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Nannotanyderinae: A new subfamily of Tanyderidae (Diptera)

Kornelia Skibińska

ABSTRACT

Wing venation and male genitalia characters were examined for fossil and extant representatives of family Tanyderidae. Based on morphological evidence, it is hypothesized that two separate evolutionary lineages at the subfamily level exist, namely Tanyderinae Osten-Sacken, 1879 and Nannotanyderinae subfam. nov. Differences between them are stated. New genus and species from Eocene Baltic amber is described and illustrated.

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Keywords: systematics, taxonomy; Baltic amber; fossil Diptera; new subfamily; new genus; new species

INTRODUCTION

Tanyderidae Osten-Sacken, 1879, is a family of Diptera including 38 extant species among 10 genera (Table 1). More than half of all described species in this family are distributed in the temperate zone of the northern or southern hemisphere, others are either in the subtropical or tropical zone. The tanyderid fossil fauna includes 27 species in seven genera (Table 2), all recorded from Eurasia. Only one genus, *Protanyderus* Handlirsch, 1909, is represented in both the fossil and extant fauna (Alexander, 1932; Krzemiński and Judd, 1997; Exner and Craig, 1976).

The family is morphologically distinct from other groups of Diptera, both in larval and adult life stages. Adults are small (6 mm body length) to large (30 mm length) in size, with patterned wings and frail, elongate legs (Figure 1). The wings are often sexually dimorphic in size, shape or intensity of banding pattern. The wing venation differs from other Diptera in a greater proportion of plesiomorphic characters (one anal vein reaching the wing margin; five radial veins reaching the wing margin; d-cell closed) (Krzemiński and Judd, 1997). Immature stages of extant species are aquatic to semi-aquatic in lotic habitats. Microhabitats include silt and gravel in stream beds, wet, sandy soil in the marginal zone of streams or the outer layers of rotting logs submerged in streams. Adult males sometimes congregate in large swarms in the evenings; spending the daylight hours among the riparian vegetation near the borders of streams (Krzemiński et al., 2013a).

Macrochile spectrum Loew, 1850, from Upper Eocene Baltic amber, was the first described species of family Tanyderidae; however, some of the earliest described tanyderids were incorrectly placed in Ptychopteridae (Loew, 1850; Alexander, 1913). In 1879, Osten-Sacken proposed Tanyderina to include three genera: *Macrochile* Loew, 1850, *Protoplasa* Osten-Sacken, 1859 and *Tanyderus* Philippi, 1865. Alexander (1920) recognized

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TABLE 1. Extant genera of Tanyderidae.

Genus	Region of distribution
Araucoderus Alexander, 1929	Neotropical (south Chile)
Eutanyderus Alexander, 1928	Australasian (Australia)
Mischoderus Handlirsch, 1909	Australasian (New Zealand)
Neoderus Alexander, 1928	Neotropical (south Chile)
Nothoderus Alexander, 1928	Australasian (Australia)
Peringueyomyina Alexander, 1921	Afrotropical (South Africa)
Protanyderus Handlirsch, 1909	Palaearctic and Oriental
Protoplasa Osten-Sacken, 1859	Nearctic
Radinoderus Handlirsch, 1909	Australasian
Tanyderus Philippi, 1865	Neotropical (central and south Chile)

Tanyderina as a family and divided it into two subfamilies, Tanyderinae and Bruchomyiinae. Subsequently, Alexander (1965) determined that Bruchomyiinae actually belonged to family Psychodidae, effectively eliminating as such the subfamilial classification in Tanyderidae.

The current work is based on an examination of many fossil tanyderids as well as representatives in the extant fauna. A new genus and species from Eocene Baltic amber is described, with particular attention given to characters of the wing and male genitalia. Some fossil and extant species can be grouped taxonomically based on similarities of these structures. Considering these characters, at the subfamily level, two evolutionary lineages in Tanyderidae are apparent; therefore, a new subfamily name is proposed here. Outcrops localities of the new subfamily are presented in Figure 2.

MATERIAL AND METHODS

Specimens examined included the extant genera *Peringueyomyina, Protoplasa, Mischoderus, Araucoderus* and *Protanyderus* (all housed in the collection of Institute of Systematics and Evolution of Animals, Polish Academy of Sciences [ISEZ PAS]) and fossil genera *Nannotanyderus* (JG. 385/2B: Acra Collection; I-F/MP/2/1621/13: ISEZ PAS; LGA 1145: Museum für Naturkunde, Germany; LGA 2222: coll. J. Ansorge; No. 2066/2182 and No. 4270/2075: Palaeontological Institute, Russian Academy of Sciences, Moscow [PIN]); *Dacochile* (Bu 1262: the American Museum of Natural History, New York, USA); *Macrochile* (MP/2920 and MP/2921: ISEZ PAS); *Podemacrochile* (MP/2922: ISEZ PAS) and a new genus described below (MP/3376 and MP/3377: ISEZ PAS).

Three specimens (two males and one female) of a new genus described below from Eocene Baltic amber were examined. Two of them (both males) are well preserved, with many pertinent characters clearly visible. The specimens housed in the Natural History Museum in Kraków, Poland.

Specimens were examined with a Leica stereomicroscope (MZFLII) equipped with a camera lucida for line drawing and Leica digital camera (DFC 295). Drawings were also completed by tracing photographs. Vein nomenclature follows that of Byers (1989) and Krzemiński and Krzemińska (2003); morphological terminology is that presented in Cumming and Wood (2009).

SYSTEMATIC PALEONTOLOGY

Order DIPTERA Linnaeus, 1758
Infraorder PSYCHODOMORPHA Hennig, 1968
Family TANYDERIDAE Osten-Sacken, 1879
Subfamily TANYDERINAE Osten-Sacken, 1879

Type Genus. *Macrochile* Loew, 1850.
Type Species. *Macrochile spectrum* Loew, 1850.
Genera included. Fossil genera *Praemacrochile*; *Podemacrochile*; *Macrochile; Similinannotanyderus* and the following extant genera *Araucoderus*, *Eutanyderus*, *Mischoderus*, *Neoderus*, *Nothoderus*, *Protanyderus* (also in fossil fauna), *Radinoderus* and *Tanyderus*.
Differential diagnosis. Male genitalia small with short and wide gonopods; gonocoxite usually broad at base and about three or four times as long as wide; specimens medium or large size compared to those of a new subfamily described below; vein Sc markedly longer than half the wing length; wing with clearly visible coloration.
Description. Species rather large size with a wing length from 7–20 mm; wings with patterning; vein Sc longer than half the wing length; rostrum short; antennae usually with 16 flagellomeres; legs elon-

TABLE 2. Fossil species of Tanyderidae.

Species	Age	Locality
Dacochile microsoma Poinar and Brown, 2004	Lower Cretaceous	Myanmar amber
Macrochile hornei Krzemiński, Krzemińska, Kania and Ross, 2013	Upper Eocene	Baltic amber
Macrochile spectrum Loew, 1850	Upper Eocene	Baltic amber
Nannotanyderus ansorgei Krzemiński, Azar and Skibińska, 2013	Lower Cretaceous	Lebanese amber
Nannotanyderus grimmensis Ansorge and Krzemiński, 2002	Lower Jurassic	Western Pomerania, Germany
Nannotanyderus incertus Lukashevich, 2011	Upper Jurassic	Shar-Teg, Mongolia
Nannotanyderus krzeminskii Ansorge, 1994	Lower Jurassic	Gerimmen and Dobbertin, Germany
Nannotanyderus kubekovensis Skibińska and Krzemiński, 2013	Upper Jurassic	Karatau, Russia
Nannotanyderus oliviae Skibińska, Krzemiński and Coram, 2014	Lower Jurassic	Dorset, England
Podemacrochile baltica Podenas, 1997	Upper Eocene	Baltic amber
Praemacrochile ansorgei Lukashevich and Krzemiński, 2009	Middle or Upper Jurassic	Karatau, Kazakhstan; Shar-Teg, Mongolia
Praemacrochile chinensis Krzemiński and Ren, 2001	Middle Jurassic	Daohuguo, China
Praemacrochile decipiens Bode, 1953	Lower Jurassic	Hondelage, schandelan and Dobbertin, Germany
Praemacrochile dobbertinensis Ansorge and Krzemiński, 2002	Lower Jurassic	Dobbertin, Germany
Praemacrochile dryasis Dong, Shih, Skibińska, Krzemiński and Ren, 2015	Middle Jurassic	Daohuguo, China
Praemacrochile kaluginae Lukashevich and Krzemiński, 2009	Middle or Upper Jurassic	Karatau, Kazakhstan
Praemacrochile ovalum Dong, Shih, Skibińska, Krzemiński and Ren, 2015	Middle Jurassic	Daohuguo, China
Praemacrochile stackelbergi Kalugina and Kovalev, 1985	Lower or Middle Jurassic	Siberia, Russia
Protanyderus astictum Dong, Shih, Skibińska, Krzemiński and Ren, 2015	Middle Jurassic	Daohuguo, China
Protanyderus invalidus Lukashevich and Krzemiński, 2009	Middle Jurassic	Siberia and Kubekovo, Russia
Protanyderus mesozoicus Kalugina, 1988	Upper Jurassic or Lower Cretaceous	Khutel Khara, Mongolia
Protanyderus nebulosus Lukashevich and Krzemiński, 2009	Upper Jurassic	Shar-Teg, Mongolia
Protanyderus savtchenkoi Lukashevich and Krzemiński, 2009	Middle or Upper Jurassic	Karatau, Kazakhstan
Protanyderus senilis Kalugina, 1992	Upper Jurassic	Shar-Teg, Mongolia
Protanyderus vetus Kalugina, 1992	Upper Jurassic	Shar-Teg, Mongolia
Protanyderus vulcanium Zhang, 2004	Middle Jurassic	Daohuguo, China
Similinannotanyderus lii Dong, Shih and Ren, 2015	Lower Cretaceous	Myanmar amber

gated; male genitalia short and wide, definitely shorter than 3/4 abdomen length.

NANNOTANYDERINAE subfam. nov.

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Type Genus. *Nannotanyderus* Ansorge, 1994.

Type Species. *Nannotanyderus ansorgei* Krzemiński, Azar and Skibińska, 2013a.

Genera included. Fossil genera *Nannotanyderus*; *Dacochile*; a new genus described below, and the extant genus *Peringueyomyina.*

Differential diagnosis. The primary feature distinguishing the new subfamily is the unique external structure of the male genitalia. Gonopods elongate, its length when at rest being at least as long as one third the length of abdomen (Figure 3.1); male terminalia either unrotated or rotated 180 degrees (inverted like in all subfamilies of Psychodidae

FIGURE 1. Extant representative of Tanyderidae: *Araucoderus gloriosus* Alexander, 1920 in natural habitat. Photograph: R. Isai Madriz.

FIGURE 2. Localities of fossil outcrops (other than "Se") and extant ("Se") members of Nannotanyderinae subfam. nov. Abbreviations: B, Baltic region (this study); Do, Dorset of UK (*Nannotanyderus oliviae*); Db, Dobbertin of Germany (*N. krzeminskii*); G, Grimmen of Germany (*N. krzeminskii* and *N. grimmensis*); K, Karatau of Kazakhstan (*N. kubekovensis*); L, Lebanon (*N. ansorgei*); M, Myanmar (*Dacochile microsoma*); S, Shar-Teg of Mongolia (*N. incertus*); and Se, South Ethiopian Region (*Peringueyomyina barnardi*). Modified from Soszyńska-Maj and Krzemiński (2013, figure 1).

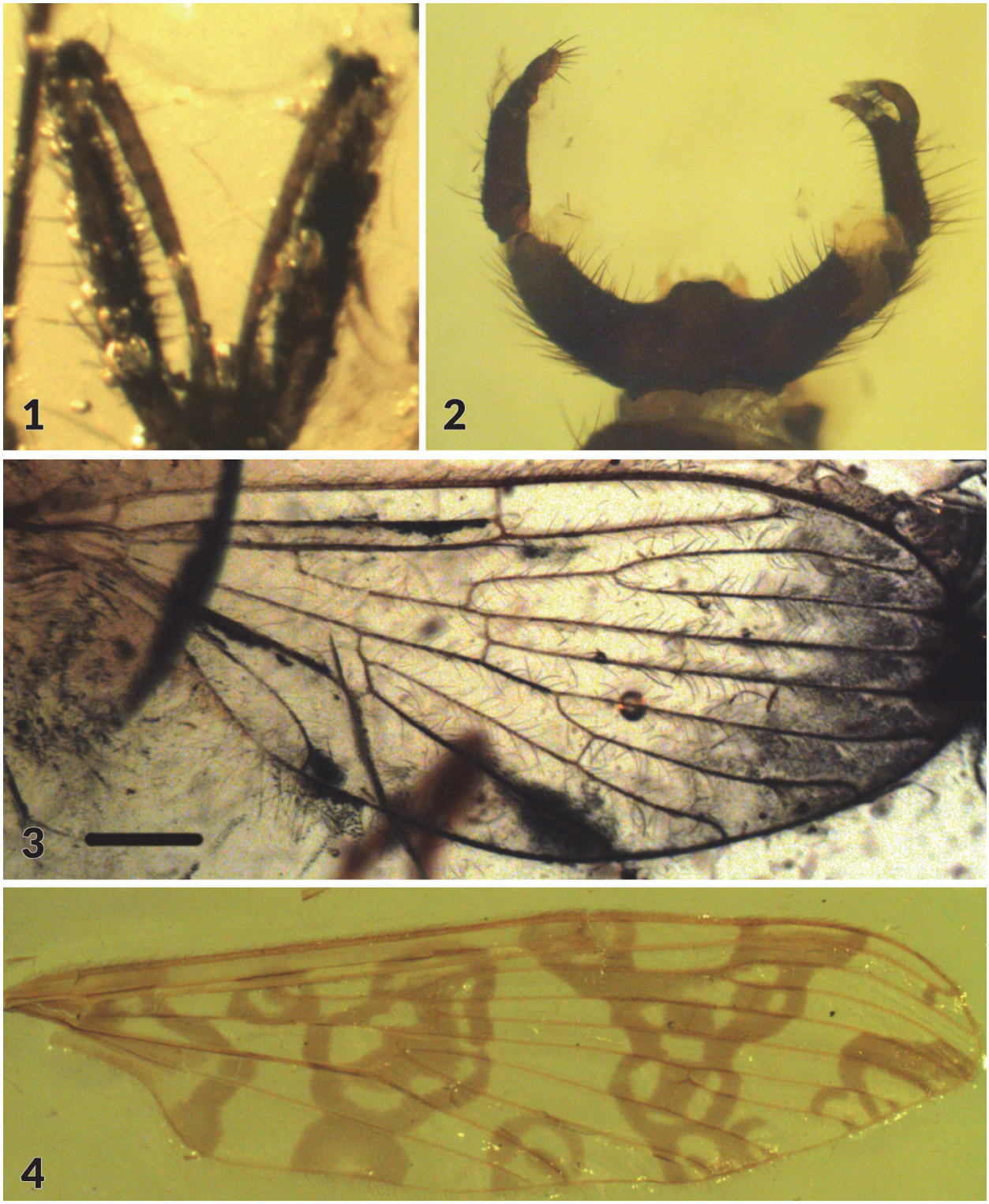

FIGURE 3. Comparison of external structure of male genitalia (**1** and **2**; in dorsal views) and wing venation (**3** and **4**; in dorsal views) in subfamilies. **1,** *Nannotanyderus ansorgei* (JG. 385/2B), Nannotanyderinae. **2,** *Mischoderus annuliferus* Hutton, 1900 (ISEZ PAN collection), Tanyderinae. **3,** a new genus of Nannotanyderinae described below (holotype, MP/3376). **4,** *Mischoderus annuliferus* (ISEZ PAN collection), Tanyderinae. Scale equals 0.5 mm.

except Sycoracinae); species small compared to those of Tanyderinae, without elongated abdominal segments (except for extant species); wing with anal lobe reduced, inconspicuous, compared to prominent in Tanyderinae; wing membrane hyaline (without patterning).

Description. Fossil species small in size, without elongated abdominal segments. Wings small with lengths ranging from 1.56–4 mm, only *Peringueyomyina* with a larger wing, approximately 10 mm in length. Wing membrane hyaline, without patterning; usually with a developed anal lobe; vein Sc short in fossil species, approximately half wing length, longer in *Peringueyomyina*; d-cell closed; Rs longer than $R_{4+5.}$ Extant species characterized by conspicuous, elongate rostrum. Antennae elongate (except in *Peringueyomyina*); usually with 16 articles (17 in *Dacochile*) with elongate, cylindrical flagellomeres. Legs elongate, each with two tibial spurs (absent in *Dacochile*). Male genitalia conspicuous, with strikingly elongate gonopods, their length when at rest being equal to as much as 3/4 abdomen length.

Genus NANNOTANYDERUS Ansorge, 1994

Type Species. *Nannotanyderus ansorgei* Krzemiński, Azar and Skibińska, 2013a.

Diagnosis. Species belonging to the genus *Nannotanyderus* are characterized by very small 1.56 mm body length with a wing length of 2–4 mm. Vein R_2 is several times shorter than vein R_{2+3}. Vein Sc ends at the mid length of the wing, usually before fork of Rs into R_{2+3} and R_{4+5}. Anal lobe present.

Species included. *Nannotanyderus oliviae*; *N. krzeminskii*; *N. grimmenensis*; *N. incertus*, *N. kubekovensis*; *N. ansorgei*

Nannotanyderus oliviae Skibińska, Krzemiński and Coram, 2014
Figure 4

Remarks. This species is represented by two specimens preserved as wing imprints in a sedimentary rock. Wing length 2.8 mm. It is the oldest record of Tanyderidae, described from the Lower Jurassic (Sinemurian, 195 Ma; Cohen et al., 2013) of England. Compared to other described species of *Nannotanyderus*, *N. oliviae* differs in that veins Rs, R_{4+5} and R_4 form a nearly straight line, and vein R_{4+5} is shorter.

Nannotanyderus krzeminskii Ansorge, 1994
Figure 5

Remarks. *Nannotanyderus krzeminskii* was the first member of the genus described based on sev-

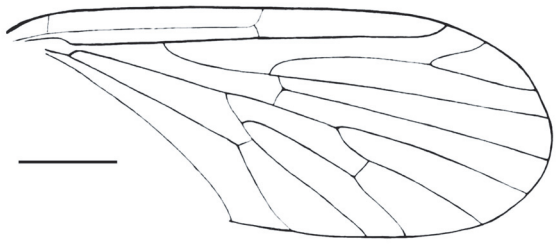

FIGURE 4. Drawing of *Nannotanyderus oliviae* wing venation (I-F/MP/1/1600/12) in dorsal view. Scale equals 0.5 mm.

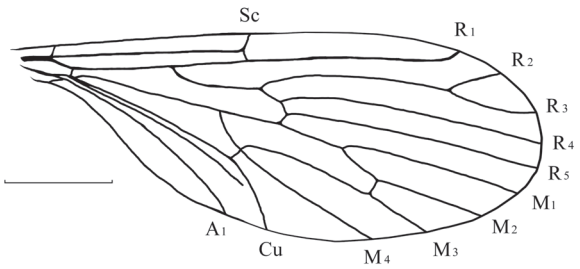

FIGURE 5. Drawing of *Nannotanyderus krzeminskii* wing venation (LGA 1145) in dorsal view. Scale equals 0.5 mm.

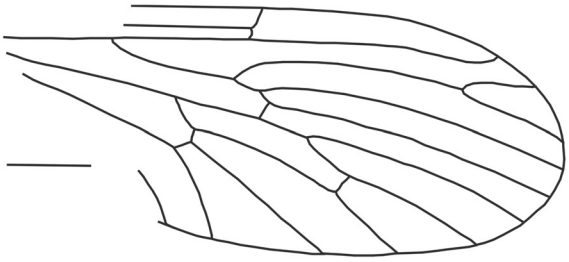

FIGURE 6. Drawing of *Nannotanyderus grimmenensis* wing venation (LGA 2222) in dorsal view. Scale equals 0.5 mm.

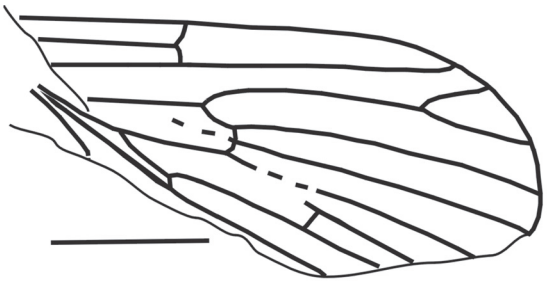

FIGURE 7. Drawing of *Nannotanyderus incertus* wing venation (No. 4270/2075) in dorsal view. Scale equals 0.5 mm.

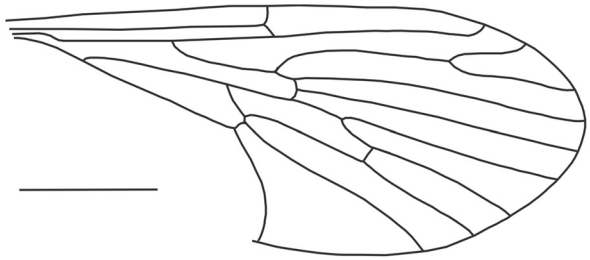

FIGURE 8. Drawing of *Nannotanyderus kubekovensis* wing venation (No. 2066/2182) in dorsal view. Scale equals 0.5 mm.

eral isolated wings from the Lower Toarcian of Grimmen, Dobbertin and Kerhhofen, Germany. It has also been found in the Lower Toarcian of Braunschweig. The species is characterized by cross vein m-cu situated exactly in the fork of M_{3+4} into M_3 and M_4, as well as the lack of a strongly angled anal lobe.

Nannotanyderus grimmenensis Ansorge and Krzemiński, 2002
Figure 6

Remarks. As for *N. krzeminskii*, this species is known from the Lower Toarcian of Grimmen, Germany. It is the largest species of this genus, with a wing length of approximately 4 mm. This species differs from other members of *Nannotanyderus* (except *N. ansorgei*) in that vein Sc ends apical to the fork of Rs into R_{4+5} and R_{2+3}. It differs from *N. ansorgei* in that vein R_1 ends apical to the fork of R_{2+3} into R_2 and R_4 and in the shorter length of vein R_{4+5}.

Nannotanyderus incertus Lukashevich, 2011
Figure 7

Remarks. *Nannotanyderus incertus* has a wing length of approximately 2 mm. Its description is based on an incomplete wing from the Upper Jurassic of Shar-Teg, Mongolia. Provisional placement of this species in *Nannotanyderus* was due to the small size, short vein R_2, three times shorter than R_{2+3}, and Sc as long as approximately half wing length.

Nannotanyderus kubekovensis Skibińska and Krzemiński, 2013
Figure 8

Remarks. The wing of *N. kubekovensis* is approximately 2.9 mm long. It is described from the Upper Jurassic of Karatau, Kazakhstan. Veins in the medial sector are markedly longer than other species in this genus. Moreover, vein M_1 in this species is longer than the length of d-cell, and cross-vein m-cu is located behind the fork of M_{3+4}.

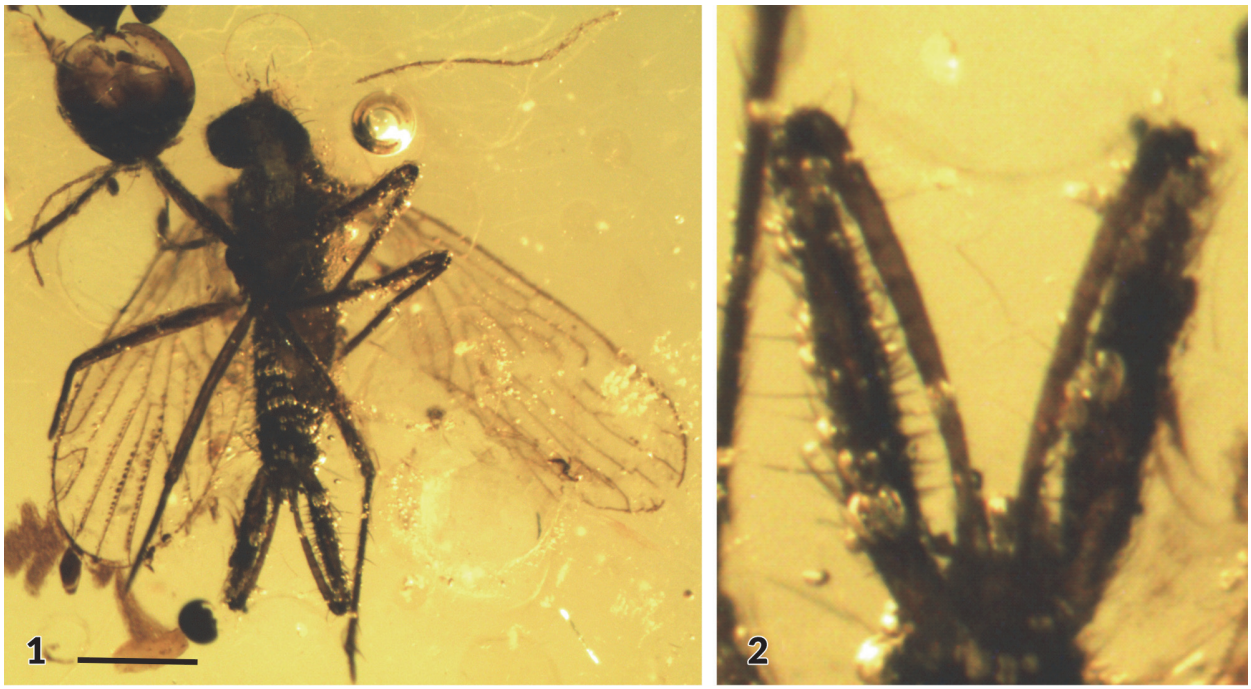

FIGURE 9. Photographs of *Nannotanyderus ansorgei* (JG. 385/2B). **1,** whole specimen. **2,** male genitalia in ventral view. Scale equals 0.5 mm.

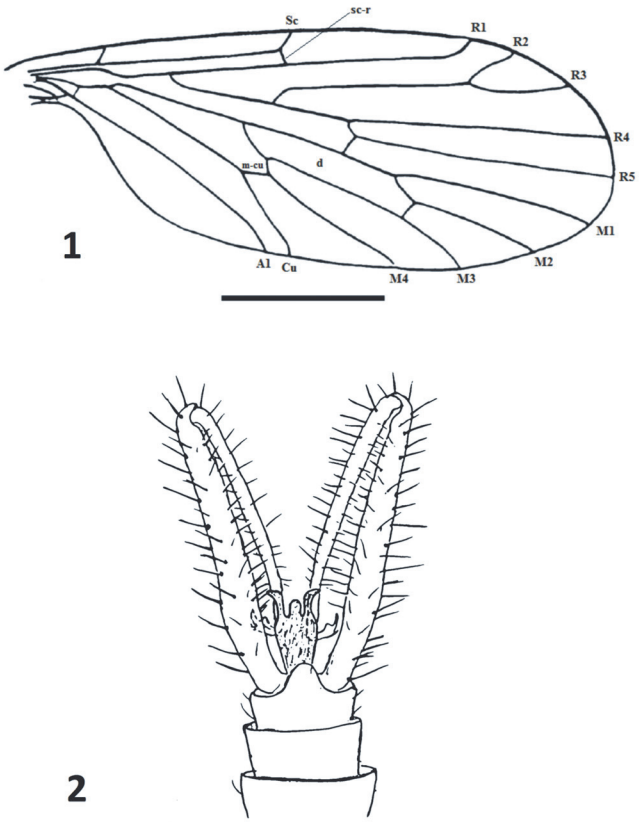

FIGURE 10. Drawings of *Nannotanyderus ansorgei* (JG. 385/2B). **1,** wing venation. **2,** male genitalia in dorsal view. Scale equals 0.5 mm.

Nannotanyderus ansorgei Krzemiński, Azar and Skibińska, 2013a
Figures 9-10

Remarks. *Nannotanyderus ansorgei* is the smallest known tanyderid, with a wing length of 1.56 mm. It is described from Lower Cretaceous Lebanese amber and is the species for which the morphology of *Nannotanyderus* could first be observed in its entirety (others described prior to this were based only on wings). The male habitus of *N. ansorgei* is exemplary of Nannotanyderinae; thus, it was selected as type species of the subfamily. The length of the gonopod at rest in this species is approximately 3/4 the total length of the abdomen (Figure 9). In the wing, vein Sc ends apical to the fork of Rs into R_{4+5} and R_{2+3} and cross-vein r-m is placed at a level approximately 2/3 along the length of the d-cell (Figure 10.1).

Genus DACOCHILE Poinar and Brown, 2004

Type Species. *Dacochile microsoma* Poinar and Brown, 2004, monotypic genus.

Dacochile microsoma Poinar and Brown, 2004
Figures 11-12

Remarks. *Dacochile microsoma* is described from Cretaceous Burmese amber and is among the smaller species of Nannotanyderinae; however, with a wing length of 2.8 mm, it is significantly larger than *N. ansorgei*. In the wing, the anal lobe is greatly reduced and vein Sc terminates at a point corresponding to one third the length of vein Rs (Figure 12.1). Woodley (2005) discussed the placement of *Dacochile* in Tanyderidae and stated that this genus should be transferred to Psychodidae. Despite a detailed explanation and justification for placing *Dacochile* in Tanyderidae, and the description of a new specimen by Poinar and Brown (2006), the taxonomic placement of this genus remained uncertain. Subsequently, Krzemiński et al. (2013a) described from Myanmar amber a male of *D. microsoma* showing pertinent characters that confirm its classification as a tanyderid.

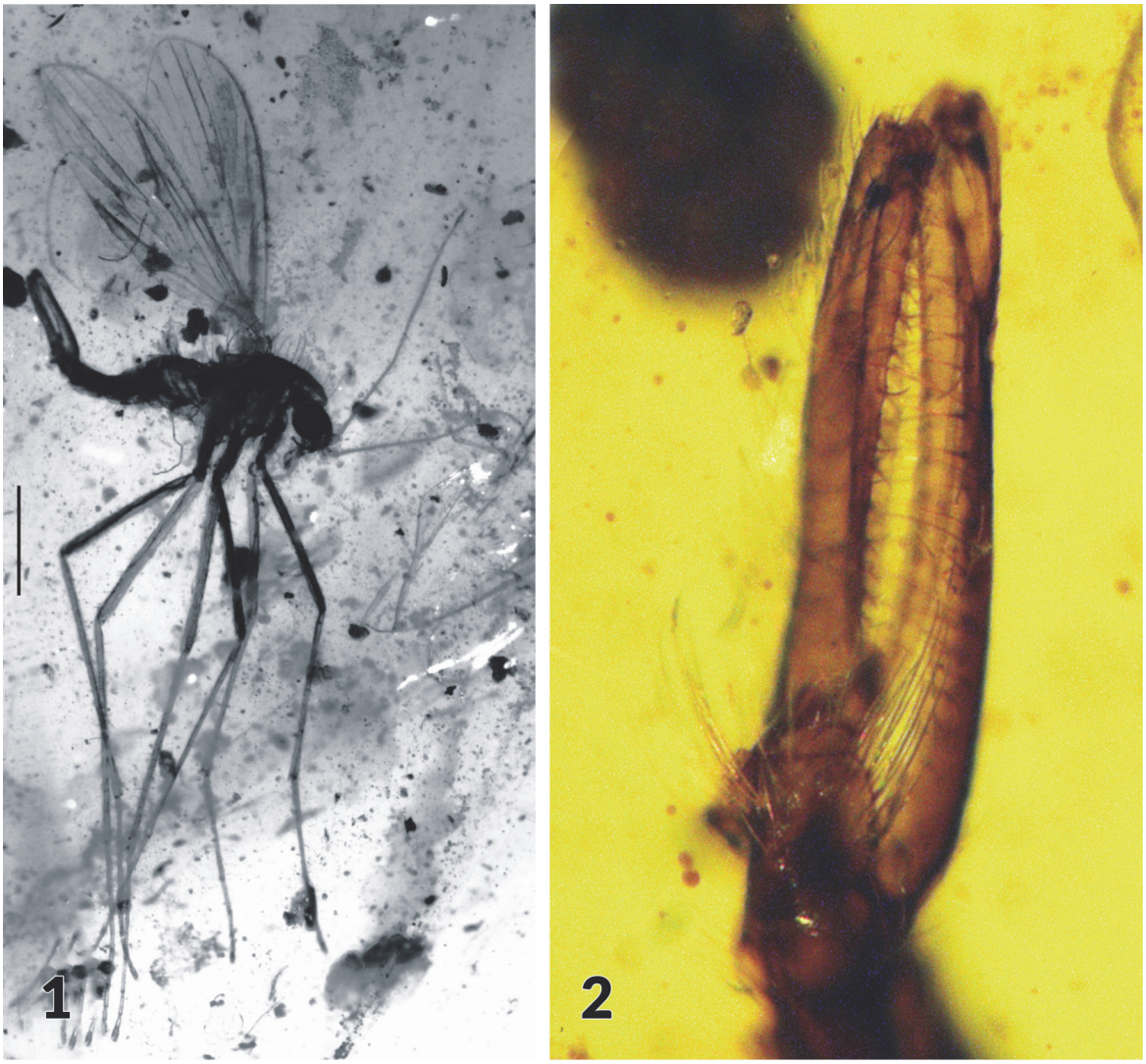

FIGURE 11. Photographs of *Dacochile microsoma* (Bu 1262). **1,** whole specimen. **2,** male genitalia in lateral view. Scale equals 1 mm.

Coramus gen. nov.

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Etymology. The new genus name is dedicated to Dr. Robert Coram for his assistance in this research.

Differential diagnosis. Wing length 4 mm; width 1.7 mm; vein R_{2+3} is short, about half the length of R_2; vein Sc apex at about one-third length of R_{2+3}; vein R_2 is long, about twice as long as R_{4+5} *Coramus* gen. nov. differs from *Dacochile* in the length of vein Sc, which in the latter ends at one-third length of Rs and in proportion of Rs to R_{2+3}. *Coramus* gen. nov. differs from *Nannotanyderus* in having a long vein R_2, about twice as long as R_{2+3}. Male genitalia with gonopods elongate; gonocoxite

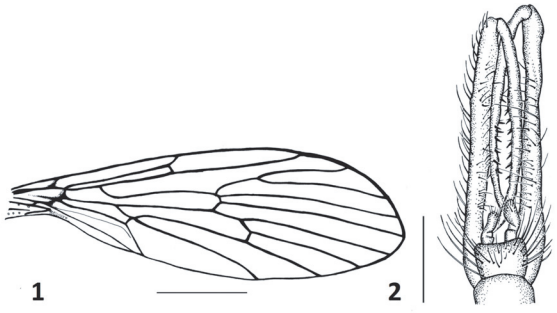

FIGURE 12. Drawings of *Dacochile microsoma*. (Bu 1262). **1,** wing venation. **2,** male genitalia in lateral view. Scale equals 0.5 mm.

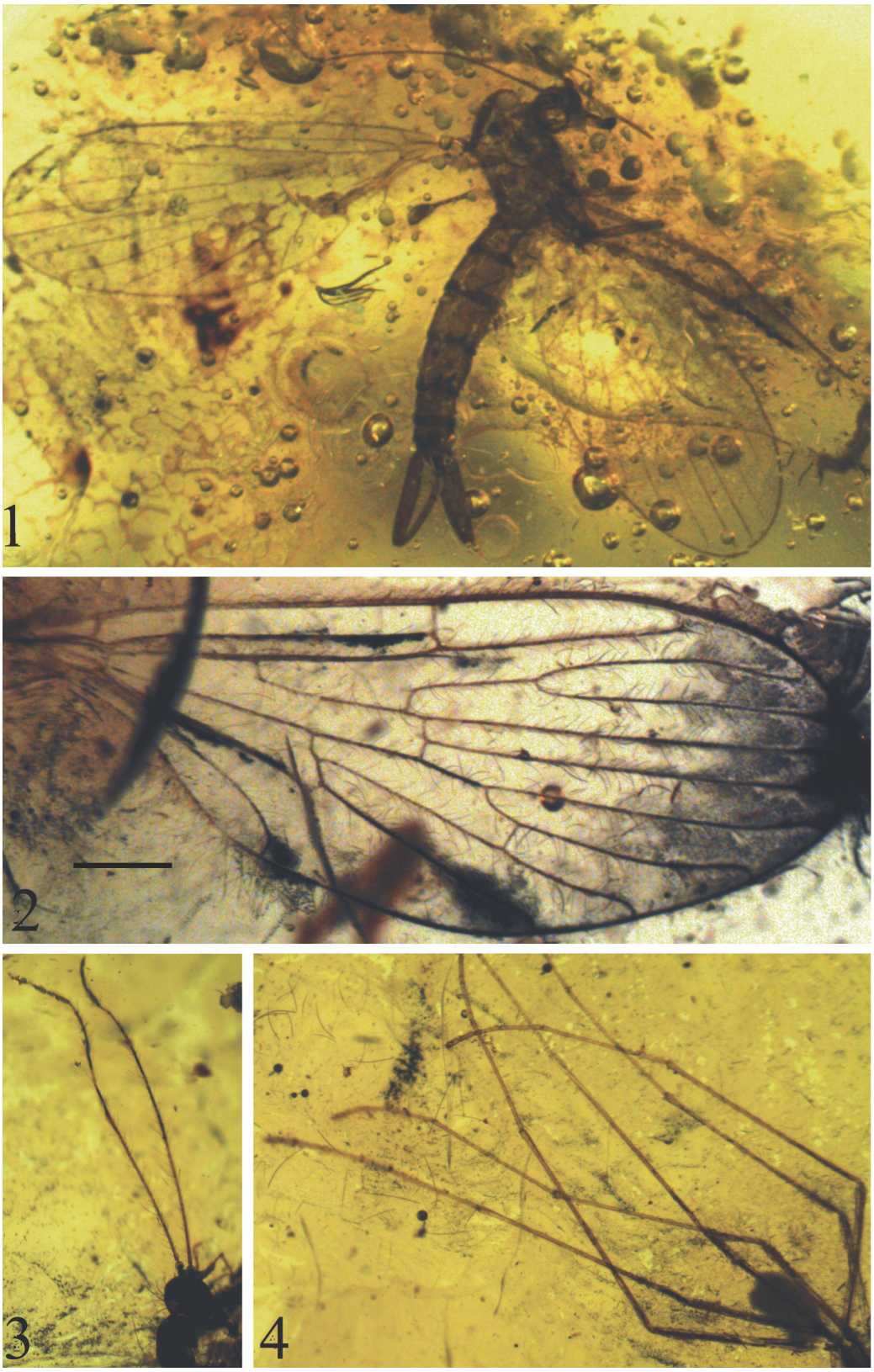

FIGURE 13. Photographs of *Coramus gedanensis* gen. et sp. nov. **1,** whole specimen (paratype, MP/3377). **2,** wing venation (holotype, MP/3376). **3,** close-up of head (holotype, MP/3376). **4,** close-up of legs (holotype, MP/3376) in lateral view. Scale equals 0.5 mm.

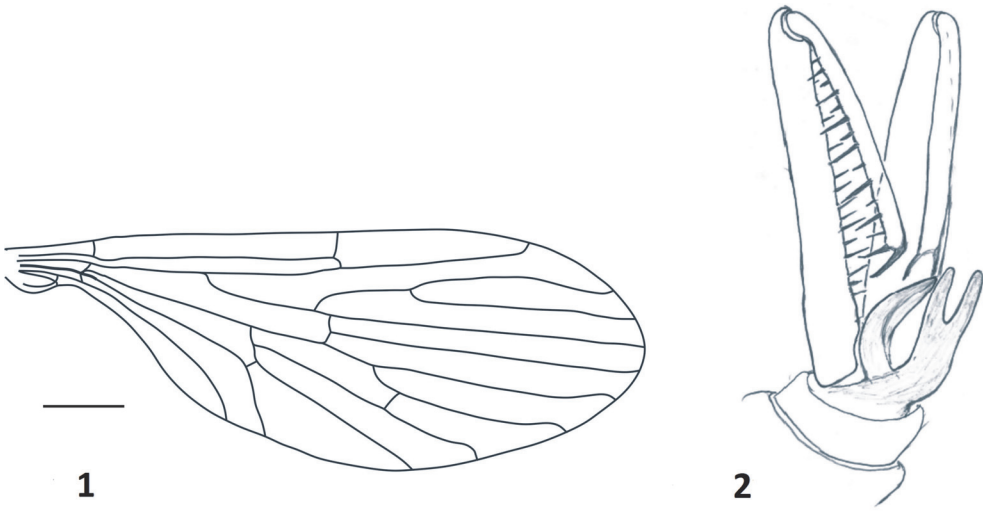

FIGURE 14. Drawings of Coramus gedanensis gen. et sp. nov. (MP/3376). 1, wing venation. 2, male genitalia in dorsal view. Scale equals 0.5 mm.

cylindrical, about five times as long as wide; gonostylus bifurcate apically, with branches of bifurcation short, their length equal to half the width of the gonostylus, each with a prominent, spiniform seta inserted apically. Aedeagal complex conspicuous, aedeagus with three phallotrema.

Description. Monotypic genus. Description of genus same as for species.

Coramus gedanensis sp. nov.
Figures 13-14

zoobank.org/81155960-C556-42C8-B299-064DCCDE537B

Etymology. "*Gedanensis*" given after old name of Gdańsk — capital of amber in Poland.

Material. Holotype No MP/3376; Paratype No MP/3377. Both from Upper Eocene Baltic amber. They are deposited in the Institute of Systematics and Evolution of Animals, PAS, Krakow, Poland.

Description. Antennae elongate, delicate, with 16 articles, slightly shorter than the whole body length (Figures 13); scapus short and cylindrical, pedicel short and ovoid, flagellomeres one and two elongate, significantly longer than remaining flagellomeres; flagellomeres 3−14 progressively shorter; flagellomeres 10−14 short and wider than all preceding flagellomeres; mouthparts shorter than the width of head (Figure 13); tibia with short and wide spine; palpus elongate, with apical segment longer than preceding segment; wing length 3.8 mm, width 1.7 mm; vein Sc ends almost opposite one-third length of R_{2+3}; Rs about 1/5 longer than R_{2+3}; R_2 twice as long as R_{2+3}; cross-vein r-m almost in a half of upper margin of d-cell length; vein m-cu situated about 1/10 length of vein M_4; d-cell almost equal in length to vein M_2; vein A_1 strongly angled at the end; anal lobe poorly developed (Figure 14.1); terminalia well developed, with slender and elongated basistylus (0.73 mm long) and gonostylus (0.64 mm long) aedeagus with three phallotrema (Figures 13.1, 14.2).

Remarks. Eocene Baltic amber is the youngest deposit in which Nannotanyderinae subfam. nov. is recorded. Wing venation and external built of hypopygium in *Coramus* gen. nov. is coincident for morphological scope of Nannotanyderinae subfam. nov. *Coramus* gen. nov. significantly differs from others genera in the wing venation (e.g., length of vein R_2; ending of vein Sc). Aedegal complex is bigger than in other genera, conspicuous, aedeadus with three phallotrema. Members of Nannotanyderinae subfam. nov. were in all probability very few because despite 150 years of research, *Coramus* gen. nov. is the first to represent this subfamily in Baltic amber. So far two fossil genera are known *Macrochile* Loew, 1850 and *Podemacrochile* Podenas, 1997, which are classifies as subfamily Tanyderinae.

Genus PERINGUEYOMYINA Alexander, 1921

Type Species. *Peringueyomyina barnardi* Alexander, 1921.

Peringueyomyina barnardi Alexander, 1921
Figures 15-16

Remarks. *Peringueyomyina* is a monotypic genus and the only tanyderid known to occur in South Africa. With a wing length of approximately 10 mm,

FIGURE 15. Photograph of *Peringueyomyina barnardi* (ISEZ PAN collection) whole specimen with elongated rostrum in lateral view. Scale equals 1mm.

P. barnardi is the largest species of Nannotanyderinae. This species is unique within extant Tanyderidae in having an elongate rostrum and a hyaline wing membrane with a lesser-developed anal lobe (Figure 15). In the wing vein Sc is longer than most other species in this subfamily, ending opposite about two-thirds the length of R_{2+3} (Figure 16.1). As with the fossil member of Nannotanyderinae, *Peringueyomyina* can be characterized by elongated gonopods (Figures 15, 16.2). However, in the latter, the number and arrangement of spiniform setae on the gonopods differs from any fossil species.

Keys

For Key to Subfamily and Key to Genera see Appendix.

DISCUSSION

Representative fossil and extant Tanyderidae were examined in this study. Differences in characters including male genitalia, wing shape and body size indicate two evolutionary lineages, in the family, treated here as subfamilies. As detailed above, the main distinguishing features between the two subfamilies are the length of wing vein Sc, shorter abdominal segments and unique structure of the male genitalia (Figures 3-16). Nannotanyderinae subfam. nov. includes mostly fossil genera *Nannotanyderus*, *Dacochile* and *Coramus* gen. nov. and one extant genus, *Peringueyomyina*. Tanyderinae is represented by the remaining extant and fossil genera.

The earliest record of subfamily Nannotanyderinae is *Nannotanyderus oliviae* from the Lower Jurassic (Sinemurian, about 190 Ma) of England (Figure 4). All Jurassic species have been described only on the basis of wing venation from isolated wing imprints in sedimentary rock. Later, the description of *Nannotanyderus ansorgei* from Lower Cretaceous Lebanese amber (about 130–135 Ma: Maksoud et al., 2014) enabled the first observation of an intact body of a Mesozoic tany-

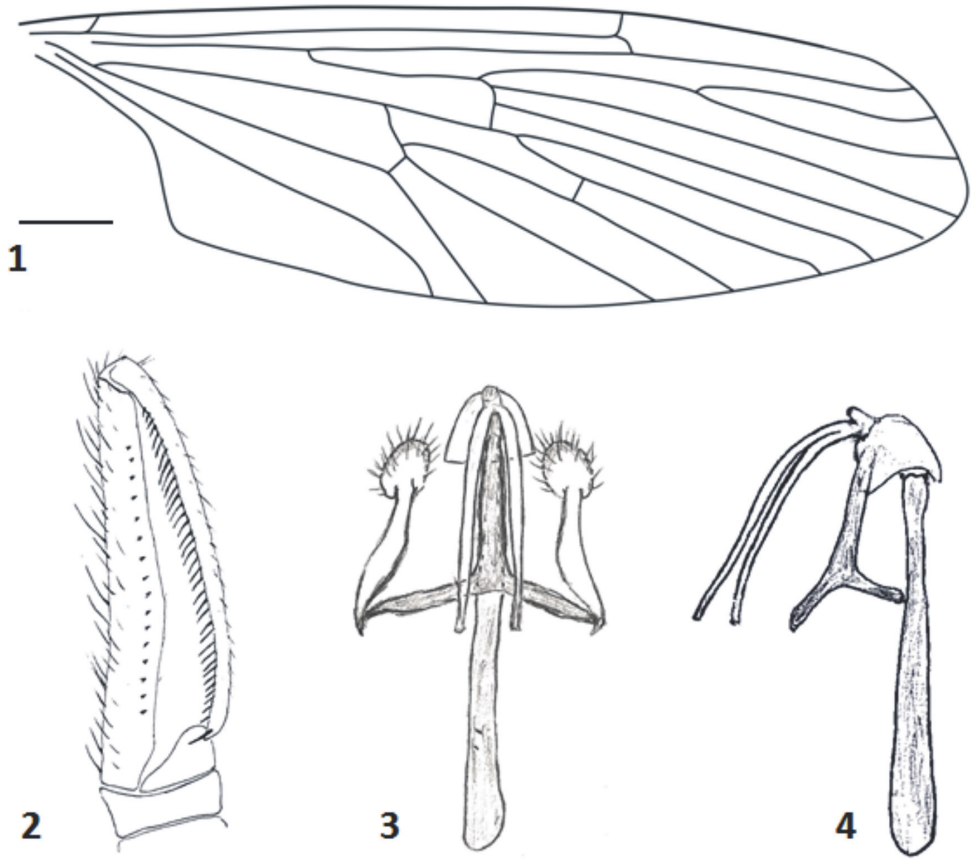

FIGURE 16. Drawings of *Peringueyomyina barnardi* (ISEZ PAN collection). **1,** wing venation in dorsal view. **2-4,** male genitalia, external built in dorsal view (**2**), aedagal complex in dorsal (**3**) ventral-lateral (**4**) views. Scale equals 1 mm.

derid. This made it possible to examine all important morphological features, particularly the male genitalia. *Coramus* gen. nov. from Eocene Baltic amber (aged within the range of 38–47 Ma: Ritzkowski, 1997; Perkovsky et al., 2007) has a male genitalia with an external structure comparable to that of genera *Nannotanyderus*, *Dacochile* and *Peringueyomyina*. The new genus, therefore, helps to bridge the temporal gap between Lower Cretaceous and extant members of the subfamily.

Tanyderidae and Psychodidae are the only extant families currently placed in suborder Diarchineura, a group hypothesized as the most ancient lineage of Diptera (Krzemiński, 1992; Krzemiński and Krzemińska, 2003). This group also includes extinct families such as Grauvogeliidae (Lower/Middle Triassic), Kuperwoodidae (Upper Triassic), Hennigmatidae (Lower Jurassic to Lower Cretaceous) and Nadipteridae (Lower/Middle Triassic to Lower Jurassic) (Krzemiński and Krzemińska, 2003; Shcherbakov et al., 1995). Recent phylogenetic studies based primarily on molecular data have found that Trichoceridae, Tipulidae, Nymphomyiidae, Deuterophlebiidae, Ptychopteridae and Blephariceridae are also among the most ancient lineages of the order (Bertone et al., 2008; Wiegmann et al., 2011). To date no phylogenetic study of Tanyderidae is existing, and its relationships within the family remain poorly understood; however, continued study of both fossil and extant species is likely to help in reconstructing the phylogeny. This will also be helpful for clarifying relationships of Tanyderidae with other families such as Psychodidae and Blephariceridae.

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APPENDIX

Key to Subfamilies

1. Gonopods of male genitalia with gonocoxites and gonostyli remarkably elongate, more than six times longer than wider; gonocoxites and gonostyli with a longitudinal row of prominent, spiniform setae on their mesial surface (Figures 3.1, 9.2, 10.2, 11.2, 12.2, 14.2, 16.2); wings in fossil species small (up to 4 mm length) (Figures 4-8, 10.2, 12.2, 14.2)	NANNOTANYDERINAE subfam. nov.
− Gonopods of male genitalia with gonocoxite shorter, usually about three of four times as long as wide, and broad at base gonocoxites and gonostyli without prominent spiniform setae; wing usually medium or large size (7–20 mm); (Figure, 3.2)	TANYDERINAE Osten-Sacken, 1879

Key to Genera

1. Vein Sc longer than half wing length (Figure 16.1); rostrum elongated (Figure 15), longer than the combined length of head and thorax.	*Peringueyomyina* Alexander, 1921
- Vein Sc reaching half wing length or shorter; head without developed rostrum	2
2. Vein R_2 short, several times shorter than length of vein R_{2+3}; vein Sc ending opposite or very close to fork of vein Rs into R_2 and R_3; at rest, gonopods about 3/4 abdomen length; (Figures 4-10)	*Nannotanyderus* Ansorge, 1994
- Vein R_2 evidently longer than R_{2+3}; vein Sc ending before fork of R_{2+3}into R_2 and R_3; gonopods shorter than 3/4 abdomen length	3
3. Vein Sc ending almost opposite one third length of R_{2+3}; vein R_2 about twice as long as Rs; aedegal complex conspicuous; (Figures 13-14)	*Coramus* gen. nov.
- Vein Sc ending opposite two third length of Rs; vein R_2 about one fifth length of Rs; complex inconspicuous (Figure 12)	*Dacochile* Poinar and Brown, 2004