TAXONOMY OF NON-BITING MIDGES OF THE TRIBE TANYTARSINI (DIPTERA: CHIRONOMIDAE) FROM EOCENE BALTIC AMBER

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This dissertation is based on a set of publications reporting results of studies on the oldest known non-biting midges of the tribe Tanytarsini, preserved as amber inclusions, from the standpoint of their taxonomy and possible courses of evolution proceeding for at least 50 million years. The Tanytarsini is one of the largest tribes in the family Chironomidae - an exceptionally diverse insect group of immense importance to the structure of aquatic ecosystems, bioindication and palaeoecology. The knowledge of Eocene Tanytarsini presented here has made it possible to explore their relationships with the extant fauna, thus providing a basis for drawing inferences regarding the taxonomy and phylogeny as well as the biogeography and evolution of this tribe's faunistic diversity.

The Tanytarsini specimens examined are part of three extensive collections: that of the Museum of Amber Inclusions, University of Gdańsk [4], that of Christel and Hans W. Hoffeins, booked to be deposited at the Senckenberg German Entomological Institute [2, 5, 6] (both collections based on inclusions in amber from Gulf of Gdańsk deposits), and that of the Institute of Zoology, National Academy of Sciences of Ukraine [1, 3] (inclusions in amber obtained from the Rovno region deposits). In line with the current concept of the origin of amber, the materials from both areas are referred to as "Baltic amber". Following a preliminary examination, the chunks selected were cut, ground and polished manually in order to obtain the highest possible transparency. This allowed examination under 400x magnification so that measurements could be taken and illustrated descriptions of diagnostic structures (in most cases within the range of several tens of micrometres) could be made. A total of nearly 1600 chironomid inclusions were examined, more than 100 of which belonged to Tanytarsini, including 68 specimens preserved well enough to be described and/or identified to species level.

Most of the taxa described in this dissertation were previously unknown. The research enabled three new fossil genera to be erected, namely: *Archistempellina*, *Corneliola* and *Eonandeva*, based on descriptions of six new species. A further 10 new species represent the genera *Caladomyia* and *Rheotanytarsus*, known so far exclusively by their extant species, as well as *Stempellinella* and *Tanytarsus*. As a result of this study, the list of Eocene

Tanytarsini from Baltic amber now includes 8 genera with 20 species, all discussed in the thesis and included in the identification keys.

†***Archistempellina*** **Giłka *et* Zakrzewska, 2013**

†***Archistempellina bifurca*** **Giłka *et* Zakrzewska, 2013**

†***Archistempellina falcifera*** **Giłka *et* Zakrzewska, 2013**

†***Archistempellina perkovskyi*** **Giłka *et* Zakrzewska, 2014**

Caladomyia Säwedal, 1981

†***Caladomyia szadziewskii*** **Giłka *et* Zakrzewska, 2013**

†***Corneliola*** **Giłka *et* Zakrzewska, 2013**

†***Corneliola avia*** **Giłka *et* Zakrzewska, 2013**

†***Eonandeva*** **Giłka *et* Zakrzewska, 2015**

†***Eonandeva helva*** **Giłka *et* Zakrzewska, 2015**

†***Eonandeva latistyla*** **Giłka *et* Zakrzewska, 2015**

Rheotanytarsus Thienemann *et* Bause, 1913

†***Rheotanytarsus alliciens*** **Giłka *et* Zakrzewska, 2013**

†***Rheotanytarsus hoffeinsorum*** **Giłka, Zakrzewska *et* Krzemiński, 2016**

Stempellina Thienemann *et* Bause, 1913

† *Stempellina exigua* Seredszus *et* Wichard, 2007

Stempellinella Brundin, 1947

†*Stempellinella bicorna* Seredszus *et* Wichard, 2007

†***Stempellinella electra*** **Giłka *et* Zakrzewska, 2015**

†***Stempellinella fibra*** **Giłka, Zakrzewska *et* Krzemiński, 2016**

†***Stempellinella ivanovae*** **Giłka *et* Zakrzewska, 2014**

Tanytarsus van der Wulp, 1874

†***Tanytarsus congregabilis*** **Giłka *et* Zakrzewska, 2013**

†***Tanytarsus crocota*** **Giłka, Zakrzewska *et* Krzemiński, 2016**

†*Tanytarsus fereci* Giłka, 2011

†***Tanytarsus glaesarius*** **Giłka *et* Zakrzewska, 2015**

†***Tanytarsus protogregarius*** **Giłka *et* Zakrzewska, 2015**

†*Tanytarsus serafini* Giłka, 2010

On account of its important position regarding the tribe's phylogeny, the dissertation also considers the only known fossil species of the genus *Nandeva*, described from Eocene Fushun amber (northern China).

Nandeva Wiedenbrug, Reiss *et* Fittkau, 1998

†*Nandeva pudens* Giłka, Zakrzewska, Baranov, Wang *et* Stebner, 2016

According to the concept of the current systematic division, the Eocene Tanytarsini are represented by genera classified within two extant subtribes: the Tanytarsina (*Caladomyia*, *Rheotanytarsus* and *Tanytarsus*) and the Zavreliina (*Stempellina*, *Stempellinella* and probably *Corneliola* and *Archistempellina*).

In Baltic amber, the subtribe Tanytarsina is represented primarily by the genus *Tanytarsus* which, in part, comprises species from groups known at present and featuring limnophilous forms: *Tanytarsus congregabilis* (the *lugens* group) [1], *Tanytarsus fereci* (the *mendax* group) [6], *Tanytarsus protogregarius* (the *gregarius* group) [4]. The exceptional structure of *Tanytarsus crocota* [6], as well as the combination of characters in *Tanytarsus glaesarius* [4], which bears an affinity to characters known from the *chinyensis*, *eminulus* and *mendax* groups, precludes assigning those species to any of the known group. Hence, one cannot rule out the possibility that further studies will recognize the need to erect new groups. *Tanytarsus serafini*, constituting a monotypic extinct group and most likely the closest to the *mendax* and *eminulus* groups [6], occupies an interesting position in the genus. The genus *Rheotanytarsus*, with two species, is recorded for the first time in the Eocene. *Rheotanytarsus alliciens* [1] and *Rheotanytarsus hoffeinsorum* [6] combine characters typical of the extant representatives of the genus with those interpreted as plesiomorphic and indicative of a distinct relationship with an ancestral group involving *Tanytarsus*. The habitat preferences of the majority of extant *Rheotanytarsus* allow one to infer that Eocene species, too, dwelled in freshwater lotic habitats. The third Tanytarsina genus found in Baltic amber is *Caladomyia*, with the only fossil species known to date, *Caladomyia szadziewskii*, the structure of which confirms its close relationship with *Tanytarsus* [2].

The subtribe Zavreliina is represented in Baltic amber by at least two genera: *Stempellina* (1 species) and *Stempellinella* (4 species). The three species described in the papers on which this dissertation is based are *Stempellinella electra* [4], *Stempellinella fibra* [6] and *Stempellinella ivanovae* [3] - each displays unique characters making it possible to interpret some evolutionary trends important for defining relationships between the Zavreliina taxa and other Tanytarsini. *Corneliola* and *Archistempellina* are also significant for understanding phylogenetic relationships in the subtribe Zavreliina and the tribe Tanytarsini. Preliminary character matrix-based analysis of all known Tanytarsini genera

assigned the monotypic genus *Corneliola* to the subtribe Zavreliina and indicated its close relations with the extant genus *Constempellina* [1]. *Archistempellina* with its three species: *Archistempellina bifurca*, *Archistempellina falcifera* and *Archistempellina perkovskyi*, in addition to the character combination of eye, antenna and wing, unique to this genus, shows a relatively simple structure of the genital apparatus (hypopygium). The primitively structured hypopygial appendages (volsellae) indicate a close relationship between *Archistempellina* and the genus *Stempellina*. Interestingly, they also show affinities with homologous structures in the sister tribe, the Chironomini. In this case, the status of *Archistempellina* as a sister group relative to both all the Zavreliina and most of the Tanytarsini genera is very likely [1, 3].

The genus *Eonandeva*, included in the tribe on the basis of two species, holds a key position in the phylogeny of Tanytarsini. *Eonandeva helva* and *Eonandeva latistyla* - despite the non-typical, exceptionally simple structure of the hypopygium - were included in the Tanytarsini based on the complete set of wing characters typical of this tribe [5]. The position of this genus within phylogenetic relationships was analysed with respect to the sister genus *Nandeva* with one known fossil species, *Nandeva pudens*, described from Chinese Fushun amber (early Eocene, 50-53 Ma). The two genera are most likely a common group dating back to the divergence point of the Tanytarsini line and the remaining tribes of the subfamily Chironominae, i.e., the Pseudochironomini or the Chironomini. Phylogenetic relationships between *Nandeva*, *Eonandeva* and other Tanytarsini remain an open question, especially in the light of the ambiguous taxonomic status of *Nandeva*, hitherto assigned to each of the three Chironominae tribes. Assuming that both the genera - *Nandeva* and *Eonandeva* - represent the Tanytarsini or are the tribe's sister group/groups, at least three possibilities emerge: 1) *Eonandeva* as a stem group of the Tanytarsini, with *Nandeva* included in the tribe; 2) *Eonandeva* + *Nandeva* as a sister group relative to the remaining/most genera, included in the tribe Tanytarsini; 3) *Eonandeva* + *Nandeva* as a sister group of the Tanytarsini but excluded from the tribe. The last possibility would, however, involve the need to verify the diagnosis of the Tanytarsini (based on wing characters), as well as the diagnoses of the remaining tribes of the subfamily Chironominae [7].

Detailed analyses of morphological characters of the taxa described, compared to the potentially closest-related extant representatives, enabled their status to be defined or redefined in the context of possible evolutionary trends. Interpretations of the antenna [1, 3, 4, 6], wing [1, 5, 7], hypopygium [1-7] character states and leg ratios [4], as well

as the homology of some structures [1-3] were presented in terms of their utility in phylogenetic analyses. To carry out such an analysis, however, requires supplementary data which can only be acquired by examining at least a few further, hitherto undescribed taxa from Eocene ambers found outside the Baltic region [in preparation].

The biogeographical aspects raised in the dissertation clearly show that the distribution pattern of Eocene Tanytarsini differs from that observed today. Evidence for this is provided by the discovery of the genus *Caladomyia* in Baltic amber [2] - nowadays recorded in the Neotropical region, and by the genus *Nandeva* in amber from northern China - known from the Neotropics and Australia in the present [7]. The remaining extant Tanytarsini genera found in Eocene amber now have a cosmopolitan distribution.

Inferences based on recent results of studies on fossil Tanytarsini regarding faunistic diversity and potential speciation rate, when confronted with analyses of the extant fauna studied for more than 200 years, can be tentative at best. Moreover, such a comparison involves regions that have been subjected to transformations for tens of millions of years. Such a juxtaposition reveals considerable disproportions: 8 genera and 20 species known from Baltic amber as opposed to 16 genera and 190 extant species recorded in Europe [6]. *Corneliola avia* and *Tanytarsus serafini*, found in all the collections examined, including amber from Ukrainian deposits, are regarded as abundant and/or frequent. Also frequent, but appearing as singletons or at best doubletons (syninclusions), are *Tanytarsus glaesarius* and *Tanytarsus protogregarius*. The most diverse of the collections examined is the one belonging to Mr and Mrs Hoffeins, as it features a total of 12 species representing 7 genera. The data collected demonstrate advanced speciation in the Tanytarsini proceeding in a region emerging in this part of the world as early as the Eocene [6].

References

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