, *Bertamyia* and *Callomyia* also occur outside these two regions (see Tab. 4).

The Callomyiinae is a monophyletic group according to molecular (TKOČ et al. 2017) and morphological data analyses (CHANDLER 2001). The morphological synapomorphies of Callomyiinae are: (i) The presence of strong bent posteroventral seta (= oxhorn seta) in fore femur in males (missing in *Platypezina*, but it is a secondary loss, because its sister genus *Grossoseta* has this character well developed); (ii) The presence of strong posteroventral seta near the base of hind femur; (iii) Eight processes (= lappets) on each larval segment; (iv) position of wings and their overlap ratio of surfaces 'in situ' in the normal resting position .

The early stages are known for some species from genera *Agathomyia*, *Callomyia* and *Bertamyia*. *Callomyia* differs remarkably in morphology of larvae and puparia from other platypezid larvae. While *Agathomyia* develop internally in polypore fungi, *Callomyia* lives externally on encrusting fungi. Larvae of *Bertamyia* live on fungi from family Phallaceae (Fig. 5a).

Table 4. Subfamily Callomyiinae. Overview of extant genera and species from the bitypic genera.

Genus	Species	Zoogeography	Author
Agathomyia	62 species	NT, NE, PA, OR, AUS	Verral, 1901
Bertamyia	*notata*	NE, NT	(Loew, 1866)
Bertamyia	*umacibise*	AT	Kessel & Clopton, 1830
Callomyia	21 species	NT, NE, PA, OR	Meigen, 1804
Grossoseta	*pacifica*	NE	(Kessel, 1948)
Grossoseta	*johnsoni*	NE	(Kessel, 1961)
Platypezina	*connexa*	PA	(Boheman, 1858)
Platypezina	*diversa*	NE	(Johnson, 1923)

Genus *Agathomyia* Verral, 1901

Genus *Agathomyia* is represented by 62 species in the world. This genus is distributed mainly in the Palaearctic and Nearctic regions and it is missing in the Afrotropical Region.

There are 26 known species of *Agathomyia* from the Nearctic Region (KESSEL 1987), but some of them are in fact described based only on one sex. The Neacrtic *Agathomyia* needs systematic revision.

Two species are known from the Neotropical Region, one from Mexico (CHANDLER 2010), *Agathomyia bella* (Williston, 1903), and one from Paraguay *A. argentata* Oldenberg, 1917.

Altogether 28 species are currently known from the Palaearctic Region (CHANDLER 1980, CHANDLER 1991; CHANDLER & SHATALKIN 1998; SHATALKIN 1985, 1992; STÅHLS et al. 2015; HAN & YANG 2017a). CHANDLER (2001) recognized four species groups for the European species of *Agathomyia* based on characters of male genitalia that corresponds with female morphological types: *Agathomyia viduella* group (one species), *A. antennata* group (four species), *A. falleni* group (two species) and *A. elegantula* group (8 species).

There are three species from the Oriental Region (CHANDLER 1994, HAN & YANG 2017b): *A. semirubra* (Indonesia: Java), *A. thoracica* (Taiwan; Philippines), and *A. yunnana* (China: Yunnan).

And finally, two species are known from the Australasian Region, *A. austrocollinella* Chandler, 1994, from the New South Wales, Australia, and *A. pluvialis* from Chimba prov., Papua New Guinea (CHANDLER 1994).

Males of *Agathomyia* (Fig. 5i) are usually not so brightly colored as the females. Coloration of females is often used as diagnostic character, it is composed of patterns of black, grey, yellow, orange, or red markings (Fig. 5g). So far known larvae live in tissues of various polypore fungi from the genera *Trametes*, *Phellinus*, *Bjerkandera*, *Inonotus*,

Ischnoderma, and *Antrodiella* (CHANDLER 2001, REEMER & DE JONG 2016, STÅHLS et al. 2015). The larvae of *A. wankowiczii* are gall-forming, they make galls on sporocarps of a polypore *Ganoderma applanatum* (Polyporales).

Genus *Bertamyia* Kessel, 1970

A genus with two species occurring in the Afrotropical, Nearctic and Neotropical regions. One species, *Bertamyia umacibise* (Kessel & Clopton, 1970), occurs in the Afrotropics, recorded from South Africa and Zimbabwe (CHANDLER 2021). It was originally described in the genus *Agathomyia*, consequently transferred to *Bertamyia* by KESSEL (1970), a genus that otherwise includes only the New World species *B. notata* (Loew, 1866), recorded from Canada to Argentina. WOODLEY (2005) recorded *B. notata* from Costa Rica, Panama, Mexico (Chiapas), and Caribbean islands.

Both sexes are black, with a pattern of metallic bluish green shiny spots (Fig. 6f, 6h). *Agathomyia* has a postsutural supra-alar seta above the wing base in front of the postalar callus, which is absent in *Bertamyia*. The biology of *B. umacibise* remains unknown, but *B. notata* is known to develop in the soft fungus *Tyromyces* (Polyporaceae) growing on wood (KESSEL 1957).

Genus *Callomyia* Meigen, 1804

The world fauna of the genus *Callomyia* is currently represented by 21 species. This genus is distributed mainly in the Palaearctic and Nearctic regions and it is apparently missing in the Neotropical and Australasian regions; in the Oriental Region it is represented by two species, *Callomyia coei* Kessel, 1966 described from Nepal (KESSEL 1966a) and *C. triangulata* Tkoč, 2012 from South China (TKOČ 2012 - **PUBLICATION 2**). Both species are known only from the female, *C. coei* was redescribed and figured by CHANDLER (1994) within his revision of the Oriental and Australasian Platypezidae.

CHANDLER (1974) recognized four species of *Callomyia* in Europe in his original revision and later described one additional species from Bulgaria (CHANDLER 1976). Thus, genus *Callomyia* has currently 5 species in Europe (CHANDLER 2001) and another four were described from Siberia and the Far East of Russia (SHATALKIN 1980, 1982, 1992). All 9 Palaearctic species are known in both sexes.

KESSEL & BUEGLER (1972) revised the genus *Callomyia* of the Nearctic Region, recognizing a total of 10 species. Only two of these species were known from both sexes,

among the remaining 8 species, 5 were described from males and three from females only. The most recent Nearctic revision of genus *Callomyia* resulted in total of 10 species CUMMING & WHEELER (2016). Three species were described as new (*C. argentea* Cumming, 2016, *C. arnaudi* Cumming, 2016 and *C. browni* Cumming, 2016), and three species were synonymized.

Males of *Callomyia* are mostly black-colored (Fig. 5k) with silver-grey patterns on thorax and abdomen in some species. Coloration of females is composed of black, yellow, brown, and grey silver dusted reflective areas (Fig. 5j). The adult characters are supplemented also by typical morphology of larvae which live on surfaces of fungal mycelia: larvae dorsoventrally flattened, their metathoracic and first abdominal segment fused, and marginal processes duplicated on each segment.

Genus *Grossoseta* Kessel & Kirby, 1968

This genus is known from Nearctic Region only. It consists of two species, *Grossoseta pacifica* and *G. johnsoni*. It is phylogenetically closely related to Holarctic genus *Platypezina* (TKOČ et al. 2017). Their resemblance is also morphological, only the males of *Grossoseta* do have the strong bent posteroventral seta (= oxhorn seta) on the base of front femur; this seta is missing in *Platypezina*. However, their biology is unknown.

Genus *Platypezina* Wahlgren, 1910

A Holarctic genus with two species, *Platypezina connexa* (Figs 5d, 5e) and *P. diversa*. Both sexes possess typical pterostigma on their wings. Males of *Platypezina* are dark brown to black colored with the wings notably brownish tinted (Fig. 5e). The females are steel grey colored, with wide frons, their wings are not so dark as in males (Fig. 5d). The larval biology is still unknown. However, the adults of *P. connexa* were repeatedly reared from strongly decayed (brown-rot) and softened trunk of spruce (*Picea abies*) (STÅHLS & KAHANPÄÄ 2006), so it is very probable that larvae feed on fungal growth of dead *Picea* trunks or branches.

The species *P. connexa* is known mainly from northern Europe. It is a rare species; however, adults could be locally abundant during the peak period of their activity (M. Tkoč, pers. obs.). The flight period in central Europe ranges from August to October (TKOČ et al. 2020 - **PUBLICATION 9**).

Figure 5. Subfamilies Melanderomyinae and Callomyiinae (Platypezidae): a – *Melanderomyia kahli* on its host fungus *Phallus ravenelii*; b – *M. kahli*, male; c – *M. kahli*, female; d – *Platypezina connexa*, female; e – *P. connexa*, male; f – *Bertamyia notata*, male; g – *Agathomyia sexmaculata*, female; h – *Bertamyia notata*, female; i – *Agathomyia falleni*, male; j – *Callomyia speciosa*, female; k – *C. amoena*, male. Photos a-c by P. Coin; photos d, e, i by J. Roháček; photo f by S. Luk; photo h by K. Schulz; photos g, j, k by D. Gavryushin.

2.6 SUBFAMILY PLATYPEZINAE

Subfamily Platypezinae includes 11 genera (Tab. 5), the genera *Grossovena* Kessel & Maggioncalda, 1968, *Penesymmetria* Kessel & Maggioncalda, 1968, *Plesioclythia* Kessel & Maggioncalda, 1968, and *Symmetricella* Kessel & Maggioncalda, 1968 are synonyms of *Lindneromyia* Kessel, 1965 (sensu CHANDLER 2001 and TKOČ et al. 2017). Most of the species are distributed in the Nearctic and Palaearctic regions as in Callomyiinae, but some species from genera *Calotarsa* Townsend, 1894, *Lindneromyia*, *Polyporivora* Kessel & Maggioncalda, 1968, and *Platypeza* Meigen, 1803 also occur in other regions (see Tab. 5).

The Platypezinae is a monophyletic group according to molecular (TKOČ et al. 2017) and morphological data analyses (CHANDLER 2001). The morphological synapomorphies of Platypezinae are: (i) first tarsomere of hind tarsus shorter than second–fourth tarsomeres together (Fig. 12); (ii) acrostichal setae absent; (iii) only short scattered frontal setae present in females. TKOČ et al. (2017) proposed additional synapomorphy for subfamily Platypezinae: the position of wings and their overlap ratio of surfaces 'in situ' in the normal resting position. Members of Platypezinae have their wings more outstretched and they overlap only by 30% at most (Figs 16 and 18 in TKOČ et al. 2017). On the contrary, members of Melanderomyiinae and Callomyiinae have 'in situ' wing overlap almost completely to about 50% of each wing surface (Figs 15 and 17 in TKOČ et al. 2017).

Table 5. Subfamily Platypezinae. Overview of extant genera and species.

Genus	Species	Zoogeography	Author
Bolopus	*furcatus*	PA	(Fallén, 1815)
Calotarsa	6 species	NE, NT	Townsend, 1894
Kesselimyia	*chandleri*	PA	Vaňhara, 1981
Lindneromyia	87 species	NT, NE, PA, AT, OR, AUS	Kessel, 1965
Metaclythia	*currani*	NE	Kessel, 1952
Pamelamyia	*stuckenbergorum*	NE	Kessel & Clopton, 1970
Paraplatypeza	7 species	NE, PA	Kessel & Maggioncalda, 1968
Platypeza	25 species	NE, PA, OR	Meigen, 1803
Polyporivora	8 species	NE, PA, OR	Kessel & Maggioncalda, 1968
Protoclythia	3 species	NE, PA	Kessel, 1949
Seri	*dymka*	NE	(Kessel, 1961)
Seri	*obscuripennis*	PA	(Oldenberg, 1917)

The early stages are known for some species from the genera *Bolopus*, *Calotarsa*, *Kesselimyia*, *Lindneromyia*, *Paraplatypeza*, *Platypeza*, *Polyporivora*, *Protoclythia*, and *Seri*. Their larvae have 6 processes (= lappets) per each segment and can be divided into

three groups according to the morphology: (i) elongate, slightly depressed dorsoventrally, but laterally rounded, mesothorax with 6 processes (*Protoclythia*, *Calotarsa*); (ii) more cylindrical larvae, not dorsoventrally depressed, mesothorax with six processes (*Seri*, *Bolopus*, *Polyporivora*); (iii) dorsoventrally depressed with more prominent marginal processes, mesothorax with only four processes (*Kesselimyia*, *Lindneromyia*, *Paraplatypeza*, *Platypeza*). The immature stages of *Metaclythia* and *Pamelamyia* are unknown. The known larvae live in tissues of various fungi from the genera *Polyporus*, *Armillaria*, *Macrolepiota*, *Agaricus*, and *Pluteus* (CHANDLER 2001). There are also other recorded genera as their host fungus, but these records need confirmation.

Genus *Bolopus* Enderlein, 1932

The genus *Bolopus* with the single European species *B. furcatus* (Fig. 7e) is known to develop in the soft polypore fungus *Polyporus squamosus* (CHANDLER 2001). Its closely related taxa are genera *Seri* and *Polyporivora* (CHANDLER 2001; TKOČ et al. 2017). Coloration of both sexes is dark greyish brown to black; thorax of males and females is slightly shiny (Fig. 7e).

Genus *Calotarsa* Townsend, 1894

Nearctic and Neotropical genus with 6 described species. Species of this genus have extensively modified tarsomeres (Figs 7a, 7b). KESSEL & YOUNG (1974) described *Calotarsa mexicana* from a single male found in Chiapas province, Mexico, confirming that this genus previously known only in the Nearctic extends into the northern Neotropical Region. Also *C. durangoensis* was described from Durango province, Mexico, in the same paper (KESSEL & YOUNG 1974).

Four species are known from the Nearctic Region, *C. calceata* (Snow, 1894), *C. insignis* Aldrich, 1906, *C. pallipes* (Loew, 1866), and *C. simplex* Kessel & Young, 1974. Biology of *C. insignis* is known, it develops in honey fungus (*Armillaria* sp.) growing on wood (KESSEL 1963).

Genus *Kesselimyia* Vaňhara, 1981

The monotypic genus *Kesselimyia* with the species *K. chandleri* (Fig. 7i) was described from the type series found in Moravia (Czech Republic) by VAŇHARA (1981). The type series was reared from an unidentified *Lepiota* (most probably *Macrolepiota procera*) (CHANDLER 2001). This Palaearctic species is also known from Hungary,

European part of Russia (CHANDLER 2001, 2014), Bulgaria (BESCHOVSKI 2004) and The Netherlands (REEMER & DE JONG 2016).

Genus *Lindneromyia* Kessel, 1965

A genus with 87 deescribed species occurring in all 6 main zoogeographical regions (CHANDLER 2021). In the current sense (CHANDLER 2001, CHANDLER 2021), the genus *Lindneromyia* includes the genera *Grossovena*, *Penesymmetria*, *Plesioclythia* and *Symmetricella* as synonymes. Similarly, all Afrotropical species described in genus *Paraplatypeza* are synonymes of *Lindneromyia* (CHANDLER 2021).

Eight species are recorded in the Neotropical Region (OLDENBERG 1916, COLLIN 1931, ACZÉL 1958, KESSEL 1966b). Nine species are known from the Nearctic Region (KESSEL 1963, KESSEL 1987, POOLE & GENTILI 1996). Six species are reported from the Palaearctic Region, three from Europe (*L. dorsalis* (Meigen, 1804)) – Fig. 7m, *L. hungarica* Chandler, 2001) – Fig. 7n; *L. tenebrica* (Shatalkin, 1981)), two from the Far East of Russia (*L. cirrhocera* (Shatalkin, 1982); *L. nigella* (Shatalkin, 1980)), and one species, occurring predominantly in Oriental Region, is recorded from Japan (*L. argyrogyna* (de Meijere, 1907)).

Thirty-eight species of *Lindneromyia* are known from the Afrotropical Region (CHANDLER 2021). Mainly from the African mainland, but some also from Comoros Is., Madagascar, and Afrotropical parts of the Arabian Peninsula (KESSEL & CLOPTON 1970, CHANDLER 2021). In the Afrotropical Region it is the most dominant genus of Platypezidae. Some of the Afrotropical species are synonyms, however, there are still many undescribed species in the collections. One Afrotropical species, *Paraplatypeza ikekeba* Kessel & Clopton, 1970, is mainly orange-yellow in body coloration (only the male is known). No identification key to Afrotropical species is currently available and the genus needs careful revision (CHANDLER 2021).

There are 16 species in the Oriental Region (CHANDLER 1994; HAN & YANG 2016; HAN & YANG 2017b). The Australasian fauna of *Lindneromyia* consists of 16 described species (CHANDLER 1994).

The males are predominantly black, velvety, the females often with grey (yellow in some species) markings on abdomen (Figs 7m, 7n). Where the biology is known, species of the genus mainly develop in terrestrial gill fungi, especially of the genus *Agaricus*.

Genus *Metaclythia* Kessel, 1952

A Holarctic monotypic genus with the species *Metaclythia currani* Kessel, 1952. *M. currani* has long been known only from the Nearctic Region, however it was also found in Far

East of Russia, Primorskiy Krai (SHATALKIN 1992). Their larval biology and host fungus are unknown. Its phylogenetical position is uncertain (CHANDLER 2021).

Genus *Pamelamyia* Kessel & Clopton, 1970

An Afrotropical endemic monotypic genus, with the single species, *P. stuckenbergorum* Kessel & Clopton, 1970, described from South Africa and later recorded also from Namibia and Kenya (CHANDLER 2021). The coloration is entirely dark in both sexes. The immature stages are unknown. TKOČ et al. (2017) confirmed that the genus belongs to a clade including *Lindneromyia* and *Paraplatypeza* (Fig. 8).

Genus *Paraplatypeza* Kessel & Maggioncalda, 1968

A Holarctic genus with 7 described species. Two species are from the Nearctic Region, *Paraplatypeza coraxa* (Kessel, 1950) and *P. velutina* (Loew, 1866). For the Palaeartic region 5 species are known; two from Europe (*P. atra* (Meigen, 1804); *P. bicincta* (Szilády, 1941) – Fig. 7l), and three from Far East of Russia (*P. angustifrons* Shatalkin, 1982; *P. rara* Shatalkin, 1982; *P. triangulata* Shatalkin, 1982). The former 5 Afrotropical species are now placed under *Lindneromyia* (CHANDLER 2021).

The males are black, with a tuft of divergent frontal setae, the females of some species have grey markings on abdomen. Both sexes have facial setae. The host fungus is known for some species, they develop in terrestrial gill fungi, especially of the genus *Pluteus*.

Genus *Platypeza* Meigen, 1803

Holarctic and Oriental genus, with uncertain number of the world species, according all information sources available to me, it is 25 species. Many species have been initially described in this genus but currently belong to *Lindneromyia* or to some other genus of Platypezinae. In fact, only two species from Burma (*P. burmensis*; *P. malaisei*) were confirmed to exist outside the Holarctic Region (CHANDLER 1994, CHANDLER 2021). Thirteen species are known from the Nearctic Region (KESSEL 1987, POOLE & GENTILI 1996), but this number is not definitive, as the Nearctic *Platypeza* needs revision. Ten species are recorded in the Palaearctic Region, four from Europe (CHANDLER 2001), 5 from Russia, and one from Japan and Kuril Island (CHANDLER & SHATALKIN 1998). The formerly Nearctic species, *P. hunteri* Kessel, 1959 was also found in Far East of Russia (CHANDLER 2001; CHANDLER & SHATALKIN 1998).

Platypeza species develop in a range of gill fungi but especially in honey fungus (*Armillaria* species) growing on wood. The males are usually dark brown to black and females grey with black pattern on abdomen (Figs 7j, 7k).

Genus *Polyporivora* Kessel & Maggioncalda, 1968

Altogether 8 species of *Polyporivora* are known from the Holarctic and Oriental Regions. Two species are in the Nearctic Region (*P. polypori, P. hunteri*). However, *P. hunteri* (described as *P. amurensis* Shatalkin, 1981) is also known from Far East of Russia in the Palaearctic Region (CHANDLER 1991). Three species are European (*P. boletina*, *P. ornata* (Fig. 7f), *P. picta* (Figs 7g, 7h)), one is from Israel (*P. canomela* Chandler, 1980) and one from Nepal and Sri Lanka (*P. nepalensis* Kessel, 1966).

All recorded rearings of larvae was from fungus *Trametes* sp. The development from *Trametes versicolor*, larval biology and distribution in Europe of the species *P. picta* (Meigen, 1830) was documented in detail by TKOČ (2011 - **PUBLICATION 6**).

Genus *Protoclythia* Kessel, 1950

A Holarctic genus, only three species of this genus are known in the world fauna: *Protoclythia modesta* (Fig. 7c), *P. rufa* (both Palaearctic), and *P. californica* (Nearctic). All three species are known to develop in *Armillaria mellea* or similar *Armillaria* sp. (CHANDLER 2001). They have autumnal flight period, together with *Calotarsa* and *Platypeza*, which are also known to develop in honey fungus (*Armillaria* sp.).

Genus *Seri* Kessel and Kessel, 1966

Genus *Seri* was described by KESSEL & KESSEL (1966) to include one rare species, *S. dymka*, originally described in *Clythia* Meigen from western North America (KESSEL 1961b). CHANDLER (1974) transferred the not-well known Palaearctic species *Clythia* (synonym of *Platypeza*) *obscuripennis* Oldenberg to *Seri* based on similar wing venation.

The genus is known from the Palaearctic, *S. obscuripennis* (Fig 7d) and Nearctic, *S. dymka*, regions. Adult specimens of *Seri* are usually recognized by their notably tinted wings, which are covered with microtrichia. The wings of other platypezids are usually glossier and clearer. CUMMING & CUMMING (2011) redescribed and diagnosed the genus *Seri*, diagnosed both species, reviewed all records and material of Nearctic *S. dymka*, and redescribed the male of this species for the first time. They supported the validity of both species.

Figure 7. Subfamily Platypezinae (Platypezidae): a – *Calotarsa insignis*, male; b – *C. insignis*, detail of tarsus; c – *Protoclythia modesta*, female; d – *Seri obscuripennis*, male; e – *Bolopus furcatus*, female; f – *Polyporivora ornata*, male; g – *P. picta*, female; h – *P. picta*, female; i – *Kesselimyia chandleri*, female; j – *Platypeza aterrima*, female; k – *P. aterrima*, male; l – *Paraplatypeza bicincta*, female; m – *Lindneromyia dorsalis*, female; n – *L. hungarica*, female. Photo a by P. Bedell; photo b by M. Hauser; photos c, g, h by J. Roháček; photos i, k, l by M. Tkoč; photos d, e, f, j, m, n by D. Gavryushin.

3. PHYLOGENY

The family was traditionally subdivided into four subfamilies: Melanderomyiinae Chandler, Microsaniinae Enderlein, Callomyiinae Rondani and Platypezinae Fallén. CHANDLER (2001) divided these four subfamilies of platypezids into two basic clades based on 19 morphological characters but identified no true synapomorphy for the family itself. The first clade consists of Microsaniinae (*Microsania*) and its sister group Melanderomyiinae (*Melanderomyia kahli*); second clade is composed of Callomyiinae (Platypezina, *Grossoseta*, *Callomyia*, *Agathomyia* and *Bertamyia*) and its sister group Platypezinae (*Protoclythia*, *Calotarsa*, *Seri*, *Bolopus*, *Polyporivora*, *Metaclythia*, *Kesselimyia*, *Platypeza*, *Paraplatypeza*, and *Lindneromyia*). According to the phylogenetic scheme of CHANDLER (2001) Microsaniinae share the following 6 adult apomorphies with Melanderomyiinae: (1) crossvein dm-cu absent; (2) vein R1 short; (3) hairs on anal lobe and alula thickened; (4) sides of prothorax bare; (5) mouth margin medially produced and (6) scape bare. The sister pair Callomyiinae + Platypezinae is supported by a single synapomorphy: tarsi of females with depressed less sclerotized areas devoid of setulae (= soles).

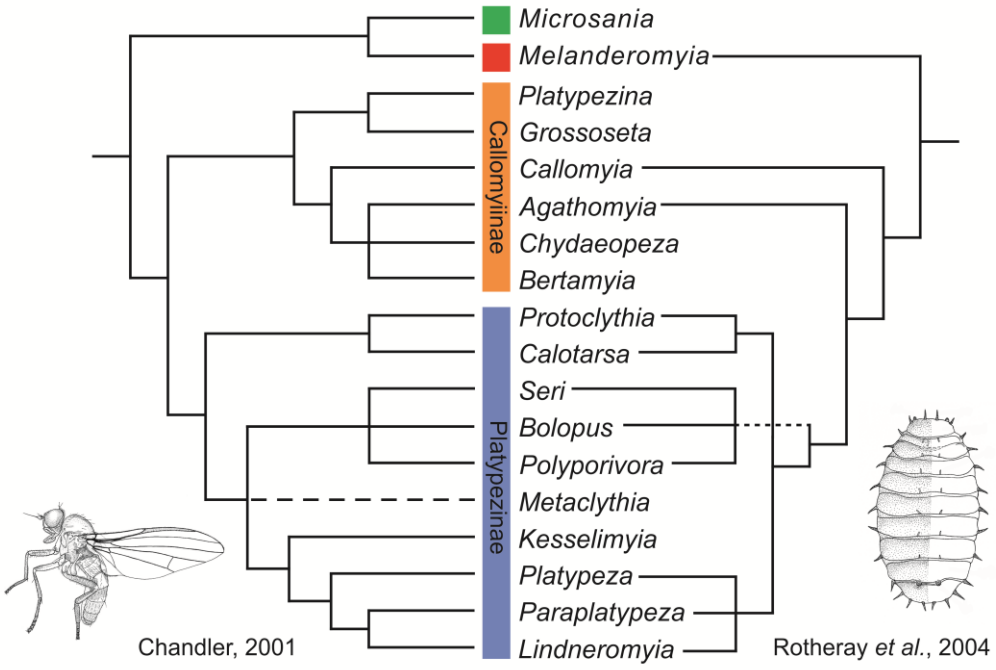

Figure 8. Summary of generic phylogenetic relationships of Platypezidae and genus *Microsania* based on morphological characters. After CHANDLER (2001) (mainly adult characters) and ROTHERAY et al. (2004) (immature characters). Long dashed line means uncertain position of the genus *Metaclythia*; green square: Microsaniinae; red square: Melanderomyinae. From TKOČ et al. (2017).

The Callomyiinae clade is defined by four apomorphies: (1) tibia and hind tarsus having uniformly dark setulae; (2) presence of strong bent posteroventral seta (= oxhorn seta) on the base of front femur of males and corresponding anteroventral notch on middle femur (missing in *Platypezina*); (3) presence of strong posteroventral seta near the base of hind femur (missing in *Bertamyia*) and (4) 8 processes per segment in the larva. The Platypezinae clade is defined by three apomorphies: (1) first tarsomere on hind leg shortened; (2) acrostichal setae absent and scutum bare between dorsocentral rows of setae; (3) frons of female with only sparsely distributed short frontal setae. ROTHERAY et al. (2004) analyzed the immature characters of 15 species belonging to 10 genera of Palaearctic Callomyiinae and Platypezinae and the Nearctic species *Melanderomyia kahli*, but their parsimony analysis results supported only the monophyly of Platypezinae. A summarizing tree of these two phylogenetic hypotheses is shown in Fig. 8.

GRIFFITHS (1972) placed Platypezidae (including *Opetia*) as sister group to Syrphoidea + Schizophora, and these all together forming sister group to Ironomyiidae + Phoridae + Sciadoceridae. MCALPINE (1989) considered Platypezidae (incl. *Opetia*) sister to all other families of Platypezoidea. A molecular study of COLLINS & WIEGMANN (2002) based on maximum likelihood analysis of 28S rDNA sequences placed *Opetia* as sister group to Lonchopteridae which together represent the sister group to Platypezidae + Phoridae; their maximum parsimony analyses showed different composition or unresolved polytomy, but in all cases *Opetia* was found to be more related to Lonchopteridae than to the Platypezidae clade. In a combined (based on molecular and morphological data) phylogenetic hypothesis Platypezidae were shown as a sister group to Phoridae + Ironomyiidae, all together forming a sister clade to Opetiidae, all together showing as sister to Lonchopteridae (WIEGMANN et al., 2011).

TKOČ et al. (2017) supported the monophyly of the Platypezidae clade, exclusive of *Microsania*. Platypezidae consists of three well-supported monophyletic clades, which are in accordance with current subfamilial classification of Platypezidae: Melanderomyiinae, Callomyiinae, and Platypezinae. The Melanderomyiinae clade is sister to the clade Callomyiinae (Fig. 9). Genus *Microsania* was resolved as a separate lineage distant from Platypezidae which clustered with Opetiidae as its sister group, both together forming a sister group to Platypezidae. *Melanderomyia* was resolved as sister to Callomyiinae subfamily.

Within Callomyiinae, the clade of *Grossoseta* + *Platypezina* was placed in a sister relationship to the rest of the subfamily. All remaining taxa from the Callomyiinae clade are sister to *Agathomyia viduella*, which would make the genus *Agathomyia* paraphyletic. This clade is composed of a branch of *Agathomyia* + *Chydaeopeza* + *Callomyia*, which is sister clade to *Bertamyia notata*. The genera *Agathomyia*, *Bertamyia*, *Chydaeopeza*, and *Callomyia* form a paraphyletic composition. However, the analysed *Agathomyia* species represent four clades which fully agree with the species groups morphologically defined by CHANDLER (2001). The genus *Agathomyia* was not resolved as a monophyletic group in the analysis. The *A. viduella* group covers the single species *A. viduella* and is the earliest branched clade of the mentioned paraphyletic group, so its position might in fact show a different generic affiliation. The *A. elegantula* group includes the analyzed species *A. elegantula*, *A. lundbecki*, *A. woodella*, and *A. zetterstedti*. The *A. antennata* group includes *A. sexmaculata* and covers also the closely related species *Chydaeopeza tibialis*, excluded from the genus *Agathomyia* by SHATALKIN (1985, 1992). Based on these results, the genus *Chydaeopeza* was synonymized with *Agathomyia*. The *A. falleni* group consists of two analyzed species *A. falleni* and *A. unicolor* and shows sister relationship to the *A. sexmaculata* + *Chydaeopeza tibialis* pair. The Callomyia clade is in the analysis (TKOČ et al. 2017) represented by three species with the following composition: *C. dives* + (*C. amoena* + *C. admirabilis*). *Callomyia* is a morphologically well-defined genus characterized mainly by its typical flattened larva and puparium with sharply pointed processes (= lappets) (Fig. S10 in TKOČ et al. 2017) and by the presence of spines on the first radial vein – R1. Its relationships to other taxa within *Agathomyia* clade remain unclear (its sister group has not been recognized).

Within Platypezinae, all the included genera form monophyletic clades (TKOČ et al. 2017). Their relationships were resolved as follows: (*Calotarsa* + *Protoclythia*) + (*Seri* + (*Bolopus* + *Polyporivora*)) + (*Kesselimyia* + (*Platypeza* + (*Pamelamyia* + (*Paraplatypeza* + *Lindneromyia*)))) (Fig. 9). A polytomy with three clades, comprising two (*Calotarsa*, *Protoclythia*), three (*Seri*, *Bolopus*, *Polyporivora*) and five genera (*Kesselimyia*, *Platypeza*, *Pamelamyia*, *Paraplatypeza*, *Lindneromyia*) form monophyletic clusters with compositions like the phylogenetic hypothesis based on morphology of CHANDLER (2001). Bifurcated setae on legs of adult Platypezidae are documented as a new synapomorphy of the family, exclusive of *Microsania*. Outstretched wings and only a small overlap of their surfaces at resting position are considered a new synapomorphy for the subfamily Platypezinae.

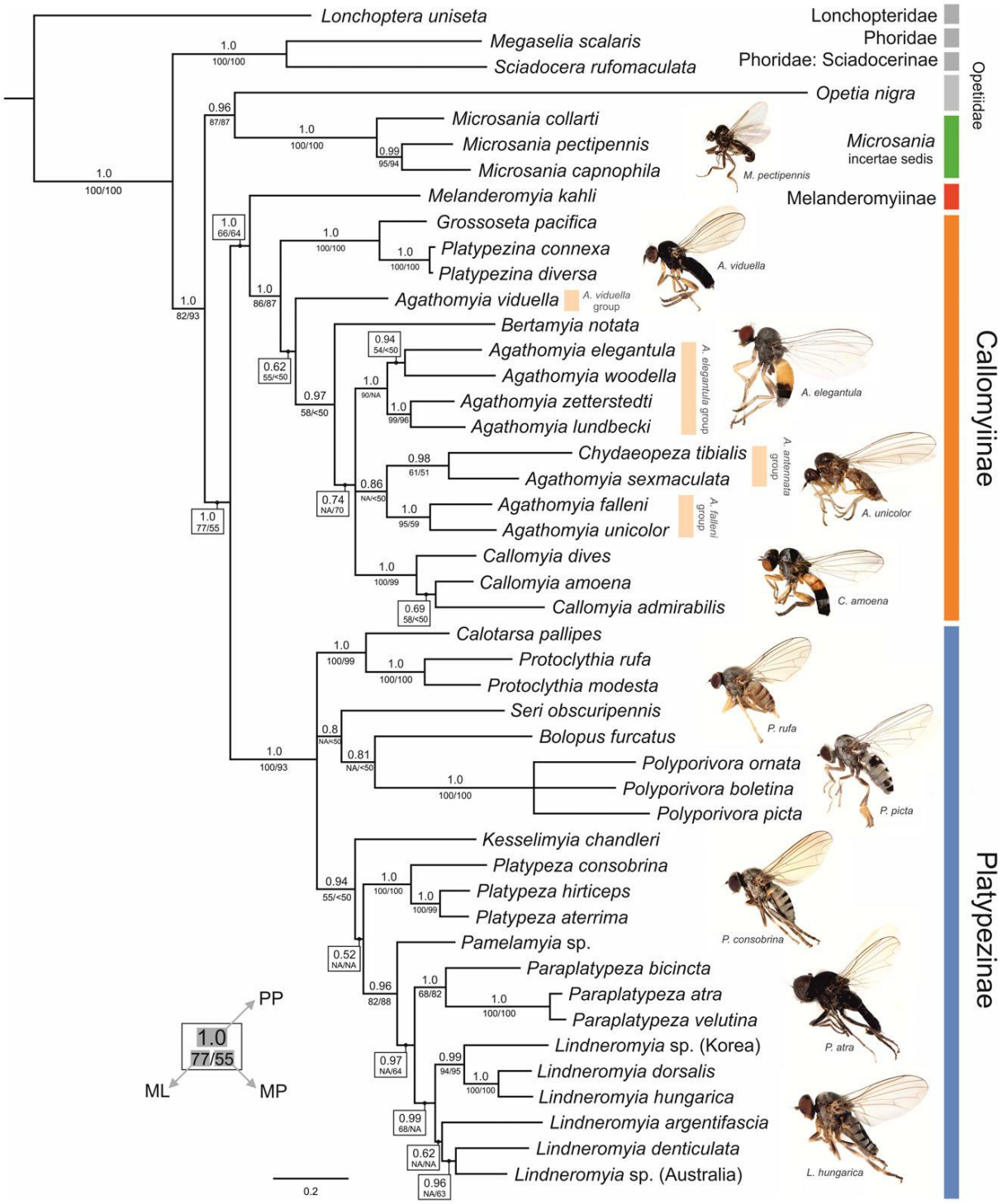

Figure 9. The phylogenetic tree of Opetiidae, *Microsania* and Platypezidae. From TKOČ et al. (2017).

Monophyly of Platypezidae

GRIFFITHS (1972) defined the monophyly of Platypezidae based on a single apomorphic character, the compressed hind tarsi. MCALPINE (1989) did not exclude *Opetia* and suggested that Platypezidae in this concept are supported by following

apomorphies: reduced prothoracic pupal spiracular horns; absence of a filter apparatus in the pharynx of the larva; presence of pad-like empodia on all tarsi. However, since the immature stages of *Opetia* spp. and *Microsania* spp. are unknown, two of these three apomorphic characters cannot be verified.

CHANDLER (2001) debated several plesiomorphic characters common to all Platypezidae genera, but he stated that there is no real synapomorphy for the family with respect to Cyclorrhapha. As probable synapomorphies he considered: uniserial acrostichal setae (lost in Platypezinae); compressed hind tarsi (however, the soles, which are the depressed less sclerotized areas without setulae, are present only in Callomyiinae and Platypezinae) and M1+2 forking beyond crossvein dm-cu (fork, crossvein or both may be lost in some genera).

The presence of uniserial acrostichal setae was also used as synapomorphy in studies of HENNIG (1976), BROWN (1992) and CUMMING et al. (1995). Additionally, the compressed hind tarsi were also considered to be a synapomorphy by HENNIG (1976) and CUMMING et al. (1995).

Most recently, TKOČ et al. (2017) supported the monophyly of the Platypezidae clade, exclusive of *Microsania*. They proposed the following synapomorphies for Platypezidae: **(i)** bifurcated setae present on femora and tibiae of all legs of both sexes (Figs 3–6 in TKOČ et al. 2017): this character is shared by all Platypezidae genera; **(ii)** compressed hind tarsi with soles (Figs 9–12 in TKOČ et al. 2017); **(iii)** larva of typical cylindrical or flattened form (Figs S9–S11 in TKOČ et al. 2017); **(iv)** mycophagous larvae (unknown in *Grossoseta*, *Platypezina*, and *Metaclythia*).

4. FOSSIL FAUNA OF FLAT-FOOTED FLIES

Although the families Opetiidae and Platypezidae are not numerous (more than 250 spp.), their fossil record is relatively rich. Thirty fossil species of flat-footed flies are currently known (Tab. 6). The fossil evidence of flat-footed flies is richer from the Cretaceous with 21 described species (ZHANG 1987, MOSTOVSKI 1995a, GRIMALDI & CUMMING 1999, GRIMALDI 2018) than it is for the Tertiary deposits – 9 species (CHANDLER 2001, GRIMALDI 2018, GREENWALT et al. 2019).

The first known fossil species of Platypezidae was *Callomyia torporata* from the Middle Eocene of the Green River Formation (Wyoming, USA) described by Scudder (1890).

New genus, *Oppenheimiella*, was erected for the species *O. baltica* from the Late Eocene of Baltic amber by Meunier (1893). Unfortunately, this species is problematic, because of uncertain family placement since the original description is ambiguous and the type specimen is lost (GRIMALDI 2018). COCKERELL (1909) described *Callomyia hypolitha* from the Green River Formation (Colorado, USA). Another species, *Eucallimyia fortis*, was described from the Early Oligocene of Florissant Formation (Colorado, USA) by COCKERELL (1911).

Table 6. List of all fossil species of Opetiidae and Platypezidae. (NT – Neotropical; NE – Nearctic; PA – Palaearctic; OR – Oriental).

Reference	Family	Genus	Species	Locality	Era / Period
Scudder (1890)	PLATYPEZIDAE	*Callomyia*	*torporata*	NE: USA	Eocene
Meunier (1893)	PLATYPEZIDAE	*Oppenheimiella*	*baltica*	PA: Baltic	Eocene
Cockerell (1909)	PLATYPEZIDAE	*Callomyia*	*hypolitha*	NE: USA	Eocene
Cockerell (1911)	PLATYPEZIDAE	*Eucallimyia*	*fortis*	NE: USA	Oligocene
Statz (1940)	OPETIIDAE	*Opetia*	*atra*	PA: Germany	Oligocene
Zhang (1987)	OPETIIDAE	*Lithopetia*	*hirsuta*	PA: China	Early Cretaceous
Zhang (1987)	OPETIIDAE	*Pseudopetia*	*exilis*	PA: China	Early Cretaceous
Zhang (1987)	OPETIIDAE	*Pseudopetia*	*grandis*	PA: China	Early Cretaceous
Mostovski (1995a)	PLATYPEZIDAE	*Maritulus*	*sospes*	PA: Russia	Early Cretaceous
Mostovski (1995a)	PLATYPEZIDAE	*Promittor*	*malus*	PA: Russia	Early Cretaceous
Mostovski (1995)	PLATYPEZIDAE	*Parnasos*	*firmipes*	PA: Russia	Early Cretaceous
Mostovski (1995)	PLATYPEZIDAE	*Parnasos*	*dissimilis*	PA: Russia	Early Cretaceous
Mostovski (1995)	PLATYPEZIDAE	*Parnasos*	*pessimus*	PA: Russia	Early Cretaceous
Mostovski (1995)	PLATYPEZIDAE	*Proplatypeza*	*parva*	PA: Russia	Early Cretaceous
Mostovski (1995)	PLATYPEZIDAE	*Proplatypeza*	*secunda*	PA: Mongolia	Early Cretaceous
Mostovski (1995)	PLATYPEZIDAE	*Proplatypeza*	*caelebs*	PA: Russia	Early Cretaceous
Mostovski (1995)	PLATYPEZIDAE	*Proplatypeza*	*amabilis*	PA: Russia	Early Cretaceous
Mostovski (1995)	PLATYPEZIDAE	*Proplatypeza*	*bontsaganica*	PA: Mongolia	Early Cretaceous
Mostovski (1995)	PLATYPEZIDAE	*Oloplatypeza*	*munusculum*	PA: Russia	Early Cretaceous
Grimaldi & Cumming (1999)	PLATYPEZIDAE	*Electrosania*	*cretica*	NE: New Jersey amber	Cretaceous
Coram et al. (2000)	OPETIIDAE	*Opetiala*	*shatalkini*	PA: UK	Early Cretaceous
Grimaldi (2018)	PLATYPEZIDAE	*Burmapeza*	*radicis*	OR: Burmese	Cretaceous
Grimaldi (2018)	PLATYPEZIDAE	*Canadopeza*	*biacrosticha*	NE: Canada	Late Cretaceous
Grimaldi (2018)	PLATYPEZIDAE	*Lebanopeza*	*azari*	PA: Lebanon	Early Cretaceous
Grimaldi (2018)	PLATYPEZIDAE	*Microsania*	sp.	PA: Baltic	Eocene
Grimaldi (2018)	PLATYPEZIDAE	*Calvopeza*	*divergens*	OR: Burmese	Cretaceous
Grimaldi (2018)	PLATYPEZIDAE	*Chandleromyia*	*anomala*	OR: Burmese	Cretaceous
Grimaldi (2018)	PLATYPEZIDAE	*Lindneromyia*	*neomedialis*	NT: Dominican	Miocene
Grimaldi (2018)	PLATYPEZIDAE	*Lindneromyia*	*dominicana*	NT: Dominican	Miocene
Tkoč in Greenwalt et al. (2019)	PLATYPEZIDAE	*Agathomyia*	*eocenica*	NE: USA	Eocene

Opetia atra, as the first known representative of Opetiidae was described from the Late Oligocene of Rott Formation by STATZ (1940). Other 5 new species attributed to four new genera of Opetiidae were described by ZHANG (1987) from the Laiyang Formation (China). Later, two of them were excluded from Platypezidae/Opetiidae and trasferred to Ironomyidae by MOSTOVSKI (1995a, 1995b). HONG & WANG (1988) described a new subfamily Sinolestinae within Platypezidae with one new species, *Sinolesta lata*, but this subfamily was also excluded from Platypezidae and later transferred into Ironomyiidae by MOSTOVSKI (1995b).

Catalogue of Fossil flies includes 11 fossil species in 9 genera of Opetiidae and Platypezidae (EVENHUIS 1994). After the works of MOSTOVSKI (1995a, 1995b) three species in three different genera should be excluded from this list (see above). MOSTOVSKI (1995) described 5 new genera and 11 new fossil species of Platypezidae from the Cretaceous deposits of Russia and Mongolia. GRIMALDI & CUMMING (1999) described a new genus and species as *Electrosania cretica* from the Late Cretaceous of New Jersey Amber (USA). CORAM et al. (2000) added a new species of Opetiidae, *Opetiala shatalkini*, from the Early Cretaceous (Berriasian age) of the Durslton Formation in Dorset (UK).

Detailed description of 8 new species found in amber was reported by GRIMALDI (2018). Five new Cretaceous genera were described from Burmese, Lebanese, and Canadian ambers. Two new species assigned to the extant genus *Lindneromyia* were described from the Miocene of Dominican amber. Additionally, an unnamed species of *Microsania* was described from the Late Eocene of Baltic amber.

The first fossil species of the genus *Agathomyia* as *A. eocenica* was described by Tkoč in GREENWALT et al. (2019 - **PUBLICATION 5**). This species was found in the Middle Eocene deposits of Kishenehn Formation at Dakin site, Montana (USA).

During the study of fossil representatives we have also discovered a specimen which does not belong to flat-footed flies, but it was so interesting in respect of morphology and taxonomy that we decided to include this new species in this dissertation thesis (TKOČ et al. 2016 - **PUBLICATION 4**). This species was described as *Microphorites moravicus* and belongs to the family Dolichopodidae (sensu lato). It was found in the Paleogene Moravian amber (Študlov locality).

5. FAUNISTIC RESEARCH

Faunistic research is essential for obtaining basic data and knowledge about the studied families and their species. Here, I am presenting the most important and recent faunistic and biodiversity research on flat-footed flies.

5.1 CZECH AND SLOVAK REPUBLIC

Based on 1742 new specimens and 1591 already published records of Opetiidae and Platypezidae, the fauna of the Czech and Slovak Republics was treated by VAŇHARA (1995). Thirty-two species were found in the Czech Republic and 27 species in Slovakia. Also, species quality index was determined, and vertical and horizontal distribution was evaluated for each species.

VAŇHARA & ROHÁČEK (1995) presented results of faunistic research in Bukovské vrchy hills is eastern Slovakia, 19 species of Opetiidae and Platypezidae were found and 7 of them were new for Slovakia. VAŇHARA (1998) published faunistic research of Pálava Biosphere reserve with following results – 19 species. VAŇHARA & BARTÁK (2000a, b) reported 15 species from Bílina and Duchcov environs (North-Wester Bohemia). VAŇHARA et al. (2005) evaluated the fauna of the Podyjí National Park, they found 19 species of Platypezidae, but *Opetia nigra* was not found. TKOČ & VAŇHARA (2008b) published 12 species from Jizerské hory Mts and Frýdlant region. The following biodiversity study of Jizerské hory Mts and its surroundings resulted in finding of 22 species (TKOČ et al. 2020 - **PUBLICATION 9**), including one new species for the Czech Republic and 8 species new for the studied area.

ROHÁČEK & ŠEVČÍK (2009) published faunistic data of Poľana Protected Landscape Area (Slovakia) with 23 species of flat-footed flies. ŠEVČÍK (2010) published a monograph of the Czech and Slovak Diptera associated with fungi, where rearing records of 10 species of Platypezidae are listed. ROHÁČEK & ŠEVČÍK 2011 also evaluated the fauna of Gemer, 18 species of Opetiidae and Platypezidae were found.

TKOČ (2011 - **PUBLICATION 6**) published a new species record for the Czech Republic, *Polyporivora picta*, and added information on its larval biology and distribution in Europe. Two new regional records from Bohemia (*Lindneromyia hungarica*, *Platypeza aterrima*) and one new record from Slovakia (*Kesselimyia chandleri*) of Platypezidae were added by TKOČ et al. (2012 - **PUBLICATION 7**). Additional two species (*Polyporivora picta*, *Seri obscuripennis*) were recorded from Bohemia and one new species (*Agathomyia cinerea*) was found in the Czech Republic for the first time (TKOČ 2016 - **PUBLICATION 8**).

5.2 EUROPE

CLAUSSEN (2013) recorded 22 species of flat-footed flies (Diptera: Platypezidae) from the district of Schleswig (Northwest Germany: Schleswig-Holstein). The material for this study was collected over the period 1989–2011 by sweeping and by rearing from the host-fungi.

The diversity of Romanian fauna was evaluated by TKOČ & ROHÁČEK (2014 - **PUBLICATION 3**) with three new country records, expanding the number of know species from Romania to 18. Biology and distribution of all species was commented. Additionally, male of *Callomyia saibhira* was redescribed and its genitalia figured in detail.

REEMER & DE JONG (2016) published detailed monographic study of Dutch flat-footed fauna. The key to all 37 Dutch (and 12 more from surrounding countries) species is supplemented with many illustrations and photographs.

Formerly, the species number for these two families in Europe was 44 (CHANDLER 2001, 2014), however two new records have been recently added by STÅHLS & RÄTTEL (2013) and STÅHLS et al. (2014). Further revision was made by STÅHLS et al. (2015), who added four more species from the genus *Agathomyia* to the European fauna, two were described as new and two were resurrected from synonymy of *Agathomyia elegantula* Chandler in Shatalkin, 1985. In Europe, these two families currently comprise 50 species in 13 genera, 34 of them are known from the Czech Republic (30 from Bohemia and 32 from Moravia) (for detailed summary see Tab. 7).

Table 7. Species numbers of Opetiidae and Platypezidae in Czech Republic & Slovakia, in Czech Republic, Bohemia, Moravia, Slovakia and Europe. (* – Czech and Slovak Diptera Checklist; ** – Fauna Europaea; BOH – Bohemia; CZ – Czech Republic; MOR – Moravia; SK – Slovakia).

Reference	CZ & SK	CZ	BOH	MOR	SK	EUROPE
VAŇHARA 2009*	36	32	25	31	31	-
ROH. & ŠEV. 2011	-	-	-	-	+1	-
TKOČ 2011	-	+1	-	+1	-	-
TKOČ et al. 2012	-	-	+2	-	+1	-
TKOČ 2016	-	+1	+3	-	-	-
CHANDLER 2001	-	-	-	-	-	44
CHANDLER 2014**	-	-	-	-	-	44
STÅHLS & RÄTTEL 2013	-	-	-	-	-	+1
STÅHLS et al. 2014	-	-	-	-	-	+1
STÅHLS et al. 2015	-	-	-	-	-	+4
TOTAL	**36**	**34**	**30**	**32**	**33**	**50**

6. CONCLUSIONS AND PROSPECTS

The flat-footed flies are not numerous, but suprisingly diverse group of Diptera with very interesting biological role in the ecosystems. In previous chapters, I have tried to summarize their diversity, systematics, biology and phylogeny. In many respects, the state of knowledge of this group is still insufficient and offers interesting topics for further study. I have contributed by attached publications to some of the knowledge of these peculiar flies. But this is not the end my scientific journey, on the contrary, this is just the beginning. Several important questions arose during my studies of flat-footed flies. Here, I will try to summarize the most important research topics, that I will try to resolve in my future studies:

(i) Identification of the morphological characters with the high phylogentical value (evolutinary novelties, real synapomorphies) and carefull construction of the morphology-based phylogenetical tree using modern computational methods. Detailed comparison with previous studies (based on larval morphology, adult characters or molecular characters).

(ii) Description of new taxa, revision of selected taxa. Currently I am working on revision of Palaearctic *Callomyia* and description of two new species of *Agathomyia* from central Europe.

(iii) Biodiversity and faunistic studies of local fauna. I am currently involved in several projects dealing with fauna of several protected areas in the Czech Republic and Slovakia. Also complete investigation of Hungarian fauna is on the way.

(iv) Compiling of catalogues and checklists. Checklist of the Czech and Slovak fauna is under preparation. A catalogue of world species is planned in the future.

(v) Further taxonomy studies with description of new fossil taxa are planned. I am currently preparing descriptions of few new species from Baltic amber. I will also continue to investigate the fauna of the Kishenehn Formation (Montana, USA).

(vi) Coevolutional, biological and ecological questions: (i) Determine the role of adults and larvae in the reproduction, distribution and evolution of their fungal hosts; (ii) Does the biological activity of flat-footed flies help the reproduction and spreading of their fungal hosts? (iii) Coevolution of flat-footed flies and the fungal hosts.

REFERENCES

Aczél M. L. 1958: Géneros y especies Argentinae de las Clythiidae (Platypezidae, Diptera) con catalogo de las especies neotropicales. *Acta Zoologica Lilloana* **15**: 47–82.

Amorim D. S., Silva V. C. & Brown B. V. 2018: *Puyehuemyia chandleri*, gen. nov., sp. nov. (Diptera: Opetiidae): Remnant of a Cretaceous Biota in Chile. *American Museum Novitates* **3892**: 1–27.

Beschovski V. 2004: Genus *Kesselimyia*, *K. chandleri* and subfamily Platypezinae (Insecta: Diptera, Platypezidae): new taxa to the Bulgarian fauna. *Acta Zoologica Bulgarica* **56**: 237–238.

Brown B. V. 1992: Generic revision of Phoridae of the Nearctic Region and phylogenetic classification of Phoridae, Sciadoceridae, and Ironomyiidae (Diptera: Phoridea). *The Memoirs of the Entomological Society of Canada* **124(Supplementum 164)**: 3–144.

Brown B. V. 1995: Response to Disney. *Journal of Natural History* **29**: 259–264.

Brown B. V., Amorim D. S. & Kung G. A. 2015: New morphological characters for classifying Phoridae (Diptera) from the structure of the thorax. *Zoological Journal of the Linnean Society* **173**: 424–485.

Chandler P. J. 1973: The flat-footed flies (Diptera, Aschiza-Platypezidae) known to occur in Kent with a key to the genera and species so far recorded from the British Isles. *Transactions of the Kent Field Club* **5**: 15–44.

Chandler P. J. 1974: Additions and corrections to the British list of Platypezidae (Diptera), incorporating a revision of the Palaearctic species of *Callomyia* Meigen. *Proceedings and transactions of the British Entomological and Natural History Society* **7**: 1–32.

Chandler P. J. 1976: A new species of *Callomyia* Meigen (Diptera: Platypezidae) from Bulgaria. *Entomologist Gazette* **27**: 257–261.

Chandler P. J. 1978: Some dipterous opportunists at Windsor Forest, Berks: the attractions for flies of bonfires, wood ash and freshly cut logs. *Entomologist's Gazette* **29**: 253–257.

Chandler P. J. 1980: Platypezidae (Diptera) from Israel, including the Description of two new species. *Entomologist's Gazette* **31**: 165–170.

Chandler P. J. 1989: Superfamily Platypezoidea. 46. Family Platypezidae. Pp. 420–421. In: Evenhuis N. L. (Ed.): *Catalogue of the Diptera of the Australasian and Oceanian Regions*. Honolulu & Leiden, Bishop Museum Press & E. J. Brill, USA & The Netherlands. 1155 pp.

Chandler P. J. 1991: Opetiidae. Platypezidae. Pp. 204–217. In: Soós Á. & Papp L. (Eds): *Catalogue of Palaearctic Diptera. Dolichopodidae – Platypezidae. Vol. 7.* Akadémiai Kiadó, Budapest, Hungary. 291 pp.

Chandler P. J. 1994: The Oriental and Australasian species of Platypezidae (Diptera). *Invertebrate Taxonomy* **8**: 351–434.

Chandler P. J. 1998: Opetiidae. Pp. 17–25. In: Papp L. & Darvas B. (Eds): *Contributions to a Manual of Palaearctic Diptera (with special reference to flies of economic importance). Vol. 3. Higher Brachycera.* Science Herald, Budapest. 880 pp.

Chandler P. J. 2001: The flat-footed flies (Diptera: Opetiidae and Platypezidae) of Europe. *Fauna Entomologica Scandinavica Volume 36*, Brill, Leiden, Boston, Köln, 276 pp.

Chandler P. J. 2010: 50. Platypezidae (Flat-footed Flies). Pp. 715–719. In: B. V. Brown, A. Borkent, J. M. Cumming, D. M. Wood, Woodley N. E. & Zumbado M. (Eds): *Manual of Central American Diptera, Volume 2*. National Research Council Press, Ottawa, Ontario, Canada. 728 pp.

Chandler P. J. 2014: Fauna Europaea: Platypezidae. In: Pape T. (Ed): *Fauna Europaea: Diptera, Brachycera. Fauna Europaea version 2.6.2.* http://www.faunaeur.org. Accessed 30.vii.2020.

Chandler P. J. 2021: Platypezidae (flat-footed flies). Pp. 1365–1374. In: Kirk-Spriggs A. H. & Sinclair B. J., (Eds): *Manual of Afrotropical Diptera. Volume 3. Brachycera–Cyclorrhapha, excluding Calyptratae. Suricata 8*. South African National Biodiversity Institute, Pretoria, Republic of South Africa.

Chandler P. J. & Shatalkin A. I. 1998: Platypezidae. Pp. 17–25. In: Papp L. & Darvas B. (Eds): *Contributions to a Manual of Palaearctic Diptera (with special reference to flies of economic importance). Vol. 3. Higher Brachycera.* Science Herald, Budapest. 880 pp.

Chvála M. 1981: Classification and phylogeny of Empididae, with a presumed origin of Dolichopodidae (Diptera). *Entomologica Scandinavica*, *Supplement* **15**: 225–236.

Chvála M. 1983: The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General Part. The Families Hybotidae, Atelestidae and Microphoridae. *Fauna Entomologica Scandinavica* **12**: 1–279.

Claussen C. 2013: Neue Nachweise von Sohlenfliegen (Diptera: Platypezidae) aus Schleswig-Holstein (Deutschland). *Studia dipterologica* **20(1)**: 3–21.

Cockerell T. D. A. 1909: Descriptions of Tertiary insects, part V. *American Journal of Science, Fourth Series* **27**: 53–58.

Cockerell T. D. A. 1911: Fossil Insects from Florissant, Colorado. *Bulletin of the American Museum of Natural History* **30**: 71–82.

Collin J. E. 1931: Platypezidae, Pipunculidae. *Diptera of Patagonia and south Chile* **6**: 49–61.

Collin J. E. 1961: Empididae. In: *British Flies, Volume 6*. Cambridge University Press, Cambridge, United Kingdom. 782 pp.

Collins K. P. & Wiegmann B. M. 2002: Phylogenetic relationships and placement of the Empidoidea (Diptera: Brachycera) based on 28S rDNA and EF–1 sequences. *Insect Systematics & Evolution* **33**: 421–444.

Coram R., Jarzembowski E. A. & Mostovski M. B. 2000: Two rare eremoneuran flies (Diptera: Empididae and Opetiidae) from the Purbeck Limestone Group. *Paleontological Journal* **34(Supplementum 3)**: S370–S373.

Cumming H. J. & Wheeler T. A. 2016: Revision of the Nearctic species of *Callomyia* Meigen (Diptera: Platypezidae) and phylogeny of the genus. *Zootaxa* **4111**: 501–554.

Cumming J. M. & Cumming H. J. 2011: The flat-footed fly genus *Seri* Kessel & Kessel (Diptera: Platypezidae). *Zootaxa* **3136**: 61–68.

Cumming J. M., Sinclair B. J. & Wood D. M. 1995: Homology and phylogenetic implications of male genitalia in Diptera – Eremoneura. *Entomologica scandinavica* **26**: 121–151.

Cumming J. M. & Wood D. M. 2009: Morphology and terminology. Pp. 9–50. In: Brown B. V., Borkent A., Cumming J. M., Wood D. M., Woodley N. E. & Zumbado M. (Eds): *Manual of Central American Diptera: Volume 1*. National Research Council Press, Ottawa, Ontario, Canada. 714 pp.

Czerny L. 1930: Clythiidae (Platypezidae). In: Lindner E. (Ed.): *Die Fliegen der palaearktischer Region 34*. Schweizerbart´sche verlagsbuchhandlung, Stuttgart, Germany. 29 pp.

Disney R. H. L. 1987: Evidence that *Opetia nigra* Meigen (Dipt., Opetiidae) is not a Muscomorphan. *Entomologist's Monthly Magazine* **123**: 47.

Disney R. H. L. 1988: The form of articulation between the pedicel and first flagellar segment of the antenna in flies (Diptera). *The Entomologist* **107**: 99–103.

Disney R. H. L. 1994: *Scuttle Flies: The Phoridae*. Chapman and Hall, London, United Kingdom. 467 pp.

Feuerborn H. J. 1922: Das Hypopygium “inversum” und “circumversum” der Dipteren. *Zoologischer Anzeiger* **60**: 189–212.

Foottit R. G. & Adler P. H. 2017: *Insect Biodiversity: Science and Society, 2nd Edition*. Wiley-Blackwell, West Sussex, United Kingdom. 904 pp.

Galinskaya T. V., Shatalkin, A. I. & Ovtshinnikova O. G. 2019: The Skeleton and Musculature of the Male Genitalia in Platypezidae (Diptera). *Entomological Review* **99**: 774–786.

Greenwalt D. E., Bickel D. J., Kerr P. H., Curler G. R., Brown B. V., Jong H., Fitzgerald S. J., Dikow T., Tkoč M., Kehlmaier Ch. & Amorim D. S. 2019: Diptera of the middle Eocene Kishenehn Formation. I. Documentation of diversity at the family level. *Palaeontologia Electronica* **22(2.50A)**: 1–56.

Griffiths G. C. D. 1972: *The phylogenetic classification of Diptera Cyclorrhapha with special reference to the structure of the male postabdomen*. Dr. W. Junk N. V. Publishers, The Hague, Netherlands. 340 pp.

Grimaldi D. A. 2018: Basal Cyclorrhapha in Amber from the Cretaceous and Tertiary (Insecta: Diptera), and Their Relationships: Brachycera in Cretaceous Amber Part IX, *Bulletin of the American Museum of Natural History* **423**: 1–97.

Grimaldi D. A. & Cumming J. 1999: Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History* **239**: 1–124.

Han S. & Yang D. 2016: Three New Species of *Linderomyia* from Laos (Diptera: Platypezidae). *Transactions of the American Entomological Society* **142(1)**: 54–72.

Han S. & Yang D. 2017a: One New Species of *Agathomyia* and Three New Species of *Lindneromyia* from Shaanxi, China (Diptera: Platypezidae). *Transactions of the American Entomological Society* **143(2)**: 153–177.

Han S. & Yang D. 2017b: One New Species of *Agathomyia* and Four New Species of *Lindneromyia* from Yunnan, China (Diptera: Platypezidae). *Transactions of the American Entomological Society* **143(2)**: 473–500.

Hennig W. 1948: *Die Larvenformen der Dipteren. Volume I.* Akademie-Verlag, Berlin, Germany. 185 pp.

Hennig W. 1976: Das Hypopygium von *Lonchoptera lutea* Panzer und die phylogenetischen Verwandtschaftsbeziehungen der Cyclorrhapha (Diptera). *Stuttgarter Beiträge zur Naturkunde*, *Serie A (Biologie)* **283**: 1–63.

Kessel E. L. 1957: Distribution and variation in *Agathomyia notata* (Loew) (Diptera: Platypezidae). Wasmann Journal of Biology **15**: 69–80.

Kessel E. L. 1960: The systematic positions of *Platycnema* Zetterstedt and *Melanderomyia*, new genus, together with the description of the genotype of the latter (Diptera: Platypezidae). *Wasmann Journal of Biology* **18**: 87–101.

Kessel E. L. 1961a: A new species of *Platypezina* from North America (Diptera: Platypezidae). *Wasmann Journal of Biology* **19**: 187–190.

Kessel E. L. 1961b: New species of flat-footed flies from North America (Diptera: Platypezidae). *Wasmann Journal of Biology* **19**: 191–227.

Kessel E. L. 1961c: The fungus hosts of *Melanderomyia* (Diptera: Platypezidae). *Wasmann Journal of Biology* **19**: 291–294.

Kessel E. L. 1963: The genus *Calotarsa*, with special reference to *C. insignis* Aldrich (Diptera: Platypezidae). *Occasional papers of the California Academy of Sciences* **39**: 1–24.

Kessel E. L. 1965: Family Platypezidae. Pp. 546–550. In: Stone A., Sabrosky C. W., Wirth W. W., Foote R. H. & Coulson J. R. (Eds.): *A catalog of the Diptera of America north of Mexico.* Agricultural Research Service, United States Department of Agriculture, Washington D.C., USA. 1696 pp.

Kessel E. L. 1966a: Diptera from Nepal, new species of *Platypeza* and *Callomyia* (Family Platypezidae). *Bulletin of the British Museum (Natural History), Entomology* **17**: 453–455.

Kessel E. L. 1966b: *Symmetricella*, a new genus of Platypezidae from Peru (Diptera). *Wasmann Journal of Biology* **23(1965)**: 235–239.

Kessel E. L. 1968: Circumversion and mating positions in Platypezidae – an expanded and emended account (Diptera). *Wasmann Journal of Biology* **26**: 243–253.

Kessel E. L. 1970: *Bertamyia*, a new genus of Platypezininae (Diptera: Platypezidae). *Wasmann Journal of Biology* **28**: 185–190.

Kessel E. L. 1987: 50. Family Platypezidae. Pp. 681–688. In: McAlpine J. F., Peterson B. V., G. E. Shewell G. E., Teskey H. J., Vockeroth J. R. & Wood D. M. (Eds): *Manual of Nearctic Diptera. Agriculture Canada Monographs, Vol. 2*. Research Branch, Ottawa, Ontario, Canada. Pp. 675–1332.

Kessel E. L. & Buegler M. E. 1972: A review of the genus *Callomyia* in North America, with the description of a new species (Diptera: Platypezidae). *Wasmann Journal of Biology* **30**: 241–278.

Kessel E. L. & Clopton J. R. 1970: The Platypezidae of the Ethiopian zoogeographic region, with descriptions of new species and a new genus (Diptera). *Wasmann Journal of Biology* **28**: 47–167.

Kessel E. L. & Kessel B. B. 1961: Observations on the mating behavior of *Platypezina pacifica* Kessel (Diptera: Platypezidae). *Wasmann Journal of Biology* **19**: 295–299.

Kessel E. L. & Kessel B. B. 1962: Mating behavior and activity – rest periodicity in *Protoclythia californica* (Diptera: Platypezidae). *Proceedings of the California Academy of Sciences, Fourth series* **32**: 57–78.

Kessel E. L. & Kessel B. B. 1966: *Seri*, a new genus of Platypezidae from North America. *Wasmann Journal of Biology* **24**: 97–100.

Kessel E. L. & Maggioncalda E. A. 1968: A revision of the genera of Platypezidae, with the descriptions of five new genera and considerations of phylogeny, circumversion and hypopygia (Diptera). *Wasmann Journal of Biology* **26**: 33–106.

Kessel E. L. & Young D. R. 1974: The genus *Calotarsa*. Description of three new species, and range extension of *C. calceata* (Snow) (Diptera: Platypezidae). *Wasmann Journal of Biology* **32**: 147–172.

Krivosheina N. P. 2008a: On biology of xylobiont platypezid larvae of the genus *Callomyia* (Diptera, Platypezidae). *Entomological Review* **88(8)**: 973–982. (Original Russian text published in *Zoologicheskii Zhurnal* **87(11)**: 1338–1347).

Krivosheina N. P. 2008b: On the larval morphology of flat-footed flies of the genera *Polyporivora*, *Seri*, and *Bolopus* (Diptera, Platypezidae) developing in fruit bodies of fungi. Entomological Review **88(8)**: 983–1001. (Original Russian text published in *Zoologicheskii Zhurnal* **87(12)**: 1476–1494).

Li X. & Yeates D. K. 2018: The first Ironomyiidae from mid-Cretaceous Burmese amber provides insights into the phylogeny of Phoroidea (Diptera: Cyclorrhapha). *Systematic Entomology* **44(1)**: 251–261.

McAlpine J. F. 1989: Phylogeny and classification of the Muscomorpha. Pp. 1397–1518. In: McAlpine J. F. & Wood D. M. (Eds): *Manual of Nearctic Diptera*, *Agriculture Canada Monographs, Vol. 3*. Research Branch, Ottawa, Ontario, Canada. Pp. 1333–1581.

Melander A. L. 1922: *Microsania*, a genus of the Platypezidae. *Psyche* **29**: 43–48.

Meunier F. 1893: Note sur les Platypezidae fossiles de l'ambre tertiaire. *Bulletin de la Société Zoologique de France* **18**: 230–232.

Milberg P., Bergman K.-O., Norman H., Pettersson R. B., Westerberg L., Wikars L.-O. & Jansson N. 2015: A burning desire for smoke? Sampling insects favoured by forest fire in the absence of fire. *Journal of Insect Conservation* **19**: 55–65.

Mostovski M. B. 1995a: New representatives of Platypezidae (Diptera) from the Mesozoic, and main directions in the evolution of the family. *Paleontologischeskii Zhurnal* **2**: 106–118.

Mostovski M. B. 1995b: New taxa of ironomyiid flies (Diptera, Phoromorpha, Ironomyiidae) from Cretaceous deposits of Siberia and Mongolia. *Paleontologicheskii Zhurnal* **4**: 86–103.

Moulton J. K. & Wiegmann B. M. 2004: Evolution and phylogenetic utility of CAD (rudimentary) among Mesozoic-aged eremoneuran Diptera (Insecta). *Molecular Phylogenetics and Evolution* **31**: 363–378.

Moulton J. K. & Wiegmann B. M. 2007: The phylogenetic relationships of flies in the superfamily Empidoidea (Insecta: Diptera). *Molecular Phylogenetics and Evolution* **43**: 701–713.

Oldenberg L. 1916: Neue europäïsche und südamerikanische Clythiiden (= Platypeziden; Dipt.). *Archiv für Naturgeschichte, Abteilung A* **82(1)**: 120–136.

Pape T., Blagoderov V. & Mostovski M. 2011: Order DIPTERA Linnaeus, 1758. Pp. 222–229. In: Zhang Z.-Q. (Ed): Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness. *Zootaxa* **3148**: 1–237.

Poole R. W. & Gentili P. 1996: *Nomina Insecta Nearctica: A Check List of the Insects of North America, Volume 3: Diptera, Lepidoptera, Siphonaptera*. Entomological Information Services, Rockville, Maryland, USA. Pp. 605–1143.

Reemer M. & De Jong H. 2016: De Nederlandse breedvoetvliegen en basterdbreedvoet-vliegen (Platypezidae & Opetiidae). *Entomologische Tabellen* **10**: 1–135. (In Dutch, English summary and key to species).

Roháček J. & Ševčík J. 2007: Faunistic records from Czech Republic and Slovakia: Platypezidae. In: Stloukalová V. (Ed): Dipterologica bohemoslovaca. Vol. 14. *Acta Zoologica Universitatis Comenianae* **47**: 255–256.

Roháček J. & Ševčík J. 2009: Opetiidae, Platypezidae. Pp. 150–155. In: Roháček J. & Ševčík J. (Eds): *Diptera of the Poľana Protected Landscape Area - Biosphere Reserve (Central Slovakia)*. SNC SR, Administration of the PLA - BR Poľana, Zvolen, Slovakia. 340 pp.

Roháček J. & Ševčík J. 2011: The fauna of Opetiidae and Platypezidae (Diptera) in the Gemer region (Central Slovakia). *Časopis Slezského Muzea Opava (A)* **60**: 41–47.

Roháček J. & Ševčík J. 2013: Diptera associated with sporocarps of *Meripilus giganteus* in an urban habitat. *Central European Journal of Biology* **8(2)**: 143–167.

Rotheray G. E. & Gilbert F. 2008: Phylogenetic relationships and the larval head of the lower Cyclorrhapha (Diptera). *Zoological Journal of the Linnean Society* **153**: 287–323.

Rotheray G. E., Chandler P. J. & Gilbert F. 2004: Final stage larvae and puparia of Platypezidae (Diptera). *Insect Systematics & Evolution* **35**: 79–105.

Scudder S. H. 1890: The Tertiary Insects of North America. *Report of the United States Geological Survey of the Territories* **XIII**: 1–734.

Shatalkin A. I. 1980: Novye vidy Platypezidae (Diptera) iz Sredney territorii Amurskoy. (New species of Platypezidae (Diptera) from Middle Amur Territory). *Entomologicheskoe Obozrenie* **59**: 660–665. (In Russian, English summary).

Shatalkin A. I. 1982: Novye vidy vrasplokh mukhi (Diptera, Platypezidae) iz Sibiri i Dal'nego Vostoka. [New species of mushroom flies (Diptera, Platypezidae) from Siberia and the Far East]. Pp. 68–75. In: Cherepanov A. I. (Ed.): *Gel'minty, kleshchi, i nasekomye. Novye i maloizvestnye vidy fauny Sibiri. Vypusk 16*. [*Helminths, mites and insects. New and little-known species of Siberian fauna. Issue 16*]. Nauka, Novosibirsk, USSR. 98 pp. (In Russian).

Shatalkin A. I. 1985: Obzor gribnykh mukh (Diptera, Platypezidae) fauny SSSR. [A review of the flat-footed flies (Diptera, Platypezidae) of USSR]. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR* **23**: 69–136. (In Russian).

Shatalkin A. I. 1992: New and little-known Palaearctic Diptera of the families Platypezidae, Psilidae and Lauxaniidae. *Russian Entomological Journal* **1(2)**: 59–74.

Sinclair B. J. & Cumming J. M. 2006: The morphology, higher level phylogeny and classification of the Empidoidea (Diptera). *Zootaxa* **1180**: 1–172.

Sinclair B. J., Cumming J. M. & Brooks S. E. 2013: Male terminalia of Diptera (Insecta): a review of evolutionary trends, homology and phylogenetic implications. *Insect Systematics & Evolution* **44**: 373–415.

Smith K. G. V. 1956: On the Diptera associated with the stinkhorn (*Phallus impudicus* Pers.) with notes on other insects and invertebrates found on this fungus. *Proceedings of the Royal Entomological Society of London, Series A, General Entomology* **31**: 49–55.

Smith K. G. V. 1980: Family Platypezidae. Pp. 480–482. In: Crosskey R. W. (Ed.): *Catalogue of the Diptera of the Afrotropical Region*. British Museum (Natural History), London, United Kingdom. 1437 pp.

Snoddy E. L. & Tippins H. H. 1968: On the ecology of a smoke fly, *Microsania imperfecta*. *Annals of the Entomological Society of America* **61**: 1200–1201.

Speight M. C. G., Blackith R. E. & Blackith R. M. 1990: *Antichaeta brevipennis*, *Leucophenga maculata*, *Polyporivora picta* and *Tephrochlamys tarsalis* (Diptera): insects new to Ireland. *Irish Biogeographical Society Bulletin* **13(2)**: 131–136.

Ståhls G. M. & Kahanpää J. 2006: New data on Platypezidae and Opetiidae (Diptera) of Finland. *Sahlbergia* **11**: 1–6.

Ståhls G. M. & Rättel E. 2013: Genus *Microsania* (Platypezidae: Microsaninae) in Finland. *Sahlbergia* **19**: 50–52.

Ståhls G. M., Rättel E. & Miettinen O. 2014: New data on genus *Callomyia* of Finland (Diptera: Platypezidae). *Sahlbergia* **20**: 9–12.

Ståhls G. M., Miettinen O. & Rättel E. 2015: mtDNA COI in efficient use: clarifying taxonomy, linking morphologically discordant sexes and identifying the immature stages of *Agathomyia* Verrall flat-footed flies (Diptera: Platypezidae). *Journal of Zoological Systematics and Evolutionary Research* **53(3)**: 219–238.

Statz G. 1940: Neue Dipteren (Brachycera et Cyclorhapha) aus dem Oberoligozän von Rott. *Palaeontographica Abteilung A* **91**: 120–174.

Stork N. E. 2018: How Many Species of Insects and Other Terrestrial Arthropods Are There on Earth? *Annual Review of Entomology* **63**: 31–45.

Szilády Z. 1941: Clythiiden (Platypezidae) aus Ungarn (Diptera). *Annales Musei Nationalis Hungarici, Zoologica* **43**: 102–104.

Ševčík J. 2004: Diptera associated with fungi in the Poloniny National Park (Bukovské vrchy Mts., East Slovakia). In: Barták M. & Kubík Š. (Eds): Dipterologica bohemoslovaca 13. *Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia* **109**: 293–304.

Ševčík J. 2010: *Czech and Slovak Diptera associated with fungi.* Slezské zemské museum, Opava, Czech Republic. 112 pp.

Tanasijtshuk V. N. 1970: 48. Sem. Platypezidae (Clythiidae). [Family Platypezidae (Clythiidae)]. Pp. 6–12. In: Stackelberg A. A. & Nartshuk E. P. (Eds): *Opredelitel nasekomykh evropeiskoi chasti SSSR. Dvukrylye, blokhi.* [*Keys to the insects of the European part of the USSR. Flies, fleas*]. Vol. 5, Part 2. Nauka, Leningrad. 944 pp. (In Russian).

Tkoč M. 2011: New records of *Polyporivora picta* (Meigen, 1830) from the Czech Republic and Greece with notes on its larval biology and distribution in Europe (Diptera: Platypezidae). *Časopis Slezského Muzea Opava (A)* **60**: 263–267.

Tkoč M. 2012: A new species of the flat-footed fly genus Callomyia (Diptera: Platypezidae) from South China. *Acta Entomologica Musei Nationalis Pragae* **52(1)**: 289–296.

Tkoč M. 2016: New records of the flat-footed flies (Diptera: Platypezidae) from the Czech Republic and Bohemia. *Acta Musei Silesiae, Scientiae Naturales* **65**: 65–70.

Tkoč M. & Barták M. 2013: Flat-footed flies (Diptera: Platypezidae and Opetiidae) of Vráž nr. Písek (Czech Republic). In: Kubík Š. & Barták M. (Eds): *Workshop on biodiversity, Jevany*. Pp. 389–395. Česká zemědělská univerzita v Praze, Praha, Czech Republic. 436 pp.

Tkoč M., Mocek B. & Barták M. 2012: New and rare records of the flat-footed flies (Diptera: Platypezidae) from the Czech Republic and Slovakia. *Klapalekiana* **48**: 275–278.

Tkoč M., Nel A. & Prokop J. 2016: Discovery of a new species of the Cretaceous genus *Microphorites* Hennig, 1971 (Diptera: Dolichopodidae s. lat.) in Paleogene amber from eastern Moravia (Czech Republic). *Insect systematics & evolution* **47**: 181–193.

Tkoč M. & Roháček J. 2014: Diversity, distribution and biology of Romanian flat-footed flies (Diptera, Opetiidae and Platypezidae) with taxonomic notes on *Callomyia saibhira* Chandler. *Zookeys* **459**: 95–118.

Tkoč M., Tóthová A., Ståhls G., Chandler P. J. & Vaňhara J. 2017: Molecular phylogeny of flat-footed flies (Diptera: Platypezidae): main clades supported by new morphological evidence. *Zoologica Scripta* **46**: 429–444.

Tkoč M. & Vaňhara J. 2008a: The puparium and mature larva of the flat-footed fly *Lindneromyia hungarica* Chandler, 2001 (Diptera: Platypezidae). *Zootaxa* **1730**: 59–64.

Tkoč M. & Vaňhara J. 2008b: Stlačenkovití (Diptera: Opetiidae a Platypezidae) Jizerských hor a Frýdlantska. Opetiidae and Platypezidae (Diptera) of the Jizerské hory Mts and Frýdlant region. *Sborník Severočeského Muzea, Přírodní Vědy, Liberec* **26**: 255–260.

Vaňhara J. 1981: *Kesselimyia chandleri* n. gen., n. sp. from Czechoslovakia (Diptera: Platypezidae). *Entomologica Scandinavica* **12**: 183–186.

Vaňhara J. 1986: The flat-footed flies (Opetiidae and Platypezidae, Diptera) in a lowland forest. Pp. 79–84. In: Olejníček J. & Spitzer K. (Eds): *Dipterologica bohemoslovaca. Vol. 4.* Jihočeské muzeum v Českých Budějovicích, Přírodní vědy, České Budějovice, Czech Republic. 148 pp.

Vaňhara J. 1995: Recent distribution of flat-footed flies (Diptera: Opetiidae and Platypezidae, Diptera) in Czech and Slovak Republics with a revised check list and species quality indexing. *Časopis Slezského Muzea Opava (A)* **44**: 43–61.

Vaňhara J. 1998: Opetiidae and Platypezidae. In: Rozkošný R. & Vaňhara J. (Eds): Diptera of the Pálava Biosphere Reserve of UNESCO. I. *Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia* **99**: 187–190.

Vaňhara J. & Barták M. 2000: Opetiidae. Platypezidae. In: Barták M. & Vaňhara M. (Eds.): Diptera in an industrially affected region (north-western Bohemia, Bílina and Duchcov environs). Vol. 1. *Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia* **104**: 203–205, 207–211.

Vaňhara J., Barták M. & Kubík Š. 2005: Platypezidae. In: Barták M. & Kubík Š. (Eds): *Diptera of Podyjí National Park and its Environs*. Pp. 183–186. Česká zemědělská univerzita v Praze, Praha, Czech Republic. 432 pp.

Vaňhara J. 2009: Opetiidae Rondani, 1856, Platypezidae Fallén, 1815. In: Jedlička L, Stloukalová V, Kúdela M. (Eds) *Checklist of Diptera of the Czech Republic and Slovakia*. Electronic version 2. http://www.edvis.sk/diptera2009/ or http://zoology.fns.uniba.sk/diptera2009 + CD-ROM. Accessed 30.vii.2018.

Vaňhara J. & Roháček J. 1995: Opetiidae, Platypezidae. Pp. 98–99. In: Roháček J., Starý J., Martinovský J. & Vála M. (Eds): *Diptera Bukovských vrchov* [*Diptera of the Bukovské hills*]. SAŽP – Správa CHKO a BR Východné Karpaty, Humenné, Slovakia. 232 pp. (In Slovakian with English summary).

Weele van der R. 2001: Platypezidae. In: Papp L. (Ed.): *Checklist of the Diptera of Hungary.* Pp. 226–228. Hungarian Natural History Museum, Budapest, Hungary. 550 pp.

Wiegmann B. M., Trautwein M. D., Winkler I. S., Barr N. B., Kim J., Lambkin C., Bertone M. A., Cassel B. K., Bayless K. M., Heimberg A. M., Wheeler B. M., Peterson K. J., Pape T., Sinclair B. J., Skevington J. S., Blagoderov V., Caravas J., Kutty S. N., Schmidt-Ott U., Kampmeier G. E., Thompson F. C., Grimaldi D. A., Beckenbach A.

T., Courtney G. W., Friedrich M., Meier R. & Yeates D. K. 2011: Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences of the United States of America* **108**: 5690–5695.

Wiegmann B. M. & Yeates D. K. 2017: Phylogeny of Diptera. Pp. 253–265. In: Kirk-Spriggs A. H. & Sinclair B. J. (Eds): *Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. Suricata 4.* South African National Biodiversity Institute, Pretoria, Republic of South Africa. 425 pp.

Woodley N. E. 2005: Distributional notes on *Bertamyia notata* (Loew), including the first report of the family Platypezidae from the Caribbean (Diptera: Platypezidae). *Proceedings of the Entomological Society of Washington* **107(3)**: 731–732.

Yeates D. K. & Wiegmann B. M. 1999: Congruence and controversy: toward a higher-level phylogeny of Diptera. *Annual Review of Entomology* **44**: 397–428.

Zatwarnicki T. 1996: A new reconstruction of the origin of eremoneuran hypopygium and its implications for classification (Insecta: Diptera). *Genus* **7**: 103–175.

Zhang J. F. 1987: Four new genera of Platypezidae. *Acta Palaeontologica Sinica* **26**: 595–603.

PUBLICATION 1

Tkoč M., Tóthová A., Ståhls G., Chandler P. J. & Vaňhara J. 2017: Molecular phylogeny of flat-footed flies (Diptera: Platypezidae): Main clades supported by new morphological evidence. *Zoologica Scripta* **46**: 429–444. [IF = 3.057]

PUBLICATION 2

Tkoč M. 2012: A new species of the flat-footed fly genus *Callomyia* (Diptera: Platypezidae) from South China. *Acta Entomologica Musei Nationalis Pragae* **52**: 289–296. [IF = 0.963]

PUBLICATION 3

Tkoč M. & Roháček J. 2014: Diversity, distribution and biology of Romanian flat-footed flies (Diptera, Opetiidae and Platypezidae) with taxonomic notes on *Callomyia saibhira* Chandler. *Zookeys* **459**: 95–118. [IF = 0.933]

PUBLICATION 4

Tkoč M., Nel A. & Prokop J. 2016: Discovery of a new species of the Cretaceous genus *Microphorites* Hennig, 1971 (Diptera: Dolichopodidae s. lat.) in Paleogene amber from eastern Moravia (Czech Republic). *Insect systematics & evolution* **47**: 181–193. [IF = 1.300]

PUBLICATION 5

Greenwalt D. E., Bickel D. J., Kerr P. H., Curler G. R., Brown B. V., de Jong H., Fitzgerald S. J., Dikow T., **Tkoč M.**, Kehlmaier Ch. & Amorim D. S. 2019: Diptera of the middle Eocene Kishenehn Formation. I. Documentation of diversity at the family level. *Palaeontologia Electronica* **22.2.50A**: 1–56. [IF = 1.616]

Note: Only the Platypezidae chapter (pp. 34–36) was written by me.

PUBLICATION 6

Tkoč M. 2011: New records of *Polyporivora picta* (Meigen, 1830) from the Czech Republic and Greece with notes on its larval biology and distribution in Europe (Diptera: Platypezidae). *Acta Musei Silesiae*, *Scientiae Naturales* **60**: 263–267.

PUBLICATION 7

Tkoč M., Mocek B. & Barták M. 2012: New records of the flat-footed flies (Diptera: Platypezidae) from the Czech Republic and Slovakia. *Klapalekiana* **48**: 269–274.

PUBLICATION 8

Tkoč M. 2016: New records of the flat-footed flies (Diptera: Platypezidae) from the Czech Republic and Bohemia. *Acta Musei Silesiae*, *Scientiae Naturales* **65**: 65–70.

PUBLICATION 9

Tkoč M., Roháček J., Preisler J. & Vonička P. 2020: Biodiversity of flat-footed flies (Diptera: Opetiidae and Platypezidae) of the Jizerské hory Mts, Frýdlant region, and Liberec environs (northern Bohemia, Czech Republic). *Sborník Severočeského Muzea*, *Přírodní Vědy* **38**: 27–54.