



Subfossil chironomids (Diptera, Chironomidae) of lakes in the Tatra Mountains: an illustrated guide

TÍMEA CHAMUTIOVÁ¹, LADISLAV HAMERLÍK² & PETER BITUŠÍK³

Department of Biology and Ecology, Faculty of Natural Sciences, Matej Bel University, Tajovského 40, SK-97401 Banská Bystrica, Slovakia

¹ peter.bitusik@umb.sk; <https://orcid.org/0000-0002-8439-4582>

² ladislav.hamerlik@umb.sk; <https://orcid.org/0000-0002-0803-8981>

³ timea.chamutiova@umb.sk; <https://orcid.org/0000-0003-4375-7727>

ABSTRACT

Here we present a summary of subfossil chironomids (Diptera: Chironomidae) found in the surface sediments of 52 Tatra Mts. lakes (Slovakia, Poland). Head capsules of 73 morphotypes of 5 subfamilies are described and illustrated. In addition to the previously documented subfossils by Brooks *et al.* (2007), we present 15 new morphotypes: *Diamesa* Tatra-type A, *Diamesa* Tatra-type B, *Pseudodiamesa branickii*-type, *Pseudodiamesa nivosa*-type, *Pseudokiefferiella parva*, *Brillia bifida*-type, *Cricotopus* (*Paratrichocladius*) *skirwithensis*-type, *Cricotopus* (*Cricotopus*) *tremulus*-type, *Cricotopus/Orthocladius* I, *Eukiefferiella brevicealcar*-type, *Eukiefferiella claripennis*-type B, *Orthocladius* (*Orthocladius*) *dentifer*-type, *O.* (*Mesorthocladius*) *frigidus*, *Orthocladius* (*Euorthocladius*) sp. and Tanytarsini indet. Most of these types have possibly broad distribution patterns in Europe. We believe that due to specific features of each region, this paper will serve as a helpful manual for limnologists and paleolimnologists working not only in the Tatra Mts. but also in the whole Carpathian region.

Keywords: non-biting midges, palaeolimnology, surface sediment samples, Slovakia, Poland, Western Carpathians

INTRODUCTION

The family Chironomidae (Diptera, Nematocera) is the most ubiquitous insect group known from all zoogeographic regions and all climatic zones from the tropics to the polar regions. The immature stages are common inhabitants of most aquatic habitats, although many species are semi- or fully terrestrial. Chironomids are among the dominant insects in brackish waters and intertidal zone of seas, while the genus *Pontomyia* is considered truly marine (Sæther *et al.* 2000). The only blind flying cave insect in the world, *Troglocladius hajdi* (Andersen *et al.* 2016) further highlight the extent of extreme biotopes colonized by chironomids.

Chironomids are very adaptable and their habitats range from marine coastal to high altitude snow fields and glaciers over 5,000 metres. Chironomid larvae often dominate aquatic insect communities of freshwater habitats both in abundance and species richness, often approaching 80 or more species and occasionally exceeding as many as 100 species per site (Ferrington 2007).

Due to their omnipresence in a variety of inland waters, high species richness and ability to response to a wide range of environmental conditions, chironomids have been used as important components of biomonitoring programmes worldwide. Many studies appearing in the last decades, demonstrated usefulness of chironomids as bioindicators for water quality assessment, lake typology, river classification, ecosystem health, etc. (see Nicacio & Juen 2015 for review) and they are considered to be a good surrogate for aquatic benthic macroinvertebrates (Ruse 2010). Compared with other groups, e.g. mayflies, stoneflies, caddisflies, dragonflies used in the recent biomonitoring, there is an obvious suitability of chironomids for palaeolimnological studies. Due to their well-preserved chitinised head capsules they remain in lake sediments for thousands of years and still can be identified to generic or morphotype level, which is very important for reconstruction of past ecological conditions of ecosystems (Brooks

et al. 2007). Qualitative and quantitative downcore changes in chironomids subfossil assemblages have been used to reconstruct past climate change, eutrophication, acidification, salinity, heavy metal pollution, macrophyte and fish community structure, lake water-level fluctuations (e.g. Walker 2001; Brodersen & Quinlan 2006; Brooks *et al.* 2007; Langdon *et al.* 2010).

Current state of Chironomidae knowledge in Slovakia is the result of many limnological, faunistic and, to a lesser extent, taxonomical studies. Recently, nearly 400 species with a valid taxonomic description is known from Slovakia (Bitušík, unpubl. data). Compared to other European countries with long history of Chironomidae research, the knowledge on the family in Slovakia reaches medium level.

Paleolimnological research in Slovakia using chironomids as palaeoindicators has short history dating back to the beginning of the 1990s. It has been developing as a part of trans-European projects, such as AL:PE, MOLAR, EMERGE, aiming to reconstruct complex physicochemical factors and aquatic communities of mountain lakes from Scandinavia to the Iberian Peninsula affected by anthropogenic acidification (for more details see Štefková & Šporka 2001; Stoklasa *et al.* 2017).

The vast majority of the Slovakian palaeo-studies has been carried out on lakes located in the Tatra Mountains (see Stoklasa *et al.* 2017 for review). This is not surprising for at least two reasons: firstly, the vast majority of natural lakes of Slovakia (and in the Western Carpathians) are concentrated in this relatively small area, secondly, the high sensitivity to climate variations ranks the Tatra Mountains among the best sites for Holocene palaeoclimate surveys in Central Europe (Gasiorowski & Sienkiewicz 2010).

Chironomids have been the most commonly used biological proxy in the Slovak palaeolimnological studies focusing mostly on basic description, general stratigraphic succession and ecological reconstruction of the lake environment (Stoklasa *et al.* 2017). However, palaeolimnological research has become more extensive over the last years in Slovakia (e.g. Hamerlík *et al.* 2016; Bitušík *et al.* 2018) and there is the tendency to quantitatively reconstruct Holocene temperature patterns in the Western Carpathians.

This paper presents an illustrated guide of subfossil larval chironomid remains sampled from surface sediments in lakes of the Tatra Mountains. Fifty-two surveyed lakes are located on both south (Slovakian) and north (Polish) parts of the mountain range, and their selection was intended to record a wide gradient of altitude, area and depth.

Here we present full diagnoses and illustrations of 73 chironomid morphotypes currently recognized in our subfossil material from the study area. Although morphological characteristics of the most of the material fit Brooks *et al.* (2007), we documented morphotype variability, and described new morphotypes, for which we included identification keys.

We hope that this guide will be useful not only for specialist working with fossil midges from lakes of the Tatra Mts. and the whole Carpathians, but also for chironomidologists dealing with recent material from alpine lakes, since it is highlighting well-visible structures for separation genera. As Larocque-Tobler (2014) pointed out, publishing local illustrated guides are essential to extend our knowledge on Chironomidae remains worldwide.

STUDY AREA

The Tatra Mountains (Tatra Mts.) with an area of ca. 778 km² are situated longitudinally along the Polish-Slovak border in the Western Carpathians (49°17'–49°06' N, 19°36'–20°20' E). It is the highest and one of the formerly most glaciated massifs in the entire Carpathians and exhibit a well-preserved glacial geomorphology with many glacial features including lakes situated in the western and central part of the mountain. This part is built mainly of crystalline (granodiorites) and metamorphic (gneiss, mica schist) rocks (Gorek & Kahan 1973).

The dominant vegetation is coniferous forest (mostly *Picea abies*, partly *Larix decidua* and *Pinus cembra*) below 1550 m a.s.l. Vegetation of the alpine zone is dominated by alpine meadows with patches of dwarf pine (*Pinus mugo*), and an increasing percentage of rocks above the upper tree line of 1800 m a.s.l. (Vološčuk 1994).

In total, 138 large and 123 small lakes (seasonal or < 0.01 ha) are present in the Tatra Mts. (Bitušík *et al.* 2006b). The lakes are situated at elevations between 1089 and 2189 m a.s.l. About 70% of them are in an alpine zone above ~1800 m a.s.l. Generally, they are small, with areas of 0.01–34.5 ha and maximum depths of 0.5–79.3 m, and are frequently seeping. The lakes are mostly fishless, except for few lakes populated with brown trout, bullhead, and brook trout.

MATERIAL AND METHODS

Surface sediment samples (i.e. the uppermost 0.0–0.5 cm layer of lake sediment, some samples include max. 1.0 cm) were taken from 52 lakes in the Tatra Mts. in summer-autumn in 2000–2019. A list of selected Tatra Mts. lakes with basic characteristics is given in Table 1. The samples were washed with distilled water to remove clay and capture small head capsules using a 60 µm sieve. If possible, a minimum of 50 head capsules were collected using a stereomicroscope at 7–40× magnification. Head capsules were mounted on microscopic slides using Berlese solution and identified at 100–400× magnification using Brooks *et al.* (2007) and Andersen *et al.* (2013a). All specimens were collected and identified by the authors, and the material is deposited as permanent slides in the collections of the Department of Biology in the Department of Biology and Ecology, Faculty of Natural Sciences, Matej Bel University in Banská Bystrica, Slovakia.

TABLE 1. Basic characteristics of the studied Tatra Mountains lakes and their chironomid communities. Data follow Bitušik *et al.* (2006b) and Stoklasa *et al.* (2017)

Lake name	Altitude (m asl)	Coordinates	Lake area (ha)	Max depth (m)	pH	No. taxa	No. head capsules
Batizovské pleso	1884	49°09'08.3"N 20°07'53.4"E	3.48	10.5	6.43	5	132
Czarny Staw Gąsienicowy	1620	49°13'56.35"N 20°01'01.7"E	17.94	51.0	6.49	14	106
Czarny Staw pod Rysami	1580	49°11'19.7"N 20°04'40.1"E	20.64	76.4	7.14	20	58
Czarny Staw Polski	1722	49°12'18.32"N 20°01'46.44"E	12.69	50.4	6.73	12	69
Čierne Kežmarské	1579	49°12'31.92"N 20°13'25.45"E	0.29	4.0	7.24	5	38
Dlhé pleso Velické	1939	49°09'54.87"N 20°08'40.63"E	0.63	5.6	6.32	4	98
Dolné Roháčske	1562	49°12'23.13"N 19°44'42.61"E	-	-	-	10	47
Dračie pleso	2020	49°09'57.30"N 20°05'18.60"E	1.72	16.0	6.93	5	105
Horné Roháčske	1728	49°12'24.14"N 19°44'06.23"E	-	-	-	8	115
Kolové pleso	1565	49°13'15.28"N 20°11'32.37"E	1.83	1.2	6.78	16	96
Kurtkowiec	1686	49°13'48.03"N 20°00'07.56"E	1.53	4.8	6.70	15	85
Ladové pleso	2057	49°11'2.65"N, 20°9'41.01"E	1.70	18.0	6.62	3	41
Ladové pleso v Zlomiskách	1925	49°09'47.3"N 20°06'19.33"E	2.25	9.7	6.70	7	98
Litvorové pleso	1860	49°10'37.20"N, 20°7'44.83"E	1.86	19.1	6.98	10	82
Litworowy Staw	1622	49°14'01.20"N 19°59'49.23"E	-	-	-	26	93
Malé Hincovo pleso	1921	49°10'26.4"N 20°03'30.6"E	2.20	6.4	7.26	7	60
Malé Žabie pleso	1920	49°10'23.82"N 20°04'28.46"E	1.21	12.6	6.67	8	113
Malé Žabie Javorové	1704	49°12'9.06"N, 20°8'58.05"E	0.18	3.1	6.95	13	306
Morské Oko	1395	49°11'50.0"N 20°04'12.7"E	34.93	50.8	7.13	27	87
Nížné Kozie pleso	1942	49°09'48.7"N 20°02'36.3"E	0.78	2.3	6.92	6	86
Nížné Rakytovské pleso	1307	49°07'29.48"N 20°01'33.57"E	0.13	2.1	5.03	16	104
Nížné Rumanovo pleso	2094	49°10'10.24"N 20°06'01.60"E	-	-	-	3	102
Nížné Spišské pleso	1993	49°11'24.17"N 20°11'50.22"E	0.62	4.3	6.26	7	97
Nížné Temnosmrečinské pleso	1677	49°11'34.4"N 20°01'50.2"E	11.70	38.1	7.33	6	287
Nížné Žabie Bielovodské	1675	49°12'01.02"N 20°05'41.44"E	4.68	20.5	6.60	12	106
Prostredné Sivé pleso	2013	49°11'2.67"N 20°10'31.01"E	1.08	4.8	6.31	9	96
Prostredné Zbojnické pleso	1960	49°10'42.03"N 20°9'38.01"E	0.60	5.3	6.76	8	78
Przedni Staw Polski	1668	49°12'44.0"N 20°02'54.7"E	7.71	34.6	7.23	17	72
Pusté pleso	2056	49°10'55.52"N 20°9'14.02"E	1.19	6.6	6.92	10	161
Slavkovské pleso	1676	49°09'09.0"N 20°11'04.9"E	0.11	2.5	5.19	11	191

...Continued on the next page

TABLE 1. (Continued)

Lake name	Altitude (m asl)	Coordinates	Lake area (ha)	Max depth (m)	pH	No. taxa	No. head capsules
Smreczynsky Staw	1226	49°13'19.02"N 19°51'48.85"E	0.75	5.3	4.95	12	82
Starolesnianske pleso	1988	49°10'48.0"N 20°10'04.1"E	0.72	4.2	5.14	10	152
Strelecké pleso	2036	49°11'02.67"N 20°11'00.39"E	-	-	-	8	103
Studené pleso	1825	49°10'47.21"N 20°10'34.86"E	-	-	-	12	98
Toporowy Staw Niżny	1089	49°17'02.00"N 20°01'50.37"E	0.62	5.7	5.57	18	43
Velické pleso	1666	49°09'24.03"N 20°09'22.95"E	2.23	4.6	6.62	15	99
Veľké Biele pleso	1615	49°13'17.09"N 20°13'50.18"E	0.97	0.8	6.69	19	150
Veľké Spišské pleso	2013	49°11'33.13"N 20°11'41.31"E	2.87	10.1	6.48	9	95
Vyšné Furkotské pleso	1698	49°8'36.76"N 20°1'47.90"E	0.41	2.4	6.52	6	57
Vyšné Račkove pleso	1697	49°11'59.17"N 19°48'16.09"E	0.74	12.3	7.49	23	103
Vyšné Satanie pliesko	1894	49°10'12.7"N 20°03'45.7"E	0.20	3.5	5.16	8	127
Vyšné Smrekovické pleso	1368	49°07'31.29"N 20°02'06.06"E	-	-	-	15	106
Vyšné Temnosmrečinské pleso	1725	49°11'20.7"N 20°02'22.2"E	5.56	20.0	7.35	10	190
Vyšné Terianske pleso	2124	49°10'04.8"N 20°01'18.5"E	0.56	4.3	5.55	7	43
Vyšné Wahlenbergovo pleso	2157	49°09'51.1"N 20°01'37.6"E	5.17	20.6	6.58	9	27
Vyšné Žabie Bielovodské pleso	1699	49°11'39.1"N 20°05'39.5"E	9.46	24.8	6.64	9	103
Wielki Staw Polski	1655	49°12'32.9"N 20°02'22.6"E	34.35	79.3	7.03	18	46
Zadni Staw Polski	1890	49°12'46.6"N 20°00'47.0"E	6.47	31.6	6.78	7	90
Zelené Kačacie pleso	1575	49°10'38.7"N 20°06'59.23"E	2.53	2.7	7.13	16	121
Zielony Staw Gąsienicowy	1672	49°13'45.26"N 19°59'51.68"E	3.84	15.1	6.85	15	93
Zmarzły Staw Gąsienicowy	1787	49°13'26.69"N 20°1'20.44"E	0.30	3.7	5.9	10	109
Žabie Javorové pleso	1878	49°11'28.89"N 20°10'7.33"E	1.13	15.3	7.16	8	124

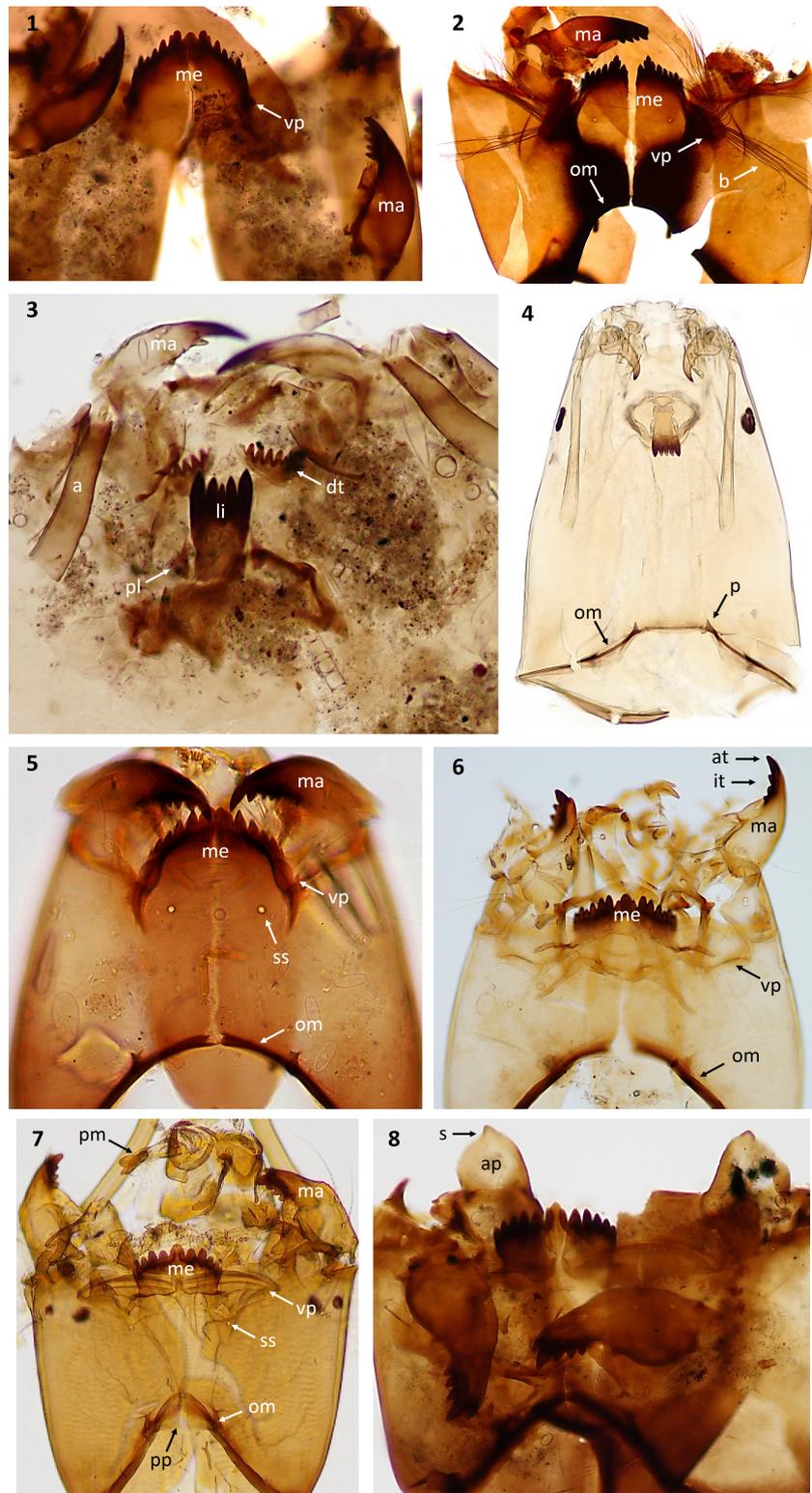
RESULTS

In total, 5,399 head capsules were analysed and identified as 73 morphotypes from 5 subfamilies: 37 morphotypes belonged to Orthoclaadiinae, 25 to Chironominae (14 to tribe Chironomini, 11 to Tanytarsini) 6 to Diamesinae, 4 to Tanypodinae and 1 to Prodiamesinae. The most frequently occurred taxa in all studied lakes were *Heterotrissocladius marcidus*-type (85%), *Procladius* sp. (73%), *Micropsectra radialis*-type (63%) and *Tanytarsus lugens*-type (60%). Diagnostic features of each subfamily are given in Figs 1–8.

Diamesinae (Fig. 1)

Head capsules of the subfamily is yellowish brown to dark brown or black with black and wide occipital margin. Surface of dorsal head mostly smooth, rarely covered with numerous short setae (*Protanypus*), or with tubercles (*Boreoheptagyia*). Third antennal segment annulated with exception of *Protanypus*. Premandible with 1–16 teeth. Mandible with apical tooth and 4–5 inner teeth. Mentum variable in shape with 4 (*Protanypus*) to 23 teeth, rarely without teeth (*Potthastia longimanus* group). Ventromental plates rudimentary to very large (*Pseudodiamesa*) (Brooks *et al.* 2007; Ilyashuk *et al.* 2010).

Larvae are rheophilic to rheobiontic, but also occur in the littoral zone as low temperature and high oxygen content combined with wave action create conditions resembling flowing waters.



FIGURES 1–8. Diamesinae, *Pseudodiamesa nivosa*: 1—head capsule. **Prodiamesinae, *Prodiamesa olivacea*:** 2—head capsule. **Tanypodinae, *Procladius*:** 3—detail of head capsule. **Tanypodinae, *Zavrelimyia*:** 4—head capsule. **Orthoclaudiinae, *Chaetocladius piger*-type:** 5—head capsule. **Chironominae (Chironomini), *Chironomus anthracinus*-type:** 6—head capsule. **Chironominae (Tanytarsini), *Micropsectra junci*-type:** 7—head capsule. **Chironominae (Tanytarsini), *Micropsectra radialis*-type:** 8—head capsule. li—ligula, pl—paraligula, dt—dorsomental teeth, a—antennae, ma—mandible, om—occipital margin, me—mentum, vp—ventromental plate, b—beard, p—projection on occipital margin, at—apical tooth of the mandible, it—inner teeth of the mandible, ap—antennal pedestal, pm—premandible, s—spur, pp—post-occipital plate, ss—seta submenti

Diamesa Meigen (Figs 9–13)

Head capsule yellow to dark brown or brown-black with robust occipital margin. Mentum with single or double median tooth (single tooth sometime with small median notch) and 7–11 lateral teeth. Arrangement of mental teeth, however, gives an appearance of 3–6 median teeth. Ventromental plates vestigial to well developed. Mandible with one apical tooth and 4 inner teeth. Premandible apically broad with 5–7 teeth.

Remarks: The most characteristic feature distinguishing subfossil *Diamesa* from other genera is the relatively large number of uniform mental teeth and remarkably wide occipital margin.

Identification of larval *Diamesa* to morphotypes/species is very difficult even in recent larvae (Rossaro & Lencioni 2015). The basic separation of living larvae is based on characters located on the body and follows with those on the head. On the contrary, identification of subfossils is limited to head coloration and few structures, such as mentum and mandible, that are, due to the feeding habit of larvae, often worn.

The following species have been recorded in the Tatra Mts.: *Diamesa laticauda* Serra-Tosio, 1964, *Diamesa tonsa* (Haliday, 1856), *Diamesa vaillanti* Serra-Tosio, 1972, *Diamesa steinboeckii* Goetghebuer, 1933, *Diamesa nowickiana* Kownacki et Kownacka, 1975, *Diamesa dampfi* (Kieffer, 1924), *Diamesa bohemani* Goetghebuer, 1932 (Bitušik 2004; Kownacki 2010, 2011).

Diamesa remains were not abundant, but relatively frequent, found in about one third of the surveyed lakes. Three morphotypes were distinguished.

Key to morphotypes:

- 1 Mentum with 5 subequal median teeth; mandible distinctive: first two inner teeth as long or slightly longer than apical tooth *Diamesa bertrami*-type
- Mentum with single median tooth; mandible of different shape 2

- 2 Mentum with a single notched median tooth wider than first laterals; first inner tooth of mandible is robust, as long or longer than apical tooth; *Diamesa* Tatra-type A
- Mentum with a single semicircular median tooth subequal to first laterals; first inner mandibular tooth not longer than apical tooth *Diamesa* Tatra-type B

Diamesa bertrami-type (Fig. 9)

Head capsule entirely dark brown. Apex of mentum with five tall, prominent teeth, median tooth single, second is taller than first, and 8 pairs of smaller lateral teeth, last one is minute. Mandible with a distinctive shape: first two inner teeth obviously long, second tooth is longer than first one.

Remarks: The *D. bertrami*-type described by Brooks *et al.* (2007) has apex of mentum with 6 teeth, i.e. median tooth is double. Rossaro & Lencioni (2015) report a single median tooth in some specimens of *D. bertrami*.

Diamesa Tatra-type A (Figs 10, 11)

This is a new morphotype, not listed in Brooks *et al.* (2007).

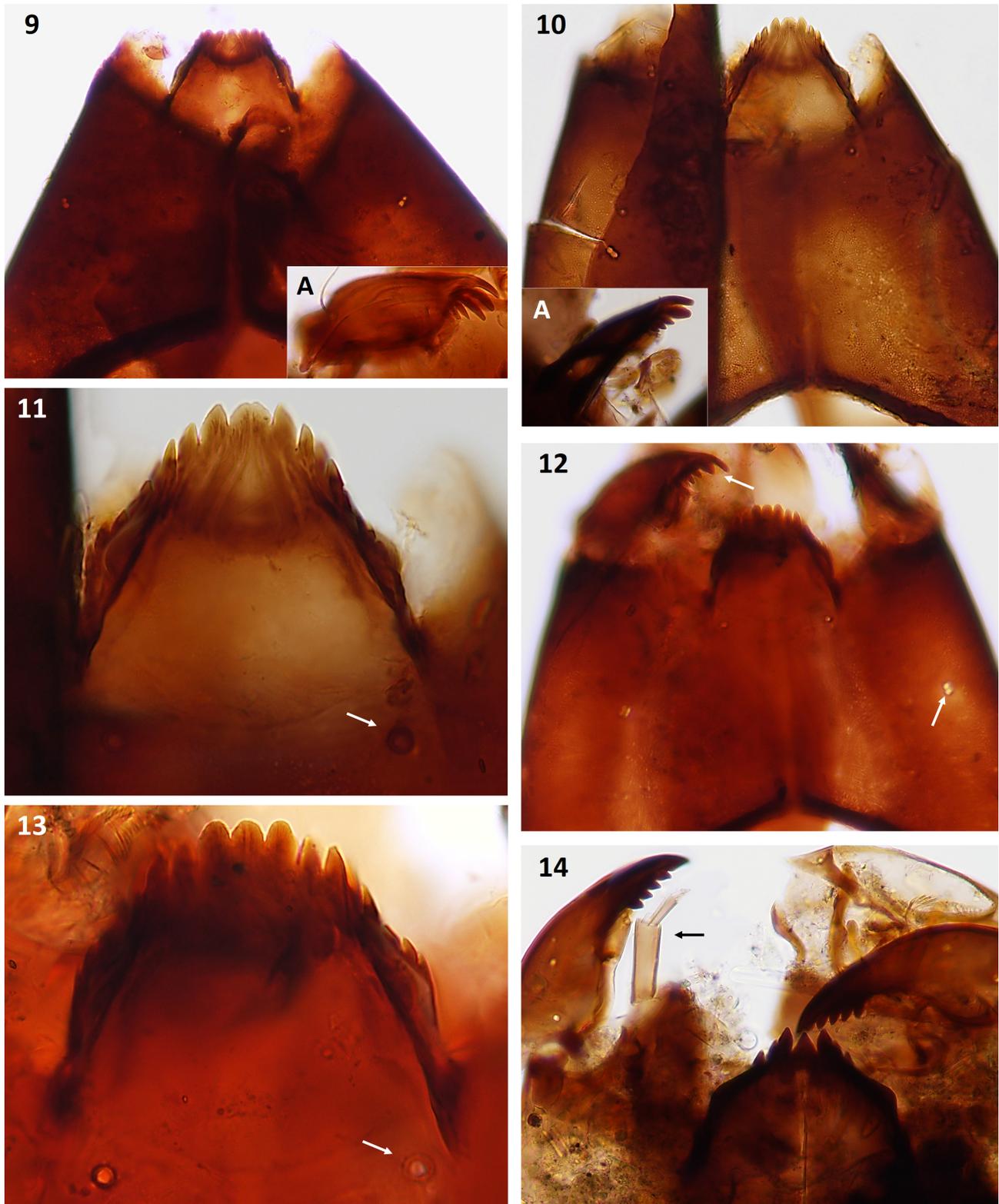
Head capsule brown, area around genal setae with two obvious lighter spots. Mentum striped, with a notched median tooth and 9 pairs of lateral teeth. Median tooth is wider than first lateral, and first lateral tooth is obviously larger than second lateral. Remaining laterals are gradually decreasing. First inner tooth of mandible is as long, or longer (and more robust) than apical tooth (Fig. 10A). Ventromental plates clearly expanded laterally. Setae submenti arising posteriorly to the base of mentum (Fig. 11).

Diamesa Tatra-type B (Figs 12, 13)

This is a new morphotype, not listed in Brooks *et al.* (2007).

Head capsule dark brown with lighter area around genal setae (Figure 12). Mentum with a single median tooth

and 9 pairs of lateral teeth. Median tooth and first pair of lateral teeth are prominent, other laterals are gradually decreasing. First inner tooth of mandible is more robust than second, but not longer than apical tooth (Fig. 12). Setae submenti positioned below the base of mentum (Fig. 13).



FIGURES 9–14. *Diamesa bertrami*-type: 9—head capsule, A—mandible. *Diamesa* Tatra-type A: 10—head capsule, A—mandible. *Diamesa* Tatra-type A: 11—mentum (arrow indicates position of seta submenti). *Diamesa* Tatra-type B: 12—head capsule (arrows indicate mandible and genal setae). *Diamesa* Tatra-type B: 13—mentum (arrow indicates position of seta submenti). *Pseudodiamesa branickii*-type: 14—head capsule (arrow indicates antenna).

Pseudodiamesa Goetghebuer (Figs 14–19)

Head capsule yellow to brown with dark brown occipital margin. Mentum with single sharp median tooth and seven pairs of lateral teeth. Median tooth is separated from first laterals by a deep V-shaped notch; second lateral lying dorsal to first lateral seems to be partially hidden behind it. Fifth and seventh lateral teeth shorter than sixth. Ventromental plates joined with median and first lateral teeth extend laterally, so only 2–4 laterals are often visible. Mandible with 4 inner teeth, apical tooth distinctly larger than first inner tooth. Premandible with 7–11 teeth.

Remarks: Three subequal teeth on the mentum apex, position of the second lateral tooth, and large ventromental plates are distinctive among the Diamesinae.

Pseudodiamesa remains are usually very abundant in alpine lakes and the intra-genus determination is very important as larvae of species groups differ in their ecological requirements. Since larvae are morphologically similar, reliable diagnosis can be difficult.

Here we follow a combination of morphological differences suggested by Serra-Tosio (1973) and Ilyashuk *et al.* (2010) and to distinguish two species-groups (*P. branickii* group and *P. nivosa* group) that are consistent with morphotypes applied to subfossil material sensu Brooks *et al.* (2007), i.e. antennal ratio, pecten epipharyngis, labrum, premandible, mandibular seta interna and mentum. Except for mentum, the above mentioned characters are usually missing in subfossils, thus only the morphology of mentum can be used for separating morphotypes.

Key to morphotypes:

- 1 Mental teeth unicolored, black, part of lateral teeth hardly visible in unflattened mentum; labral lamellae absent *Pseudodiamesa branickii*-type
- Mentum with a slightly lighter median tooth relative to black lateral teeth, outermost lateral teeth clearly visible in unflattened mentum; labral lamellae present. *Pseudodiamesa nivosa*-type

Pseudodiamesa branickii-type (Figs 14–16)

This is a new morphotype, not listed in Brooks *et al.* (2007).

Antennal ratio (length of basal segment/ length of flagellum) < 2.5 (Fig. 14). Pecten epipharyngis consists of seven, weakly sclerotized scales. Labral lamellae absent. Premandible with 7–9 teeth (Fig. 16). Mandibular seta interna consists of 9–15 branches (Fig. 15). All teeth of mentum unicolored, black, fourth to seventh lateral teeth are hardly visible in unflattened mentum (Fig. 14).

Remarks: Subfossil remains have been recorded only in three lakes. In the Tatra Mts. lakes, the morphotype contains a single species, *P. branickii* Nowicki, 1873 (Bitušik *et al.* 2006a; Novikmec *et al.* 2015).

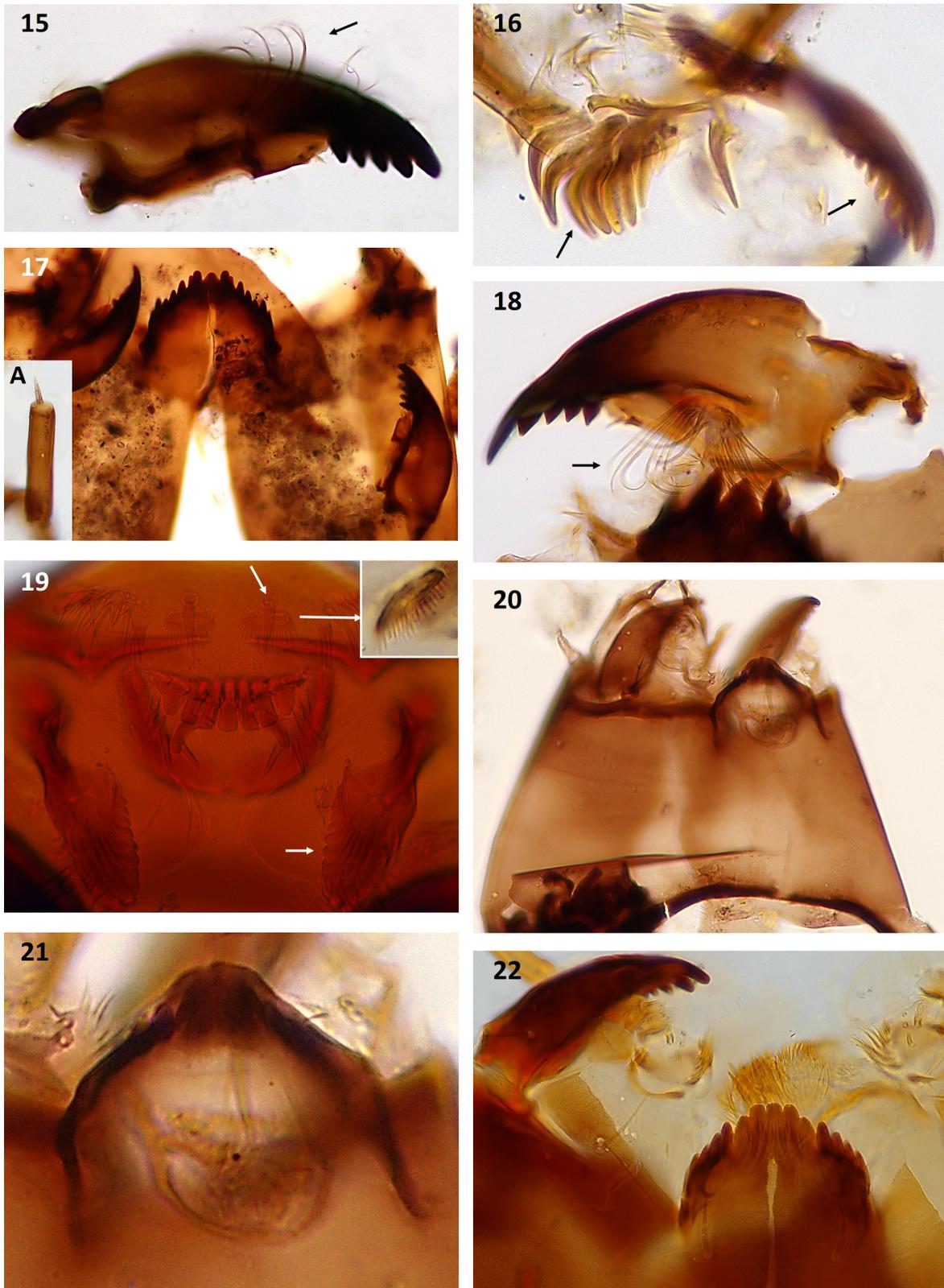
Pseudodiamesa nivosa-type (Figs 17–19)

This is a new morphotype, not listed in Brooks *et al.* (2007).

Antennal ratio ≥ 2.5 (Fig. 17A). Pecten epipharyngis is characterized by even number (3–4 pairs) strongly sclerotized scales. Labral lamellae present between bases of SI setae. Premandible with more than 10 teeth (Fig. 19). Mandibular seta interna consists of 14–24 branches (Fig. 18).

Mentum with a lighter median tooth compared to the black lateral teeth; outermost lateral teeth are more visible in unflattened mentum (Fig. 17). However, be aware of the fact that first and second instar larvae of both morphotypes has broad median mental tooth that is lighter than the blackish lateral teeth (Figs 20, 21), thus young instars are not sufficient for morphotype identification.

Remarks: This morphotype was the most frequent Diamesinae remain in surface sediments of the Tatra Mts. lakes. Its distribution is consistent with the knowledge of the ecology of the *nivosa* species group. It is more cold-adapted than the *P. branickii* group, which occurs under more moderate conditions (Ilyashuk *et al.* 2010; Hamerlík *et al.* 2017). One species of the species group, *P. nivosa* Goetghebuer, 1928, was recorded in the Tatra Mts. (Novikmec *et al.* 2015).



FIGURES 15–22. *Pseudodiamesa branickii*-type: 15— mandible (arrow indicates branches of seta interna). *P. branickii*-type: 16—detail of pecten epipharyngis and premandible (arrows indicate seven scales of pecten epipharyngis and 8–9 teeth of the premandible). *Pseudodiamesa nivosa*-type: 17—head capsule, A—antenna. *P. nivosa*-type: 18—mandible (arrow indicates branches of seta interna). *P. nivosa*-type: 19—detail of pecten epipharyngis and premandible (arrows indicate premandible teeth, SI setae and detail of labral lamellae). *Pseudodiamesa*: 20—young instar head capsule. *Pseudodiamesa*: 21—detail of mentum. *Pseudokiefferiella parva*: 22—head capsule.

***Pseudokiefferiella parva* (Edwards, 1932) (Fig. 22)**

This is a new morphotype, not listed in Brooks *et al.* (2007).

Head capsule dark-brown. Mentum striped, with one median tooth and 7 pairs of lateral teeth. Median tooth is subequal to first lateral tooth in size, second lateral tooth is obviously smaller and fused to the first lateral. There is a distinct space between the lighter second and darker third laterals; third to seventh laterals are darker and create a distinct cluster. Ventromental plates are small. Setae submenti situated below bases of mentum. First inner tooth of mandible is as long as apical tooth.

Remarks: Larvae of *Pseudokiefferiella* are similar to *Diamesa* and reliable diagnose is based on larval body. Comparing subfossil heads with recent larval material, we suggest that remains of both genera are distinguishable by shape and coloration of mentum.

Subfossil remains were recorded in small number of studied lakes. *P. parva* (Edwards, 1932) belongs to inhabitants of cold alpine streams and lake inlets and outlets in the Tatra Mts. (Novikmec *et al.* 2015).

Prodiamesinae (Fig. 2)

Head capsule of the subfamily Prodiamesinae differ from that of Chironominae, Orthocladiinae and Diamesinae by large ventromental plates without striae and with numerous and dense setae creating a ventromental beard, often visible even under low magnification (Brooks *et al.* 2007).

***Prodiamesa* Kieffer (Fig. 23)**

Head capsule large, yellow with black occipital margin and with dark brown pattern on postmentum.

Mentum consisting of 2 low median teeth and 8 pairs of lateral teeth; first lateral tooth high, trifid and fifth lateral teeth higher than fourth and sixth, respectively. Ventromental plates long and broad with long beard exceeding the edge of the head, well visible under lower magnification. Mandible with one apical tooth and 4 inner teeth.



FIGURE 23. *Prodiamesa* sp.: 23—head capsule.

Remarks: The unique shape of mentum together with well-developed ventromental plates bearing dense and long beard distinguish this morphotype from other chironomids.

Recently, *P. olivacea* (Meigen, 1818) has been recorded in the Tatra Mts. lakes (Bitušík *et al.* 2006a; Novikmec *et al.* 2015).

Remains were collected rarely in small number of lakes at lower altitude. Morphology of the mouthparts correspond to description of *P. olivacea* in the current taxonomic literature (e.g. Schmid 1993, Sæther & Andersen 2013).

Tanypodinae (Figs 3, 4)

Head capsules of the subfamily Tanypodinae can be distinguished from the other subfamilies at first glance. The most obvious feature, unique for this subfamily, is the presence of ligula and a pair of paraligulae at each side of the base of the ligula. Another typical feature is the absence of distinct mentum and ventromental plates. If toothed dorsomentum present, it is less notable and of different shape as in other subfamilies (Fig. 3). Mandible curved, tapered towards apex into dark apical tooth with one (rarely more) inner teeth. Distal part of mola swollen into lobe appearing as a large tooth (in older literature called also basal tooth (Fittkau & Roback 1983). Features used to distinguish morphotypes are mainly number of teeth, shape and colour of ligula, presence/absence of dorsomenta teeth and the shape and colour of occipital margin. Unfortunately, in the subfossil material ligula (and frequently also other structures important for identification) is often missing. In that case, position of cephalic setae and sensory pores can be used for generic diagnosis. Our manual does not focus on this character, but there is a relatively extensive literature dealing with it (see Kowalyk 1985; Rieradevall & Brooks 2001; Brooks *et al.* 2007; Cranston & Epler 2013).

***Ablabesmyia* Johannsen (Fig. 24)**

Head capsule narrow, yellowish-brownish. Dark occipital margin with two thorn-like projections (Fig. 24). Mandible with single long apical tooth with dark tip and bluntly rounded inner tooth, mola protruding as large blunt or pointed tooth. Basal segment of maxillary palp subdivided into 2–6 segments (in subfossil material often 2–3 segments segments are visible) (Fig. 24A). Dorsomenta teeth absent Ligula with 5 dark teeth, median tooth is the shortest, other gradually increase in size. Paraligula bifid, pecten hypopharyngis consists of up to 20 teeth of unequal size (Fig. 24B). In the fourth instar larvae, however, larvae of the third instar have pecten with 6–8 teeth of equal size.

Remarks: Important diagnostic features to distinguish heads of mature larvae from other Tanypodinae genera include segmented maxillary palp, thorn-like projections on occipital margin and unequal-sized teeth of pecten hypopharyngis. However, some of these structures occur in *Zavrelimyia* (s.str.), which has thorn like projection on occipital margin, and *Zavrelimyia* (*Paramerina*) that has segmented basal segment of maxillary palp (always 2 segments). Central European species of *Ablabesmyia* can be distinguished from these taxa by moderately to strongly concave row of ligula teeth, which is straight in *Zavrelimyia* (s. str.) and its subgenus *Paramerina*.

It is present only in small Tatra Mts. lakes/ponds of low altitudes and relatively high trophic (Novikmec *et al.* 2015; Hamerlík *et al.* 2017).

Remains of the genus were only recorded in small amounts in eight surveyed lakes/ ponds located mostly in coniferous forest zone at lower altitude.

***Macropelopia* Thienemann (Fig. 25)**

Head capsule broad, yellowish to orange in life, subfossil heads rather reddish-brown. Occipital margin rather dark. Mandible slender, uniformly curved; mola with 1 distal and 1 or more marginal teeth, with small dorsolateral tooth (difficult to see from lateral view). Dorsomentum with 7–9 teeth. Ligula with 5 teeth, tooth row deeply concave, outer tooth 2x as long as the median one The middle part of each tooth is quite transparent (Fig. 25A). Paraligula is bifid. Pecten hypopharyngis with 15–25 subequal teeth.

Remarks: Based on the shape of inner ligula teeth our subfossil *Macropelopia* remains belong to the *nebulosa*-group. While points of inner teeth are rather straight in larvae of this group, they are distinctly curved outwards in *notata*-group (see Cranston & Epler 2013). As this diagnostic character seems to be reliable, the morphotype *Macropelopia nebulosa*-type is suggested.

The related genus *Apsectrotanypus* differs from *Macropelopia* in having only 4 large and 1 smaller dorsomenta teeth (note that younger larval instars of *Macropelopia* have reduced number of dorsomenta teeth), and brown head with light fields around eye spots and median pale stripe on ventral side of the head capsule.

In the Tatra Mts. lakes, *M. nebulosa* has been confirmed (Bitušik *et al.* 2006a), however recently Michailova *et al.* (2014) reported the presence of *M. rossaroi* in two lakes on the Polish side of the Tatra Mts. Both species belong to the *nebulosa*-group.

Macropelopia subfossils were recorded in ten alpine lakes, generally situated at altitude below 2000 m a.s.l.

***Procladius* Skuse (Fig. 26)**

Large, oval head capsule whitish to yellowish in colour. Mandible slender, uniformly curved with dark black tip of the apical tooth; mola distally expanded to a large, broad tooth with bluntly rounded apex (Fig. 26). Dorsomenta teeth (6–8) present. Ligula with 5 dark teeth, their apex is blackish brown. Paraligula multibranching with more or less prominent main spine (Fig. 26A). Shape of paraligula is diagnostic to differ the subgenera *Holotanypus* and *Psilotanypus* (Cranston & Epler 2013). Pecten hypopharyngis with 10–15 teeth and some smaller teeth in a supplementary row.

Remarks: *Procladius* remains differ from all other Tanypodinae with dorsomenta teeth, in blackish-brown coloration of distal part of ligula and apex of mandibula, and in large, blunt mandibular mola expansion.

Detailed survey based on pupal exuviae study revealed presence of two species in the Tatra Mts.: *P. (Holotanypus) choreus* (Meigen, 1804) and *P. (Holotanypus) tatrensis* Gowin, 1944. While *P. tatrensis* is widespread with exception of the coldest lakes, *P. choreus* was repeatedly found in one, strongly acidified lake (Bitušik *et al.* 2006a).

Subfossil remains were common in most of studied lakes. All of them belong to subgenus *Holotanypus*.

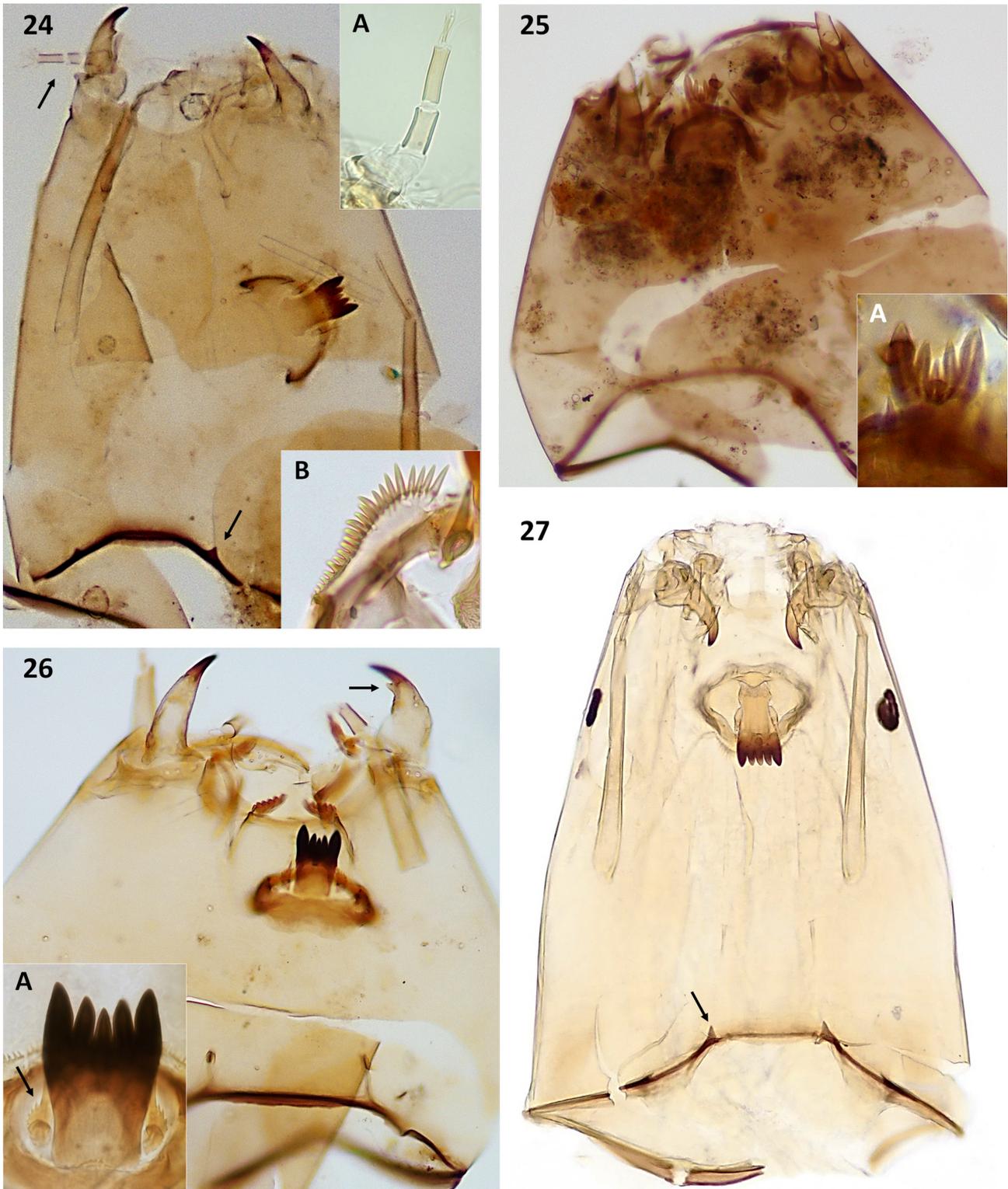
***Zavrelimyia* Fittkau (Fig. 27)**

Head capsule narrow yellowish-brown, in some species partially dark in proximal part. Occipital margin darker with two thorn-like projections on ventral side (Fig. 27). Mandible moderately curved with long apical tooth and large inner tooth. Mola expanded into large, blunt tooth (Fig. 27). Dorsomentum without teeth. Ligula with 5 brown subequal teeth. Paraligula is bifid. Pecten hypopharyngis with 9–15 teeth, inner tooth and some middle teeth enlarged. Remarks: Recently, *Zavrelimyia* includes formerly separate genus *Paramerina* as its subgenus (Silva & Ekrem, 2016), which also has basal segment of maxillary palps subdivided always into 2 parts resembling some species of *Ablabesmyia*. However, arrangement of teeth on ligula in straight row should distinguish *Zavrelimyia* and *Paramerina* from *Ablabesmyia* (with concave row of ligula teeth). For more information see description of *Ablabesmyia*. Pupal exuviae material from the Tatra Mts. lakes was identified as *Z. punctatissima* (Hamerlík & Bitušik 2008).

Zavrelimyia was the second most abundant tanypod remain mostly occurring in the surface sediments of sub-alpine lakes.

Orthoclaadiinae (Fig. 5)

Head minute to large, yellow to brown or brown-black, occipital margin can be darkened, dark brown or black. Antenna not longer than head with 4–7 (usually 5) segments (with the exception of *Corynoneura*, where antennae exceed length of head), third segment never annulate. Labrum and pecten epipharyngis with variable shaped structures (labral setae, labral lamellae) important for identification, however these characteristics usually missing from subfossils. Premandible with 1–6 teeth. Mandible with single apical tooth and usually 3 inner teeth. Mentum is very variable, mostly curved, with 3–29 teeth; mainly 4–6 pairs of lateral teeth are present. Ventromental plates vestigial to relatively large, never with striae; setal beard is present in some genera.



FIGURES 24–27. *Ablabesmyia longistyla*-type: 24—head capsule (arrows indicate thorn-like projection and segmented maxillary palp), A—maxillary palp, B—pecten hypopharyngis. *Macropelopia nebulosa*-type: 25—head capsule, A—detail of ligula. *Procladius*: 26—head capsule (arrow indicates broad tooth on the mandible), A—detail of ligula (arrow indicates paraligula). *Zavrelimyia*: 27—head capsule (arrow indicates thorn-like projection).

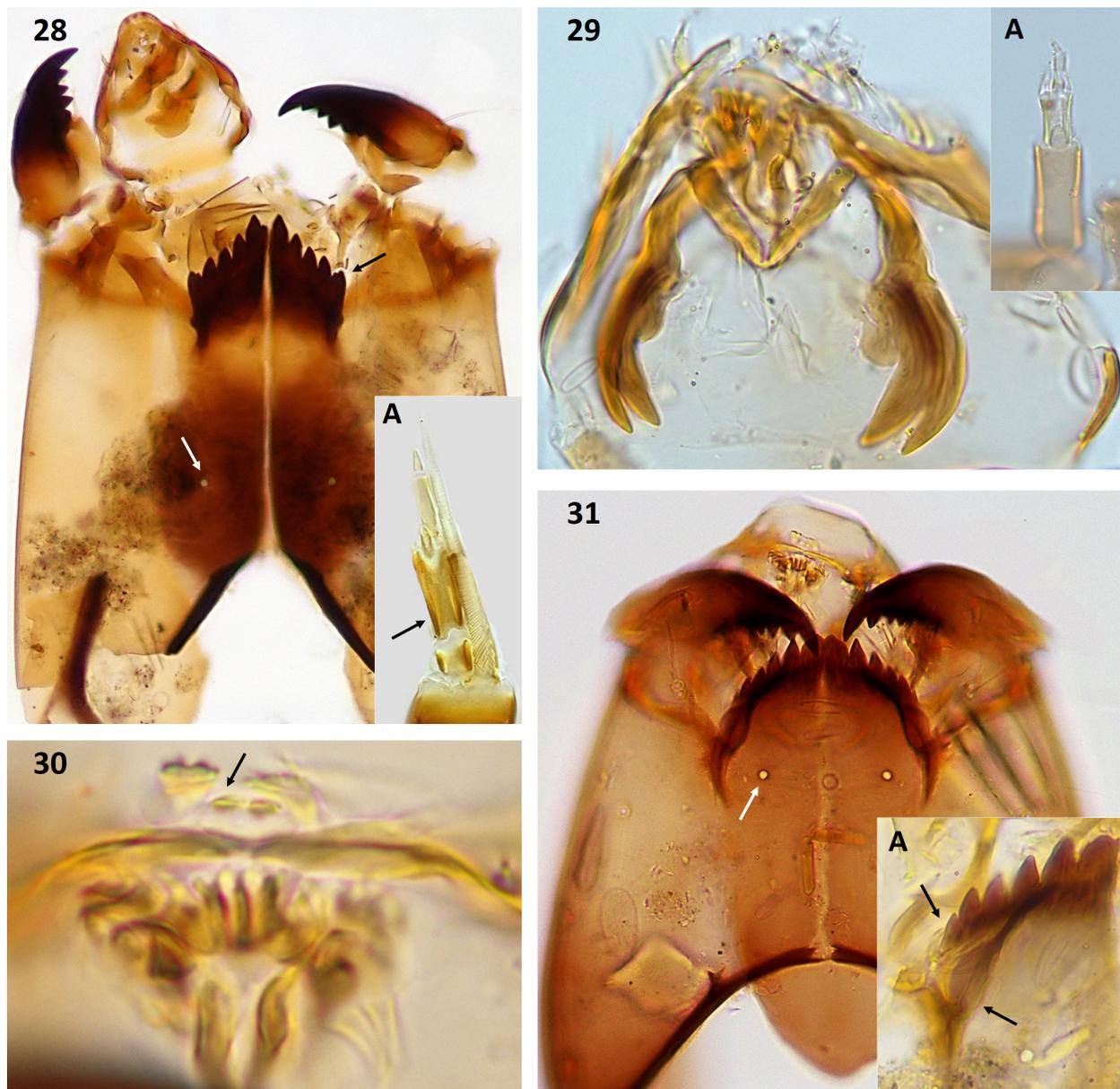
Orthoclaadiinae head capsules can be separated from Chironominae by absence of striate on ventromental plates, and by the eye-spots (if visible), which often are usually contiguous or, when separate with a dorsal eye-spot posterior to a ventral eye-spot. Diamesinae can be distinguished from orthoclaids by having annulate third antennal

segment (unfortunately, antenna very often missing) generally higher number of lateral teeth and more robust head occipital margin. The most important characters for subfossil identification are shape, number and arrangement of teeth together with the shape of ventromental plates.

Most of recorded head capsules belong to rheophilic to rheobiontic genera, in less extent to typical lentic and semiterrestrial/ terrestrial genera are present.

***Brillia* Kieffer (Fig. 28)**

Head capsule triangular and yellow. Antenna with 4 segments, second segment divided into small proximal and longer (~3x) distal part (Fig. 28A). Premandible bifid, weak notch between teeth. Mandible with 4 inner teeth. Mentum dark brown with two long median teeth, a very small tooth usually present in between bases of them, and 5 pairs of lateral teeth. Ventromental plates small, triangular. Setae submenti positioned on the submentum closer to occipital margin than base of mentum (Fig. 28).



FIGURES 28–31. *Brillia bifida*-type: 28—head capsule (arrows indicate fourth and fifth lateral teeth of the mentum and position of seta submenti), A—antenna (arrow indicates second segment). *Chaetocladius piger*-type: 29—bifid premandible, A—antenna. *C. piger*-type: 30—labral lamellae (arrow indicates its position). *C. piger*-type: 31—head capsule (arrow indicates seta submenti), A—detail of mentum (arrows indicate minute last lateral tooth and bulbous ventromental plate).

Remarks: Larval *Brillia* is similar to *Euryhapsis* and *Eurycnemus* and can be differentiated by details on antennae and labrum, even though these structures are usually absent in subfossil material. However, neither of these genera have been recorded in Slovakia and their occurrence in the Tatra Mts. is unlikely.

Two subfossil morphotypes of *Brillia* can be distinguished corresponding to *modesta* and *flavifrons* species groups following Oliver & Roussel (1983). As the valid name of *B. modesta* is *B. bifida* (see Moller Pillot 2013), the morphotype is named *B. bifida*-type.

Only one morphotype was found in the studied lakes.

Brillia bifida-type

This is a new morphotype, not listed in Brooks *et al.* (2007).

Head capsule yellow, postoccipital margin blackish. Well sclerotized specimens have distinct brown-black oval patch on the postmentum. Fourth and fifth lateral teeth are adpressed to each other (Fig. 28).

Remarks: This morphotype corresponds to *B. bifida*, the only species from *bifida*-group known in Europe. It was rare, only found in two surveyed lakes.

Chaetocladus Kieffer (Figs 29–31)

Head yellow to light brown with darkened occipital margin. Antenna 5 segmented, never strongly reduced (Fig. 29A). Premandible bifid with 1–2 blunt inner teeth (Fig. 29). Labral lamellae of various shape usually well developed between labral setae SI, but can be vestigial or absent (Fig. 30). Apical mandibular tooth shorter than combined width of 3 inner teeth. Mentum with 1–2 median teeth and 5 pairs of lateral teeth, the outermost tooth may be reduced. Ventromental plates usually large, rounded and extending beyond outer lateral mental tooth.

Remarks: The shape of mentum is often the only character that can be used for the identification of subfossils. *Parametriocnemus*, *Paraphaenocladus*, *Heterotrissocladus* have mentum with double median tooth, and 5 pairs of laterals, combined with large ventromental plates extending beyond the outer lateral teeth without beard. Setae submenti of *Chaetocladus* are arising under the ventromental plates (Fig. 31) while there are located much higher in *Parametriocnemus* and *Paraphaenocladus* (see Fig. 58). The outermost mental tooth is not reduced in *Heterotrissocladus*. *Metriocnemus*, *Hydrobeanus* and *Thienemannia* have similar menta, however without large ventromental plates and obviously narrower median teeth/ tooth.

The only *Chaetocladus* identified to species level from the Tatra Mts. is *C. bitusiki* Moubayed, 2019 (Moubayed & Bitusik 2019).

The morphotype recognized in our material corresponds to Brooks *et al.* (2007).

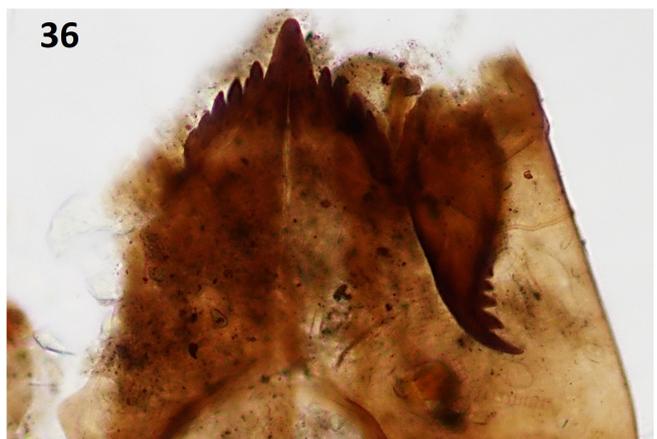
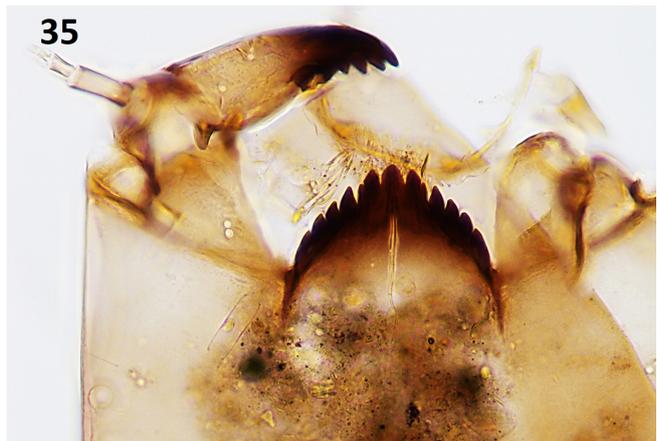
Chaetocladus piger-type (Fig. 31)

Mentum with paired median teeth, and 5 pairs of lateral teeth, outermost lateral is minute. Ventromental plates are broad and bulbous (Fig. 31A).

Remarks: Head capsules were found in eleven lakes without obvious respect to altitude, however, recent larvae of the genus were typical for lakes and ponds of higher elevations with significant fluctuation of water level (Hamerlík *et al.* 2017).

Corynoneura Winertz, 1846 (Figs 32–34)

Head capsule very small (thus easy to overlook), narrow and yellow, often sculpturing on surface. Occipital margin pale to black. Antennae 4 segmented, subequal or longer than head, second and third segments are frequently darkened. Premandible with up to 12 minute teeth. Apical mandibular tooth smaller than any of 4 inner teeth. Mentum with 2–3 median teeth and 5 pairs of lateral teeth. Ventromental plates narrow.



FIGURES 32–36. *Corynoneura arctica*-type: 32—head capsule (arrow indicates net-like reticulation). *Corynoneura edwardsi*-type: 33—head capsule. *Corynoneura lobata*-type: 34—head capsule (arrow indicates wrinkled sculpturing). *Cricotopus intersextus*-type: 35—head capsule. *Cricotopus (Isocladius) sylvestris*-type: 36—head capsule.

Remarks: The unique feature of the genus is the extremely long 4 segmented antenna (often broken off in the subfossil material). *Thienemanniella* has similar shape of mentum but the 5-segmented antenna is shorter than head,

third segment is shorter than second (while longer than second in *Corynoneura*); moreover, the head capsule is often pigmented (while usually pale in *Corynoneura*) without reticulation.

Two species, *Corynoneura scutellata* Winnertz, 1846 and *C. lobata* Edwards, 1924 were confirmed from the Tatra Mts. lakes (Bitušík 2004).

Corynoneura remains were found in lakes covering a broad altitudinal range, missing only in the uppermost Tatra Mts. lakes (Hamerlík *et al.* 2017). Three morphotypes were distinguished following Brooks *et al.* (2007).

Corynoneura arctica-type (Fig. 32)

Head capsule yellow, with strong, clearly visible net-like reticulation. Occipital margin dark brown. Mentum with three median teeth, while middle tooth small, and 5 pairs of subequal lateral teeth. This is the most frequent morphotype in the Tatra Mts. lakes.

Corynoneura edwardsi-type (Fig. 33)

Head capsule pale and not reticulated. Mentum similar to above mentioned morphotype, however middle tooth is more developed than in *C. arctica*-type. Lateral teeth subequal.

Corynoneura lobata-type (Fig. 34)

Head capsule brownish with weak wrinkled sculpturing. Occipital margin dark brown. Middle tooth of mentum strongly reduced, first lateral teeth visibly reduced.

***Cricotopus van der Wulp* (Figs 35–40)**

Head capsule yellow to blackish brown, occipital margin pale to black. Antenna usually 5-segmented. Premandible with one, rarely two apical teeth. Mandible with short apical tooth (shorter than combined width of inner teeth) and 3 inner teeth. Outer margin is usually crenulated, sometimes smooth. Mentum with one median, and usually 6 (rarely 5 or 7) lateral teeth. Ventromental plates narrow.

Remarks: *Cricotopus* larvae are extremely similar to *Orthocladius* and *Paratrichocladius* (recently placed within *Cricotopus* as subgenus, Cranston & Krosch, 2015).

Tuft of setae on the body segments of most species can distinguish *Cricotopus* from *Orthocladius*, however this feature is inapplicable in subfossil material, and the same goes for characters on antennae (Andersen *et al.* 2013b). In general, the following characters seem to be more typical for *Cricotopus* than *Orthocladius* (though can be present in some *Orthocladius* as well): outer margin of mandible strongly crenulated, second lateral tooth smaller than first one and/or reduced and fused to first lateral tooth, and outer four lateral teeth forming a distinct group. Brooks *et al.* (2007) state that lateral teeth of *Cricotopus* are usually more rounded and pointed apically and the median tooth is relatively narrow, while in general, *Orthocladius* have lateral teeth more rectangular and median tooth can be broad (>3 times broader than first lateral). *Paratrichocladius* is usually distinguished by having the first lateral tooth of the mentum constricted at base so that broader in the middle than at the base. This tooth of *Cricotopus* and *Orthocladius* is widest at the base.

Cuppen & Tempelman (2018) have proposed a key to recognize *Cricotopus* subgenera that may be applied to sub-fossil remains. Subgenus *Isocladius*: Median mental tooth usually rounded, triangular in shape, always < 2.5 times as wide as first lateral tooth; second lateral mental tooth strongly reduced and for the largest part fused with the first lateral tooth. Subgenus *Cricotopus*: Median mental tooth of varying size, either small or up to 3 or 4 times as wide as first lateral tooth, second lateral not reduced (e.g. Fig. 39).

Up to date, *Cricotopus* (*Cricotopus*) *pilosellus* Brundin 1956, *Cricotopus* (*Isocladius*) *perniger* (Zettstedt, 1850) and *C. (I.) cf. tricinctus* (Meigen, 1818) were identified from pupal exuviae material (Bitušík 2004; Bitušík *et al.* 2006a).

Cricotopus was relatively frequently recorded from the lakes situated at lower altitudes. Five morphotypes were recognized, three of them are not listed in Brooks *et al.* (2007).

Key to morphotypes:

- | | | |
|---|---|---------------------------------------|
| 1 | Second lateral tooth of mentum reduced and partly fused with first lateral tooth | 2 |
| - | Second lateral tooth of mentum subequal or only slightly smaller than first lateral tooth and not fused with it. | 3 |
| 2 | Median tooth of mentum prominent, more than twice height of first lateral tooth | <i>Cricotopus sylvestris</i> -type |
| - | Median tooth of mentum subequal to slightly longer than first laterals. | <i>Cricotopus intersectus</i> -type |
| 3 | Mentum rather horizontal in appearance | <i>Cricotopus/Orthocladius</i> I |
| - | Mentum triangular in shape | 4 |
| 4 | Head capsule light brown; median mental tooth up to 2 times width of first lateral tooth; first lateral tooth rounded, wider in middle than at base; first inner tooth of mandible robust, larger than apical tooth | <i>Cricotopus skirwithensis</i> -type |
| - | Head capsule dark brown; median mental tooth narrow, equal to or slightly wider than first lateral tooth; inner teeth on mandible subequal in size | <i>Cricotopus tremulus</i> -type |

Cricotopus (Isocladius) intersectus-type (Fig. 35)

Head capsule yellow with dark brown occipital margin. Mentum with single broad median tooth taller than the first lateral tooth. Second lateral tooth minute and fused to the first lateral. Median tooth and first two laterals form a distinct group separated from the other laterals.

Cricotopus (Isocladius) sylvestris-type (Fig. 36)

Head capsule yellow to light brown. Mentum with very large rounded median tooth and 6 pairs of lateral teeth. Second lateral tooth is small and fused to the first one. Premandible apically bifid.

Cricotopus (Paratrichocladius) skirwithensis-type (Figs 37, 38)

This is a new morphotype, not listed in Brooks *et al.* (2007).

Head capsule light brown with dark brown occipital margin and mandibular teeth. Mentum triangular in shape with a single median tooth up to 2 times width of first lateral tooth. First lateral tooth of the mentum is clearly rounded, wider in the middle than at the base. Remainder of lateral teeth pointed. First inner tooth of the mandible large, noticeably broader than apical tooth, but not taller (Fig. 37); outer margin of mandible smooth or only with a vague indication of crenulation. Setae submenti positioned between the bases of ventromental plates. Premandible with one apical tooth (however, there may be a faint indication of a notch) (Fig. 38).

Cricotopus (Cricotopus) tremulus-type (Fig. 39)

This is a new morphotype, not listed in Brooks *et al.* (2007).

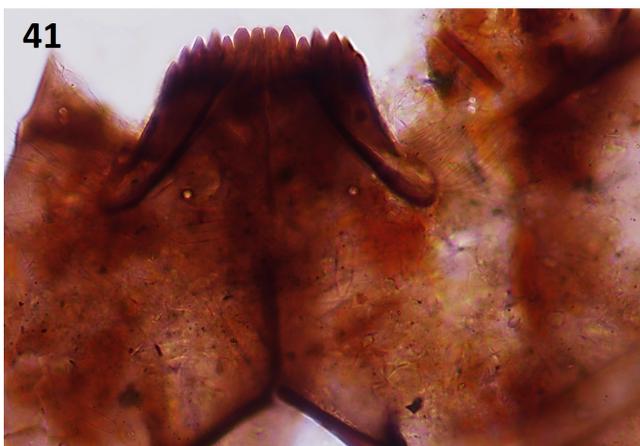
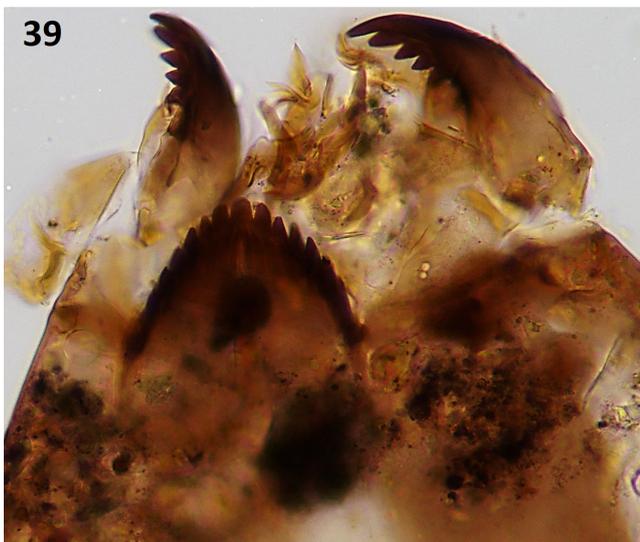
Head capsule dark brown with black occipital margin and mandibular teeth. Teeth of mentum dark brown to black in colour; single narrow median tooth, equal to or only slightly wider than the first lateral tooth. Mandible with crenulated outer margin. Premandible with single tooth.

Cricotopus/Orthocladius I (Fig. 40)

This is a new morphotype, not listed in Brooks *et al.* (2007).

Head capsule light brown to yellow in colour. Mentum rather horizontal in shape, all teeth brown. Single me-

dian tooth, about 1.5 times width of first lateral tooth; first lateral teeth obviously rounded. Second lateral tooth reduced and partly fused to first lateral. Setae submenti situated below the bases of mentum.



FIGURES 37–42. *Cricotopus (Paratrichocladius) skirwithensis*-type: 37—head capsule (arrow indicates first inner tooth of the mandible). *C. (P.) skirwithensis*-type: 38—detail of premandible. *Cricotopus (Cricotopus) tremulus*-type: 39—head capsule. *Cricotopus/Orthocladus* I: 40—head capsule. *Diplocladius cultriger*: 41—head capsule. *D. cultriger*: 42—detail of the head capsule (arrow indicates long and dense beard).

***Diplocladius* Kieffer (Figs 41, 42)**

Head capsule dark brown, occipital margin black. Antenna 5-segmented, premandible bifid. Mandible with 4 inner teeth, their combined width is larger than length of apical tooth. Mentum broad with two median teeth and 6 pairs of lateral teeth. The first lateral tooth is subequal to median tooth and second lateral tooth is smaller than first lateral and third lateral. Ventromental plates are long and broad with noticeably long and dense beard (Fig. 42).

Remarks: The unique shape of mentum with long beard is distinctive for the genus.

Diplocladius cultriger Kieffer, 1908, is the only species known in the Holarctic. It was found in one lake of our lake set.

***Eukiefferiella* Thienemann (Figs 43–46)**

Head capsule narrow, yellow to dark brown. Occipital margin darkened, broad. Antenna with 4–5 segments, premandible broad with one apical tooth. Mandible with 3–4 inner teeth, apical tooth shorter than combined width of inner teeth; mola with 1–5 spines. Mentum striped, with 1 or 2 median and 4–5 lateral teeth. Ventromental plates are narrow, creating an appearance of a dark triangle below the last lateral tooth of mentum.

Remarks: *Eukiefferiella* is very similar to *Tvetenia* and the most reliable character separating their subfossils is the position of setae submenti that are close to the base of the mentum in *Eukiefferiella* but well below the mentum in *Tvetenia*. Moreover, head capsule of *Tvetenia* is usually pale, while head capsule of *Eukiefferiella* is light brown to dark brown (Schmid 1993).

Eukiefferiella claripennis (Lundbeck, 1898), *E. coerulescens* (Kieffer, 1926), *E. minor* (Edwards, 1929)/ *fittkau*i Lehmann, 1972 and *E. brevicealcar* (Kieffer, 1911)/ *tirolensis* Goetghebuer, 1938 have been so far recorded in the Tatra Mts. lakes (Bitušík 2004; Novikmec *et al.* 2015).

Subfossil remains occurred relatively frequently in lakes situated at lower altitudes, especially in lakes with strong inlet stream.

Four morphotypes were distinguished.

Key to morphotypes:

- | | | |
|---|---|---|
| 1 | Mentum with single median tooth | 2 |
| - | Mentum with bifid median tooth | <i>Eukiefferiella claripennis</i> -type B |
| 2 | Mentum with 4 lateral teeth | <i>Eukiefferiella devonica</i> -type |
| - | Mentum with 5 lateral teeth | 3 |
| 3 | Median mental tooth relatively narrow, about 2x as broad as first lateral tooth | <i>Eukiefferiella brevicealcar</i> -type |
| - | Median mental tooth broad, more than 3x as broad as first lateral tooth | <i>Eukiefferiella fittkau</i> i-type |

***Eukiefferiella brevicealcar*-type (Fig. 43)**

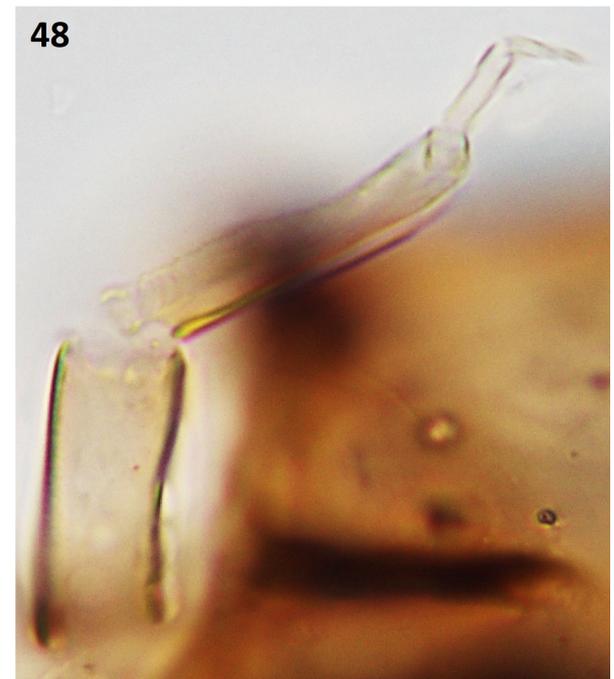
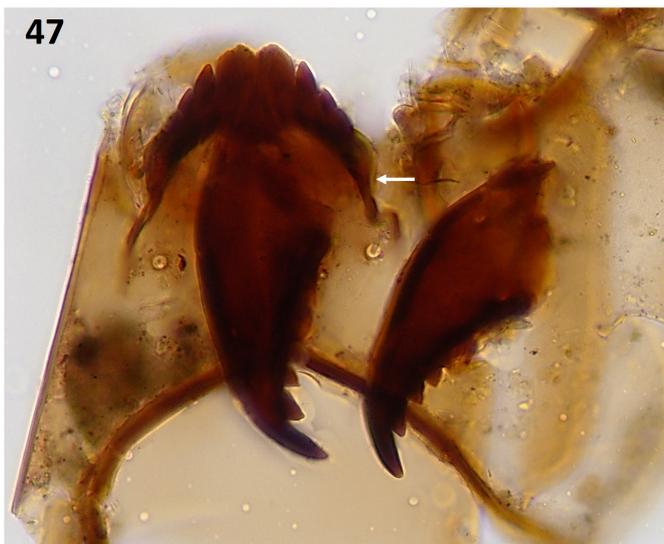
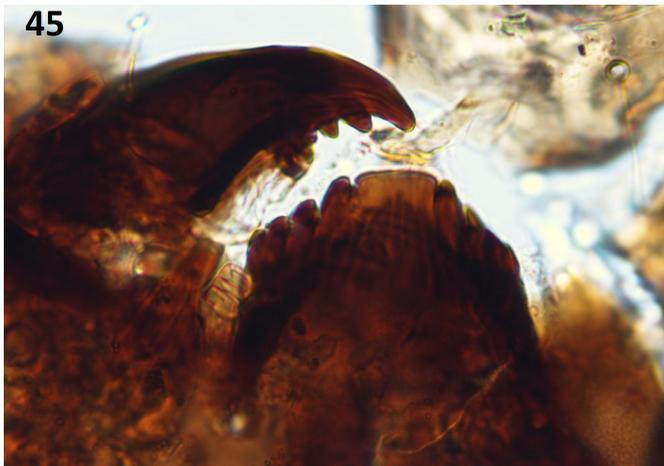
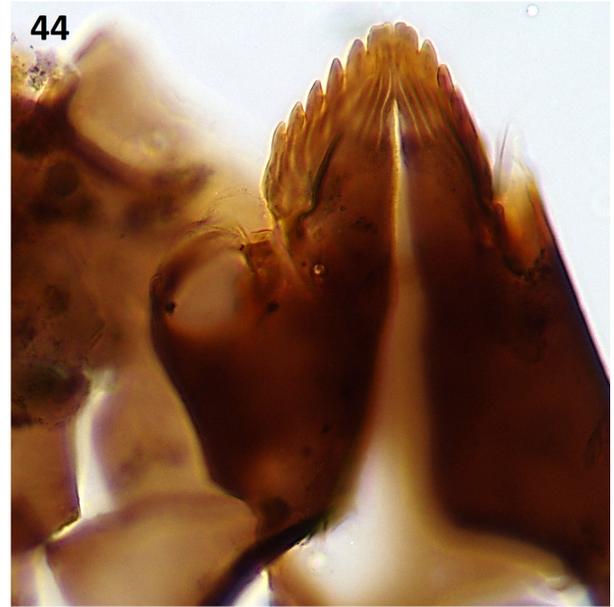
This is a new morphotype, not listed in Brooks *et al.* (2007).

Head capsule brown. Mentum with a single median tooth, about 2.0 times width of first lateral tooth. Second lateral tooth pressed to first lateral leaving obvious gap between it and group of three outermost lateral teeth.

***Eukiefferiella claripennis*-type B (Fig. 44)**

This is a new morphotype, not listed in Brooks *et al.* (2007).

Head capsule dark brown. Mentum with two median teeth and 5 pairs of equidistant lateral teeth. Brooks *et al.* (2007) present only one *Eukiefferiella* morphotype with double median tooth, *E. claripennis*-type, which differs in some minor but obvious features from the type found in the Tatra Mts. In our case the median teeth are well-sepa



FIGURES 43–48. *Eukiefferiella brevicar*-type: 43—head capsule. *Eukiefferiella claripennis*-type B: 44—head capsule. *Eukiefferiella devonica*-type: 45—head capsule. *Eukiefferiella fittkaii*-type: 46—head capsule. *Gymnometriocnemus*/*Bryophaenocladus*: 47 (arrow indicates ventromental plate). *Heterotrissocladus marcidus*-type: 48—antenna.

rated and broader than the first lateral teeth that are clearly separated from the median teeth with a deep notch; in Brooks *et al.* (2007), median teeth are narrow and weakly separated, and first lateral teeth are appressed to medians. The former reminds *E. rectangularis* group, recently placed to *Tokunagaia rectangularis* group. We assume that our morphotype represents this taxon occurring in cold springs (Bitušík 2000) and lakes (Hamerlík *et al.* 2017) in the High Tatra Mts. and sediment cores from the high alpine Nižné Terianske pleso lake (Bitušík & Kubovčík 1999). To distinguish the two morphotypes, we named the one recorded in the Tatra Mts. lakes *E. claripennis*-type B.

Eukiefferiella devonica-type (Fig. 45)

Dark brown head capsule. Strongly pigmented mentum with a single broad median tooth, 2–3 times width of first lateral tooth and 4 pairs of lateral teeth.

Eukiefferiella fittkawi-type (Fig. 46)

Head capsule brown. Mentum with a single, broad median tooth more than 4 times width of first lateral tooth and 5 pairs of lateral teeth.

Gymnetriocnemus Edwards/ *Bryophaenocladus* Thienemann (Fig. 47)

Head capsule yellow to light brown, occipital margin pale or darkened. Antenna with 5 segments of variable lengths. Premandible with 3 teeth. Apical mandibular tooth shorter than combined width of 3 inner teeth. Mentum dark brown with paired, relatively broad and rounded median teeth and 4 pairs of lateral teeth gradually decreasing in size. Ventromental plates distinct, sclerotized, not extending beyond outer lateral tooth, reminding ears and visible at the first sight (Fig. 47).

Remarks: Without body and antennae, larval *Gymnetriocnemus* virtually cannot be distinguished from *Bryophaenocladus*.

Bryophaenocladus muscicola (Kieffer, 1906) and *B. cf. subvernalis* (Edwards, 1929) are known from the Tatra Mts. lakes (Bitušík 2004).

Subfossils were recorded in low abundance but relatively frequently in the studied lakes.

Heterotrissocladus Spärck (Figs 48–50)

Head capsule yellow, occipital margin pale or darkened. Antenna 7-segmented, seventh segment vestigial (Fig. 48). Premandible with two indistinct teeth (Fig. 49). Apical mandibular tooth shorter than combined width of 3–4 inner teeth. Mentum with two (rarely one) median teeth (sometimes accessory teeth are present) and 5 pairs of lateral teeth. First and second lateral teeth clearly longer than other three lateral teeth. Ventromental plates distinct, bulbous, extended beyond margin of mentum.

Remarks: *Heterotrissocladus* is similar to *Paratrissocladus*, however the latter has 4 lateral mental teeth. Subfossil remains without antennae and labro-epipharyngeal region could be confused with *Psectrocladius* and *Chaetocladus* that have distinct ventromental plates. However, the outmost lateral tooth is usually reduced in *Chaetocladus*, and ventromental plates of obviously triangular shape with weak beard in *Psectrocladius*.

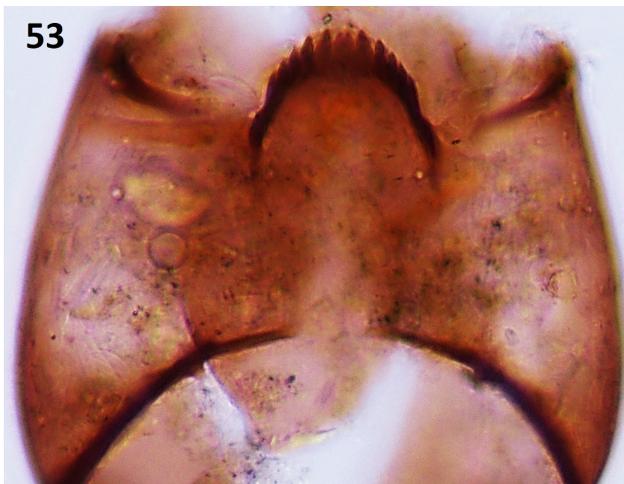
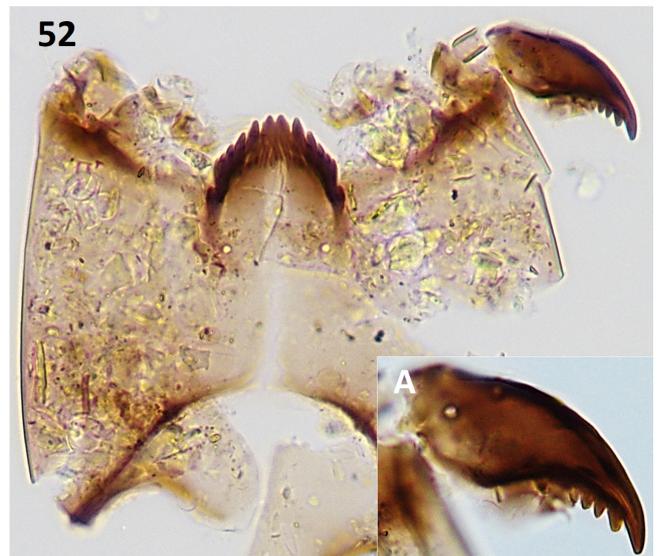
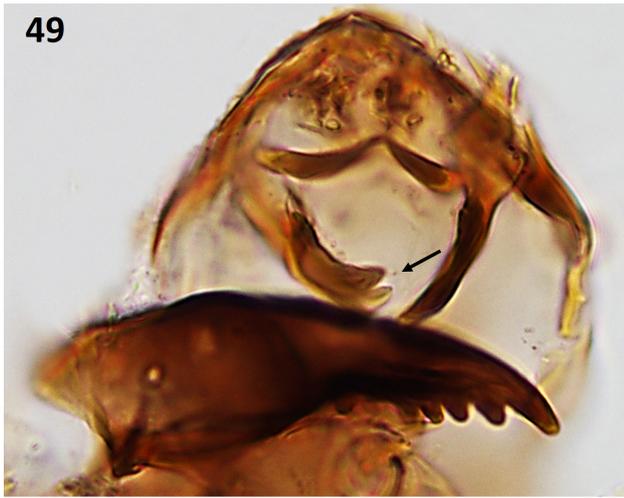
One morphotype was distinguished.

Heterotrissocladus marcidus-type (Fig. 50)

Mentum with two median teeth. Submentum entirely pigmented, darker than the rest of the head capsule.

Remarks: *Heterotrissocladus marcidus* (Walker, 1856) is the only known species in the Tatra Mts. lakes, and it is considered to be the most common chironomid inhabiting the Tatra Mts. lakes (Bitušík *et al.* 2006a).

Subfossil remains were abundant in most of the studied lakes.



FIGURES 49–53. *Heterotrissocladius marcidus*-type: 49—premandible. *H. marcidus*-type: 50—head capsule. *Limnophyes/Paralimnophyes*: 51—head capsule. *Paralimnophyes*: 52—head capsule, A—detail of mandible. *Metriocnemus eurynotus*-type: 53—head capsule.

***Limnophyes* Eaton/ *Paralimnophyes* Brundin (Figs 51, 52)**

Head capsule yellow, occipital margin pale or darkened. Antenna 5-segmented. Premandible with two apical and two inner teeth. Apical mandibular teeth shorter than combined width of 3 (*Limnophyes*) or 4 (*Paralimnophyes*) inner teeth (Fig. 52A). Mentum with two median teeth slightly higher than first lateral of 5 lateral teeth. Fourth and fifth laterals obviously smaller and narrower than others. Mentum frequently with pale stripes in the median region

Ventromental plates widened and sclerotized posterolaterally into rounded dark pigmented plate projecting below outermost lateral tooth and appearing as additional basal tooth separated by notch (Fig. 52A).

Remarks: When mandibles are missing from subfossils *Paralimnophyes* and *Limnophyes* are indistinguishable. Shape of mentum with two median teeth and 5 pairs of laterals, presence of stripes resembles *Eukiefferiella*, however widely separated median teeth and presence of dark brown bulge at the end of ventromental plates is distinctive for *Limnophyes/ Paralimnophyes*. *Heleniella* has a similar pattern of mentum but unlike *Limnophyes/ Paralimnophyes* the fifth lateral tooth is longer than the fourth and there is a U-shaped gap between median teeth.

Remains were found in small number of Tatra Mts. lakes. Generally, the occurrence of *Limnophyes* larvae, like other semi-terrestrial taxa (in the uppermost lakes) may be indicative for water-level fluctuation in these lakes (Hamerlík *et al.* 2017).

***Metriocnemus van der Wulp* (Figs 53, 54)**

Head capsule yellow to dark brown, occipital margin pale or darkened. Antenna with 5 segments and variable in structure, sometimes reduced. Premandible with 2–4 apical teeth. Apical mandibular tooth short, 4–5 inner teeth are present. Mentum with 1–4 median teeth, usually lower than first of 5–6 pairs of lateral teeth. Ventromental plates very weak (Figures 53, 54).

Remarks: The shape of mentum with lower and narrower median teeth than the first laterals is routinely distinctive for the genus, however, the same pattern of mentum is typical for *Thienemannia*, so heads of both genera are indistinguishable in subfossil material. However, *Thienemannia* has not been recorded from the Tatra Mts.

Based on pupal exuviae material, two species: *Metriocnemus fuscipes* (Meigen, 1818) and *Metriocnemus* cf. *obscuripes* (Holmgren, 1869) were identified from the Tatra Mts. lakes (Bitušík 2004).

Subfossil *Metriocnemus* remains were recorded rarely.

Two morphotypes were distinguished following Brooks *et al.* (2007).

Metriocnemus eurynotus-type (Fig. 53)

Head capsule brown. Mentum with two short median teeth and with 5 pairs of lateral teeth gradually decreasing in size, first lateral tooth broader than median teeth.

Metriocnemus fuscipes-type (Fig. 54)

Head capsule dark brown. Mentum with two short median teeth and with 5 pairs of lateral teeth, first and second lateral teeth longer and broader than median and other laterals.

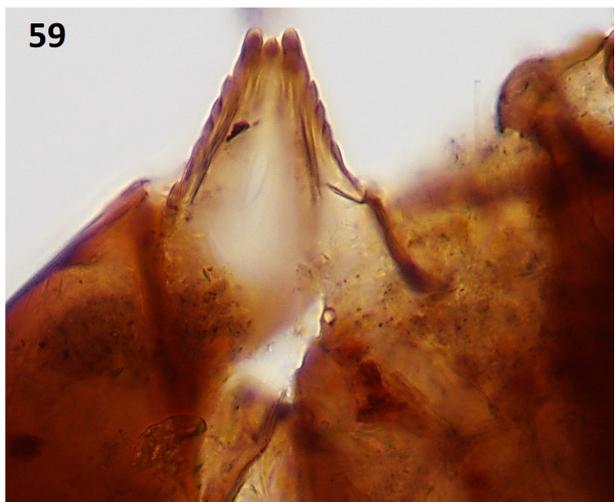
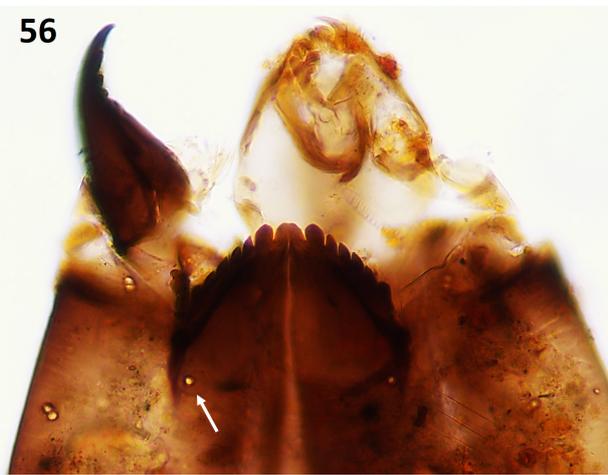
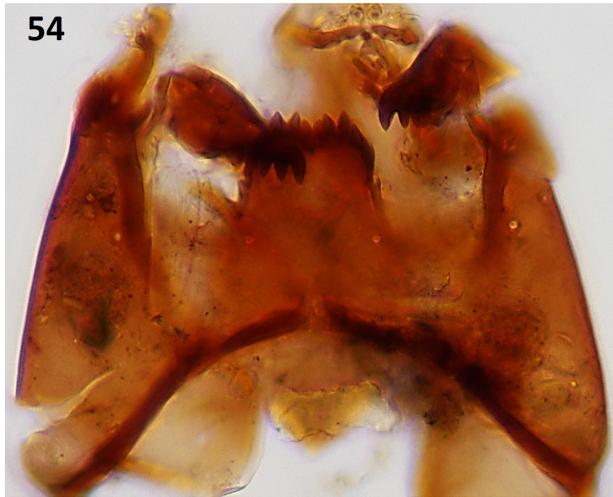
***Orthocladius van der Wulp* (Figs 55–57)**

Head capsule yellow, brown to dark brown, or reddish brown, occipital margin usually darkened. Antenna 5-segmented (rarely with 4 segments). Premandible with one (frequently notched) or two apical teeth. Mandible with 3 inner teeth, apical tooth usually short, longer in some species of subgenera *Euorthocladius* and *Symposiocladius*. Mentum with one median and usually with 6 pairs of lateral teeth, sometimes 7–9 laterals are present (*O. (Symposiocladius) lignicola* has unusual mentum with single elongate median tooth and 2 pairs of lateral teeth). Ventromental plates narrow and short, beard absent (with the exception of subgenus *Pogonocladius*).

Remarks: Subfossil head capsules of *Orthocladius* with 6 pairs of lateral mental teeth and without beard are essentially indistinguishable from *Cricotopus* (incl. *Paratrithocladius*) as mentioned above (see remarks to *Cricotopus*).

The following *Orthocladius* species have been recorded in the Tatra Mts. lakes: *O. (Eudactylocladius) fuscimanus* (Kieffer, 1908), *O. (Eudactylocladius) olivaceus* (Kieffer, 1911), *O. (Euorthocladius) rivicola* Kieffer, 1921, *O. (Euorthocladius) rivulorum* Kieffer, 1909, *O. (Mesorthocladius) frigidus* (Zetterstedt, 1838) (Bitušík 2004; Novikmec *et al.* 2015).

The remains identified as *Orthocladius* were recorded very rarely in small number of the surveyed lakes. Three morphotypes were distinguished following Schmid (1993) and Soponis (1977), none of them is listed in Brooks *et al.* (2007).



FIGURES 54–59. *Metriocnemus fuscipes*-type: 54—head capsule. *Orthocladius (Orthocladius) dentifer*-type: 55—head capsule. *Orthocladius (Mesorthocladius) frigidus*: 56—head capsule (arrow indicates seta submenti). *Orthocladius (Euorthocladius)*: 57—head capsule. *Parametriocnemus/Paraphaenocladius*: 58 (arrow indicates seta submenti). *Parorthocladius*: 59—head capsule.

Key to morphotypes:

- 1 Median mental tooth extending considerably beyond apices of first laterals; mentum noticeably triangular in shape; median tooth with first two lateral teeth paler than remaining laterals. *Orthocladius dentifer*-type
- Median and first lateral teeth subequal in lengths 2
- 2 Mandibular teeth black; ventromental plates short and narrow; seta submenti located close to bases of ventromental plates, 2 setal pores present *Orthocladius frigidus*
- Mandibular teeth brown; ventromental plates long extended well below seta submenti, angling inwards apically, setae submenti positioned below the base of ventromental plates *Orthocladius (Euorthocladius)*

Orthocladius (Orthocladius) dentifer-type (Fig. 55)

This is a new morphotype, not listed in Brooks *et al.* (2007).

Head capsule yellow to light brown with brown occipital margin and mandibular teeth. Mentum triangular in shape with clearly separated teeth. Median tooth with first two lateral teeth lighter than the remaining laterals. First lateral teeth clearly pointing outwards. Mandible with crenulated outer margin, inner teeth subequal in size.

Orthocladius (Mesorthocladius) frigidus Zetterstedt, 1838 (Fig. 56)

This is a new morphotype, not listed in Brooks *et al.* (2007).

Head capsule brown with black occipital margin. Mentum with single median tooth and 6 pairs of lateral teeth, all black. Median and first lateral tooth rounded, median and first laterals are subequal. Seta submenti is located between the narrow ventromental plates, very close to them; 2 setal pores present above each other, a bigger anterior and smaller posterior. Outer margin of mandible crenulated.

Orthocladius (Euorthocladius) (Fig. 57)

This is a new morphotype, not listed in Brooks *et al.* (2007).

Head capsule dark brown with black occipital margin. Mentum triangular in shape with weak striation and light brown teeth. Median tooth and first lateral teeth rounded, first lateral narrower at the base. Ventromental plates characteristic: darkly pigmented, extended well below seta submenti, angling inwards apically, with an obvious bulb at the base. Setae submenti positioned below the base of ventromental plates. Mandible with first inner tooth large, outer margin smooth.

Parametriocnemus Goetghebuer/ *Paraphaenocladus* Thienemann (Fig. 58)

Head capsule yellow, occipital margin slightly darker. Antenna usually 5-segmented, when 6-segmented, last segment vestigial. Premandible with 2–6 teeth. Mandible with 3 inner teeth, apical tooth short. Mentum with paired median teeth and five pairs of lateral teeth, fifth lateral minute. Ventromental plates distinct, extending beyond the last lateral tooth, with second plate inside main plate. Setae submenti are positioned high on mentum, about at the level of the outermost lateral teeth (Fig. 58).

Remarks: Subfossil larval head of *Parametriocnemus* essentially cannot be distinguished from *Paraphaenocladus*. If premandibles are present, specimens with two and more than three apical teeth can be allocated to *Parametriocnemus* as premandible of *Paraphaenocladus* consists of 3 apical teeth.

Limnophyes superficially resembles *Parametriocnemus/ Paraphaenocladus* but it differs from it by having darkly pigmented lobe below outermost lateral tooth, subequal lateral teeth, and weakly developed ventromental plates (Fig. 51).

Only one species of the *Parametriocnemus* genus (*P. boreoalpinus* Gouin, 1942) was recorded from the Tatra Mts. lakes (Bitušík 2004).

Subfossil remains were found rarely.

***Parorthocladius* Thienemann (Fig. 59)**

Head capsule brownish, triangular in shape. Occipital margin dark brown. Antenna 5-segmented. Premandible simple, with one apical tooth. Apical mandibular tooth shorter than combined width of 3 inner teeth. Mentum subtriangular with three equal sized median teeth and 4 pairs of lateral teeth steeply sloping reminding a ladder. Ventromental plates narrow with beard consisting of a tuft of long setae (often missing in the subfossil material).

Remarks: The larval head of *Parorthocladius* and *Synorthocladius* are very similar, however *Synorthocladius* has two very long median teeth on mentum, while *Parorthocladius* three (and not as long). The only known species from the Tatra Mts. lakes is *P. nudipennis* (Kieffer, 1908) (Bitušík 2004).

Subfossil remains were found rarely.

***Psectrocladius* Kieffer (Figs 60–62)**

Head capsule yellow to light brown, occipital margin pale or darkened. Antenna 5-segmented, premandible with one tooth. Apical mandibular tooth shorter than or 2.5x longer than combined width of 3 inner teeth. Mentum with one or two median teeth and 5 pairs of subequal lateral teeth. When single median tooth, then either with one or two nipple-like median projections. Ventromental plates broad, extending beyond outermost mental teeth and forming a noticeable triangle at the apex. Beard consisting of variable number of setae present, but not always visible in subfossils.

Remarks: *Psectrocladius* is a relatively uniform genus, and subfossil head capsules provide a combination of characteristics that are distinctive: large acutely pointed ventromental plates with beard (beard is often missing in subfossil material), simple premandible, five lateral mental teeth.

Recently, 5 species: *Psectrocladius* (*Allopectrocladius*) *obvius* (Walker, 1856), *P. (A.) platypus* (Edwards, 1929), *P. (Mesopsectrocladius) barbatipes* Kieffer, 1923, *P. (Psectrocladius) octomaculatus* Wülker, 1956, *P. (P.) oxyura* Langton, 1985 were identified based on pupal exuviae material collected from the Tatra Mts. lakes (Bitušík 2004; Novikmec *et al.* 2015).

Psectrocladius remains belong to the most common orthoclads in the Tatra Mts. lakes, mostly found in lakes situated at lower altitude.

Three types were distinguished following Brooks *et al.* (2007).

Psectrocladius (*Mesopsectrocladius*) *barbatipes*-type (Fig. 60)

Mentum with one very broad median tooth with two small median projections.

Psectrocladius (*Psectrocladius*) *psilopterus*-type (Fig. 61)

Mentum with single broad median tooth with pair of median nipple-like projections. Only 3 inner teeth of mandible darkened (Fig. 61A).

Psectrocladius (*Psectrocladius*) *sordidellus*-type (Fig. 62)

Mentum with paired median teeth, with a short median projection. All or only 3 inner teeth darkened. If only half of head capsule is preserved, it can be difficult to distinguish this morphotype from *P. psilopterus*-type.

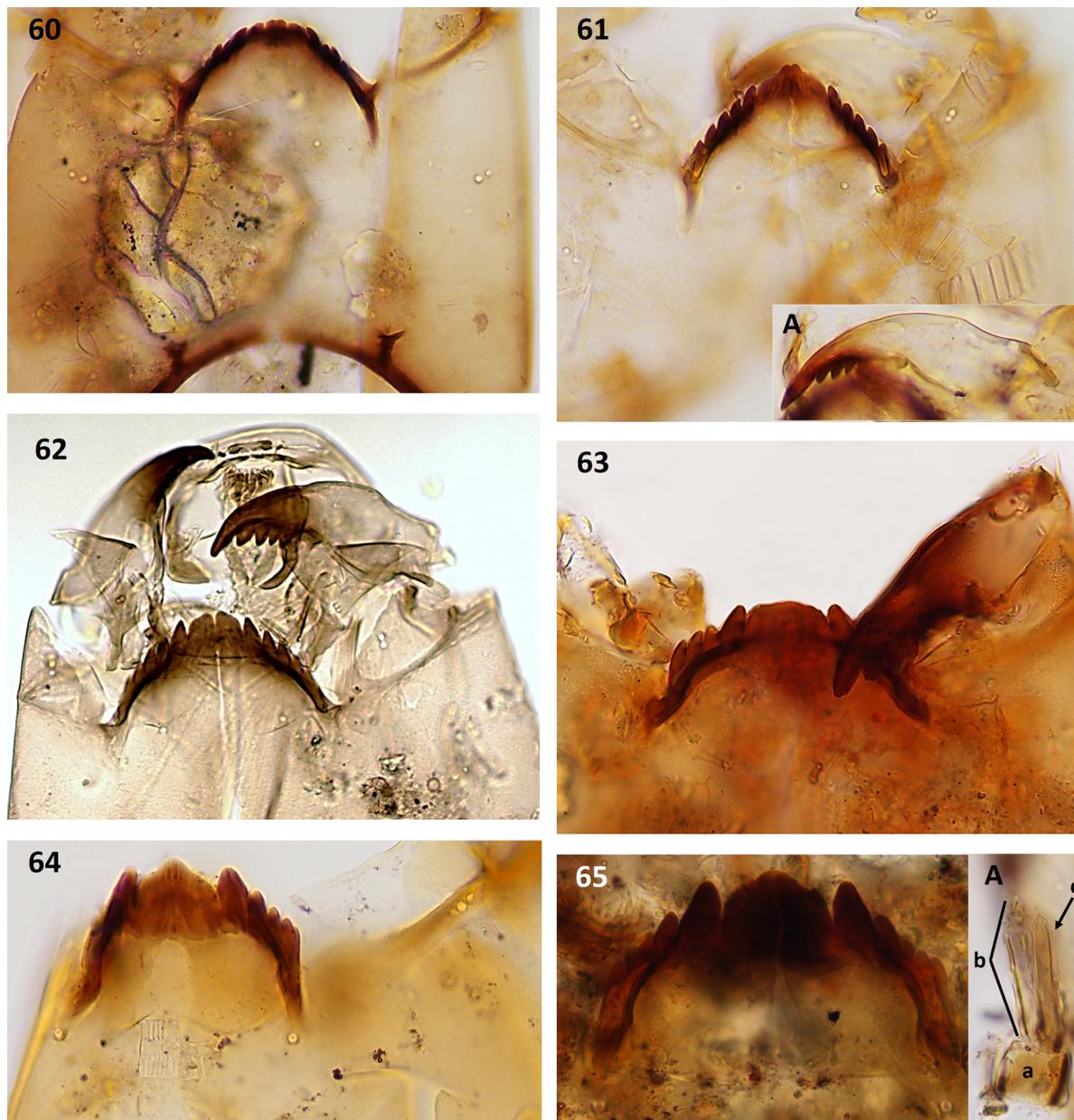
***Pseudosmittia* Edwards (Fig. 63)**

Head capsule yellow, occipital margin pale to brown. Antenna reduced (only $\frac{1}{4}$ length of mandible), with 4 segments. Premandible with 2 apical teeth and 1–2 inner more or less tooth-like projections can be present. Mandible

with 3–4 inner teeth. One very broad median mental tooth with more or less obvious median projection and 4 pairs of lateral teeth gradually decreasing in size. Ventromental plates large, not extending beyond outermost teeth.

Remarks: The shape of mentum is distinctive among other Orthoclaadiinae with exception of *Camptocladius*, however its larvae are full terrestrial, so their presence in lake sediments is very unlikely. *Pseudosmittia* could be confused with *Pseudorthocladius* when its median mental teeth are worn but setae submenti is arising further below outermost lateral teeth compared to that of *Pseudosmittia*.

Only one head capsule was found.



FIGURES 60–65. *Psectrocladius* (*Mesopsectrocladius*) *barbatipes*-type: 60—head capsule. *Psectrocladius* (*Psectrocladius*) *psilopterus*-type: 61—head capsule, A—detail of mandible. *Psectrocladius* (*Psectrocladius*) *sordidellus*-type: 62—head capsule. *Pseudosmittia*: 63—head capsule. *Smittia*/*Parasmittia*: 64—head capsule. *Smittia*/*Parasmittia*: 65—mentum, A—*Smittia* antenna (a—basal segment, b—flagellum, c—blade).

Smittia Holmgren/ *Parasmittia* Strenzke (Figs 64, 65)

Head capsule yellow to brownish, occipital margin pale or darkened. Antenna reduced, with 4 segments. Blade well developed and as long as flagellum (*Smittia*, Fig. 65A) or considerably longer (*Parasmittia*). Premandible with

2 apical teeth and 1 variably developed inner tooth. Mandible with 3 inner teeth and short apical tooth. Mentum with one broad median tooth with projecting nipple (may be domed in *Smittia*) and 5 pairs of subequal lateral teeth. Ventromental plates well developed, not extending outermost teeth.

Remarks: *Smittia* and *Parasmittia* are indistinguishable in specimens with missing antennae.

In the Tatras, only *Smittia edwardsi* Goetghebuer, 1932 was determined based on adults (Bitušík 2004).

Remains of *Smittia/ Parasmittia* were recorded infrequently in the studied lakes. As mentioned above (see *Limnophyes/ Paralimnophyes*), presence of subfossils of semiterrestrial/ terrestrial taxa such as *Smittia/ Parasmittia* could have indicative value in the reconstruction of water-level oscillation.

***Synorthocladus* Thienemann (Figs 66, 67)**

Head capsule yellow, triangular in shape. Antenna 5-segmented. Premandible with one apical tooth. Mandible with 3 inner teeth and short apical tooth, mola with one strong spine (Fig. 67). Mentum triangular with two median teeth and 4 or 5 pairs of lateral teeth sloping steeply (Fig. 66A). Ventromental plates narrow and long with strong beard (may be missing in subfossil material).

Remarks: Larval *Synorthocladus* and *Parorthocladus* are similar, however the mentum of *Synorthocladus* has 2 median teeth on its apex.

Only one Holarctic species, *Synorthocladus semivirens* (Kieffer, 1909) is known and it was identified from several Tatra Mts. lakes (Bitušík 2004).

Subfossil remains were found rarely, only in two studied lakes.

***Thienemanniella* Kieffer (Fig. 68)**

Head capsule yellow to brown, occipital margin dark brown. Compared with other orthoclads (with exception of *Corynoneura*), head capsule is prolonged in shape and very small, easy to overlook. Antenna at least 1/2 but no more than 3/4 length of head; 5-segmented; segment 3 is frequently darkened. Premandible with one apical tooth. Mandible with 4 inner teeth, first one can be longer than apical tooth. Mentum with three subequal median teeth (exceptionally with two) clearly above the 5 pairs of subequal lateral teeth.

Remarks: *Thienemanniella* resembles *Corynoneura*, which also has a narrow, triangular mentum with three prominent median teeth and long antennae, however, in case of *Thienemanniella* antenna is shorter than head and with 5 segments. Antennae are often missing in subfossils, but the head capsule is usually darker and always without net-like reticulation on the surface (note that in some *Corynoneura* species/types reticulation may be indistinct, too).

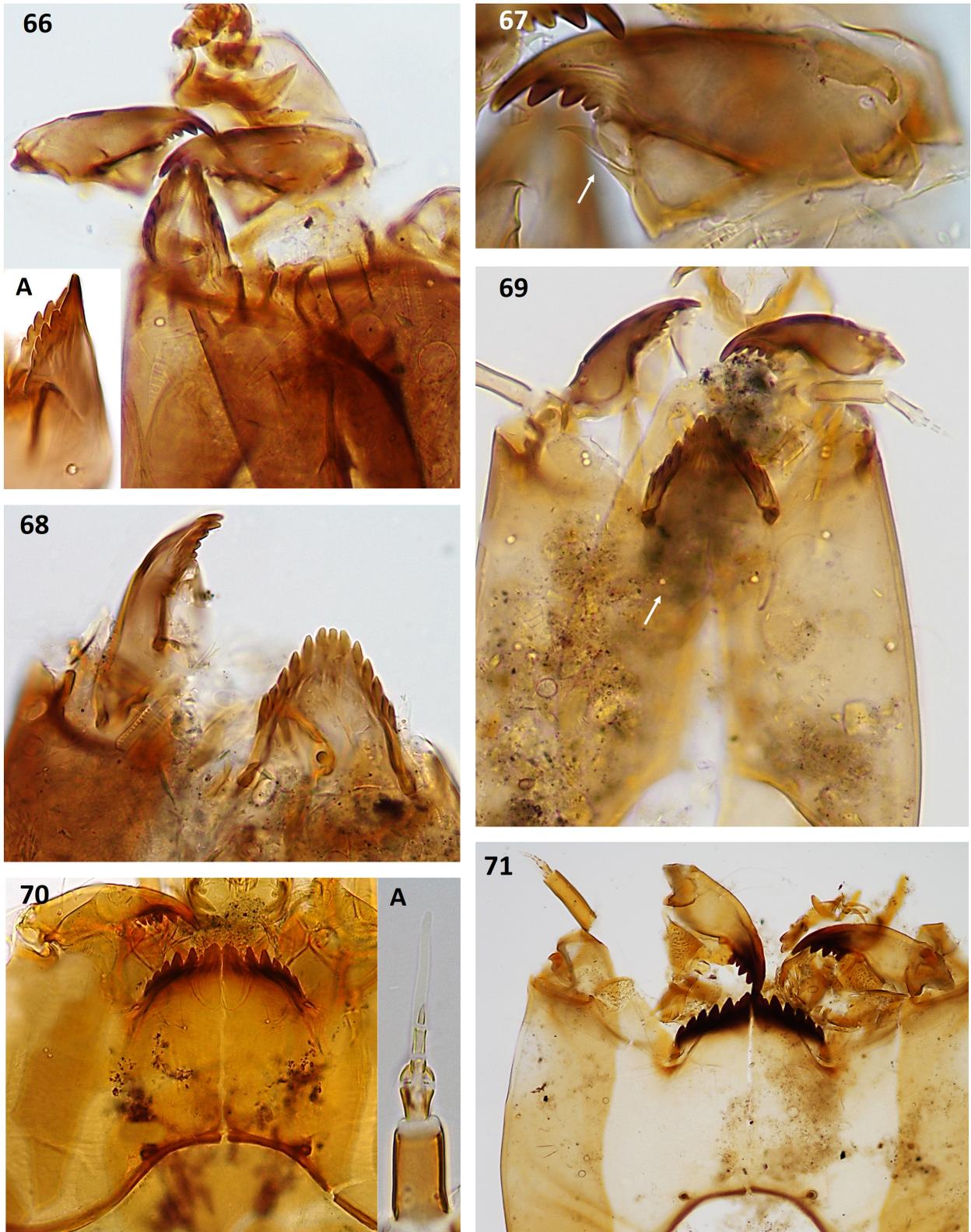
Head capsule remains were found in low abundance in several lakes located at lower altitudes. One morphotype was identified following Brooks *et al.* (2007).

***Thienemanniella clavicornis*-type (Fig. 68)**

Central median tooth is approximately the same length than the outer pair of median teeth, first inner tooth of mandible as long as apical tooth.

***Tvetenia* Kieffer (Fig. 69)**

Head capsule yellow to light-brown, occipital margin pale or dark brown. Antenna 5-segmented, premandible with one apical blunt tooth. Apical tooth of mandible shorter than combined width of 3 inner teeth, mola usually with 2–3 spines, some species without spines. Mentum striped, with 1 or 2 median teeth and 5 pairs of lateral teeth. Ventromental plates narrow creating an appearance of dark bulge below last lateral tooth of mentum. Setae submenti arising either well below mentum (in *T. bavarica* group) or just below bases of mentum (*T. discoloripes* group).



FIGURES 66–71. *Synorthocladius*: 66—head capsule, A—detail of mentum. *Synorthocladius*: 67—mandible (arrow indicates spine). *Thienemanniella clavicornis*-type: 68—head capsule. *Tvetenia bavarica*-type: 69—head capsule (arrow indicates seta submenti). *Zalutschia mucronata*-type: 70—head capsule, A—antenna, blade longer than flagellum. *Zalutschia* type B: 71—head capsule.

Remarks: *Tvetenia* closely resembles *Eukiefferiella*, however, some *Eukiefferiella* types/species can be easily distinguished from *Tvetenia* if they possess one of the following features: dark, heavily pigmented head (yellow in

Tvetenia), very broad median mental tooth (e.i. ca 4x width of first lateral tooth, which is always less in *Tvetenia*), 4 lateral teeth (always 5 in *Tvetenia*). *Tvetenia bavarica*-type can be distinguished by the position of seta submenti, arising well below mentum while being close to the bases in *Eukiefferiella*. Species with similar coloration of head, number of lateral teeth and position of seta submenti cannot be distinguished with certainty in subfossils.

Tvetenia bavarica (Goetghebuer, 1934) is the only species recorded from the Tatra Mts. lakes (Bitušik *et al.* 2006a; Novikmec *et al.* 2015).

Subfossil remains were rarely found in small number of investigated lakes. One morphotype was identified following Brooks *et al.* (2007).

Tvetenia bavarica-type (Fig. 69)

Head capsule yellow with pale occipital margin. Mentum with two median teeth and 5 pairs of lateral teeth. Setae submenti arising well below mentum.

***Zalutschia* Lipina (Figs 70, 71)**

Head capsule yellow with brown occipital margin. Antenna with 6 segments, sixth segment vestigial. Premandible bifid apically with one inner tooth. Apical mandibular tooth shorter than combined width of 3 inner teeth. Mentum usually dark with double median tooth and 6 pairs of lateral teeth, first lateral reduced, occasionally with 2–3 light coloured median teeth and first and sixth lateral teeth reduced. Ventromental plates well developed extending beyond mentum with fine beard.

Remarks: *Zalutschia* is a distinctive genus. It resembles *Hydrobaenus* which has similar shape of mentum however without beard. *Zalutschia* may be confused with *Psectrocladius* due to distinct ventromental plates and beard, however mentum of *Psectrocladius* has only five lateral teeth.

Zalutschia tatica (Pagast, 1935) is considered to be typical inhabitant of small, acidified Tatra Mts. lakes (Bitušik *et al.* 2006a; Kownacki 2011). Recently, larvae belonging to *tornetraeskensis* species group were found (Novikmec *et al.* 2015).

Subfossil *Zalutschia* remains were recorded from small number, mostly acidified lakes.

Two morphotypes were recognized.

Key to morphotypes:

- 1 Mandible and mentum lighter than occipital margin; outermost mental tooth reduced in size; third inner mandibular tooth not significantly smaller than second tooth *Zalutschia mucronata*-type
- Mandible and mentum darker than occipital margin; outermost mental tooth not significantly reduced; first and second mandibular teeth subequal in size, third tooth markedly smaller *Zalutschia* type B

Zalutschia mucronata-type (Fig. 70)

Head capsule light brown, occipital margin dark brown. Teeth of mandible and mentum lighter than occipital margin. Outermost mental tooth reduced in size. Inner mandibular teeth decreasing in size, third inner tooth not significantly smaller than second tooth. Head capsules with preserved antenna can be identified further: longer blade than flagellum (Fig. 70A) indicates *Z. tatica* (see Sæther 1976, Bitušik 2000).

Zalutschia type B (Fig. 71)

This morphotype corresponds to *Zalutschia* type B sensu Brooks *et al.* (2007), however, Medeiros & Quinlan (2011) pointed out conflicts of this morphotype with numerous other publications and suggest to refer to it as *Zalutschia*

lingulata pauca-type. Head capsule yellow, occipital margin light brown. Teeth of mandible and mentum strongly pigmented, darker than occipital margin. Outermost mental tooth not significantly reduced. Mandible with first and second teeth subequal in size, third tooth markedly smaller. Basal antennal segment longer than flagellum (length of blade unknown, but larvae with long basal antennal segment have blade at most as long as flagellum, see Sæther 1976).

Chironominae

Head capsules small to very large, usually yellow, brown patches may be present dorsally, submentum may be fully darkened or darker patch may be limited to the part above the occipital margin. Antennae always well developed, 5–8 segmented. They arise from rounded protuberances (Chironomini, Pseudochironomini) or on distinct pedestals, frequently with distal spur (Tanytarsini). Premandibles invariably present and well developed, with 1–7 teeth. Sometimes median teeth or entire mentum pale or poorly sclerotized. Mandible with several inner teeth and usually with dorsal tooth. Mentum with 9–16 dark teeth, median area (ventromentum) maybe visibly delineated from the lateral regions (dorsomentum). Beard absent. Ventromental plates variable in shape but usually well developed and striated.

Chironomini (Fig. 6)

Antennae not placed on distinct pedestals, Lauterborn organs not situated on pedicels. Seta submenti situated ventrally, on the opposite side of mandible from seta interna. Ventromental plates variable in shape but with very few exceptions well-developed and striated (reduced only in the *Stenochironomus* complex). A useful character to separate the genera within Chironomini is the structure of sclerites on dorsal surface of head: frons (frontal apotome), clypeus and labrum. Frons is either discrete or fused with clypeus and forms frontoclypeus (rarely, all dorsal sclerites fused to form frontoclypeolabrum – *Stenochironomus*). In some genera there is a distinct fenestra (Fig. 78) at anterior frons or frontoclypeus, sometimes reduced to smaller mark, line or area with different cuticle. Anterior margin of frons or frontoclypeus can be straight, curved, expanded laterally, sometimes crenulated, or with tubercles on surface.

Chironomus Meigen (Figs 72–75)

Head capsule yellow, often with more or less obvious pigmented on frontoclypeus and on submentum. Occipital margin dark brown to black. Antenna 5-segmented. Premandible usually with 2 teeth. Mandible usually with 2 pale dorsal teeth (often hardly visible), dark apical tooth, and 2–3 inner teeth. Mentum with trifid median tooth, 6 pairs of lateral teeth, first 2 mostly closely appressed. Ventromental plates broad, usually each plate about as wide as mentum or somewhat wider.

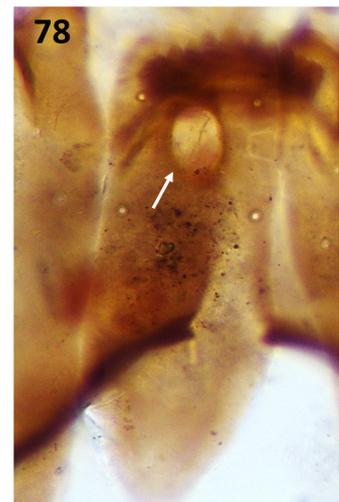
Remarks: The shape of the three median teeth is distinctive among other Chironomini with exception of *Einfeldia pagana*-type (Brooks *et al.* 2007), which has large heart-shape fenestra on frontoclypeus.

Recently, two species were reliably identified from the lakes in the Tatra Mts.: *Chironomus* (*Chironomus*) *striatus* Strenzke, 1959 and *C. (Lobochironomus) montuosus* Ryser, Wülker & Scholl, 1985 (Matěna & Frouz 2000; Bitušík 2004).

Chironomus subfossils were found only in acidified Tatra Mts. lakes. Two morphotypes were recognised following Brooks *et al.* (2007).

Chironomus anthracinus-type (Figs 72, 73)

Fourth lateral tooth of mentum shorter than the other laterals. Mandible with two inner teeth.



FIGURES 72–78. *Chironomus anthracinus*-type: 72—head capsule (arrow indicates two inner teeth of the mandible). *C. anthracinus*-type: 73—head capsule (arrow indicates three inner teeth of the mandible). *Chironomus plumosus*-type: 74—head capsule (arrow indicates three inner teeth of the mandible). *C. plumosus*-type: 75—head capsule (arrow indicates two inner teeth of the mandible). *Cladopelma lateralis*-type: 76—head capsule. *Dicrotendipes nervosus*-type: 77—frontal apotome (arrow indicates crenulated anterior margin). *Dicrotendipes notatus*-type: 78—frontal apotome (arrow indicates antero-median fenestra).

Chironomus plumosus-type (Figs 74, 75)

Fourth lateral tooth of the mentum longer than fifth. Mandible with three inner teeth.

In our material, however, there are also individuals combining the *plumosus*-type mentum with *anthracinus*-type mandible and the other way around (Fig. 73 and 75). In this case, the shape of the mentum should be indicative for the type. Considering the great amount of *Chironomus* species, more study is needed to define more morphotypes.

Cladopelma Kieffer (Fig. 76)

Head capsule light, greyish with brownish patch on submentum, occipital margin dark brown. Antenna with 5 segments, premandible bifid. Dorsal tooth on mandible absent, 1–2 flat inner teeth present. Mentum with usually double median tooth (or at least notched medially) and 7 pairs of lateral teeth. Outermost lateral teeth set forward in relation to slope of remaining lateral teeth, while 5th and 7th lateral are short and the 6th lateral is taller and broader. Ventromental plates broad, with fine striation distinct at base, anterior margin often crenulated.

Remarks: Mentum with double median tooth and more or less separated group of outer lateral teeth is distinctive for *Cladopelma*. *Cryptotendipes* and *Microchironomus* have a similar pattern of the lateral teeth, however median tooth is distinctly trifid in *Microchironomus* while single in *Cryptotendipes*; if laterally notched it may appear trifid but the mentum is much steeper than in *Cladopelma*.

Subfossil remains were recorded from two dystrophic lakes situated in the forest zone of the Tatra Mts.

One morphotype was recognized (Brooks *et al.* 2007).

Cladopelma lateralis-type (Fig. 76)

Three outermost lateral teeth separated from remainder by a deep notch, and forming a separate group.

Dicrotendipes Kieffer (Figs 77–82)

Head capsule yellow, occipital margin darkened. Frontal apotome separated from clypeus (except for a European species, *Dicrotendipes lobiger* (Kieffer, 1921)), and there is an antero-median fenestra (oval to round or linear) on the frontal apotome (Figs 77, 78); anterior margin of frontal apotome may be crenulated (Fig. 77). Antenna 5-segmented, segment 4 exceptionally long. Premandible with 3 teeth, second one and third broad and blunt. Mandible with pale dorsal tooth, 1–2 small surficial and 3 inner teeth. Median tooth of mentum robust, sometimes laterally notched, 6 pairs of lateral teeth. First and second pairs sometimes partially fused. Sixth lateral tooth sometimes reduced into a broad lobe, so only five laterals are clearly visible. Ventromental plates narrow, visibly fan-shaped, completely striated, about half width of mentum; anterior margin smooth or crenate.

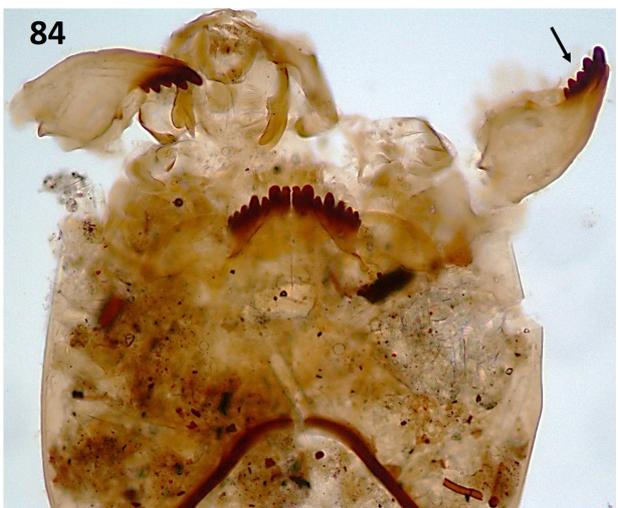
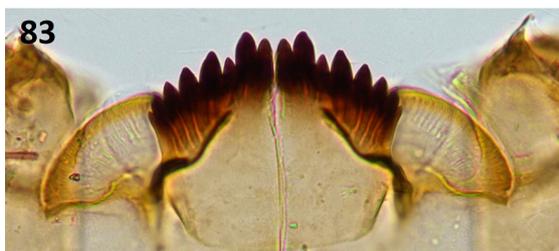
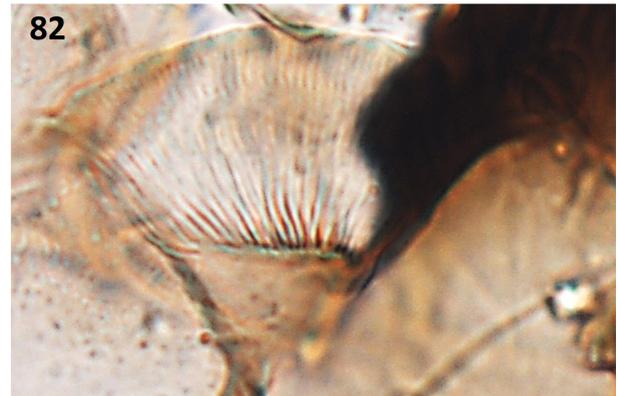
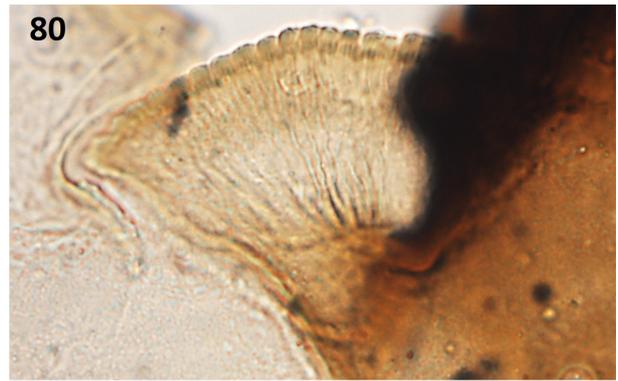
Remarks: Mentum of *Dicrotendipes* is especially similar to that of *Glyptotendipes*, *Einfeldia* and *Kiefferulus* (all having fenestra in frons or frontoclypeus), however ventromental plates of these genera are much longer, (equaling to or exceeding width of mentum), while distinctly short in *Dicrotendipes*.

Subfossil remains were rare, found in lakes with higher trophy.

Two morphotypes were distinguished following Brooks *et al.* (2007).

Dicrotendipes nervosus-type (Figs 79, 80)

Ventromental plates crenulated at anterior margin.



FIGURES 79–84. *D. nervosus*-type: 79—head capsule. *D. nervosus*-type: 80—ventromental plate. *D. notatus*-type: 81—head capsule. *D. notatus*-type: 82—ventromental plate. *Endochironomus impar*-type: 83—detail of mentum and ventromental plates. *E. impar*-type: 84—head capsule (arrow indicates four inner teeth of the mandible).

Dicrotendipes notatus-type (Figs 81, 82)

Ventromental plates with smooth anterior margin.

Endochironomus Kieffer/ *Synendotendipes* Grodhaus (Figs 83, 84)

Head capsule large, yellow, occipital margin dark brown. Antenna 5-segmented, premandible with 2 apical teeth and 1 inner tooth. Mandible with slender apical tooth and 3–4 inner teeth, dorsal tooth pale, hardly visible. Mentum

with 3–4 protruding median teeth (central ones lower than outer pairs) and 6 pairs of lateral teeth; the first lower than second and medians. Ventromental plates relatively narrow and gently curved with smooth anterior margin and continuously striated (Fig. 83).

Remarks: Genus *Synendotendipes* was erected based on immature stages previously placed in *Endochironomus* (= species group B, Pinder & Reiss, 1983). As the subfossil heads may lack important characters allowing separation of these genera (mandibula, maxilla), it is reasonable to keep both genera together. In specimens where mandible is present, 4 inner teeth is separating *Synendotendipes* from *Endochironomus* with 3 inner teeth.

Subfossils were recorded from dystrophic and acidified lakes of the studied region. These findings correspond very well with known distribution of *Endochironomus*/*Synendotendipes* in the Tatra Mts. lakes (Novikmec *et al.* 2015).

One morphotype following Brooks *et al.* (2007) was found.

Endochironomus impar-type (Figs 83, 84)

Outer median teeth are longer than central teeth and first laterals are clearly shorter than second lateral teeth; mandible with 4 distinctive inner teeth. This morphotype corresponds to genus *Synendotendipes* sensu Epler *et al.* (2013).

***Lauterborniella* Thienemann & Bause (Fig. 85)**

Head capsule small, yellow occipital margin darkened. Antenna 6-segmented, large Lauterborn organs alternate on segments 2 and 3. Premandible with 3 distinct apical teeth and 1 blunt inner tooth. Mentum pale brown in colour; dorsal tooth very strong, apical tooth only slightly larger than 2 inner teeth. Mentum weakly pigmented with two rounded median teeth and 6 pairs of lateral teeth; first lateral tooth very short. Ventromental plates distinctly triangular in shape (Fig. 85).

Remarks: *Lauterborniella* may be confused with *Zavreliella* and perhaps with *Polypedilum nubeculosum*-type. The first and the second lateral teeth of mentum are distinctly separate in *Lauterborniella*, while partially fused in *Zavreliella*. Shape of setae submenti (if preserved in subfossils) is also indicative: it is branched in *Lauterborniella*, while simple in *Zavreliella*. Ventromental plates in *Lauterborniella* are triangular, while fan-shaped in *Polypedilum nubeculosum*-type (Fig. 89).

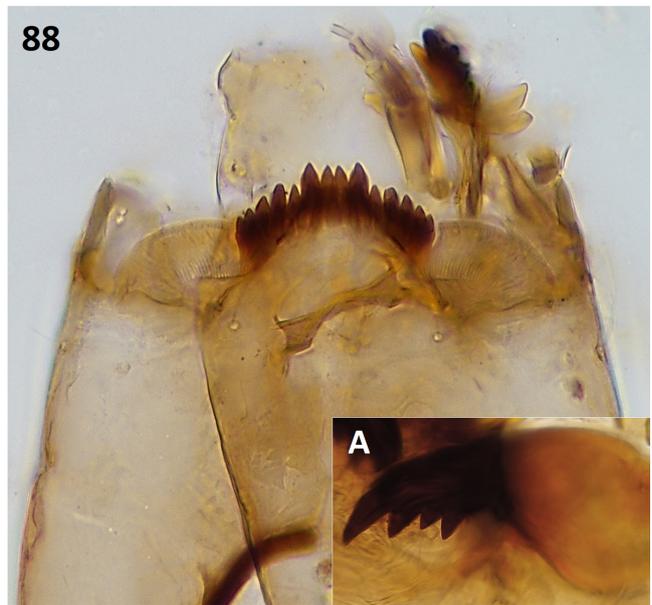
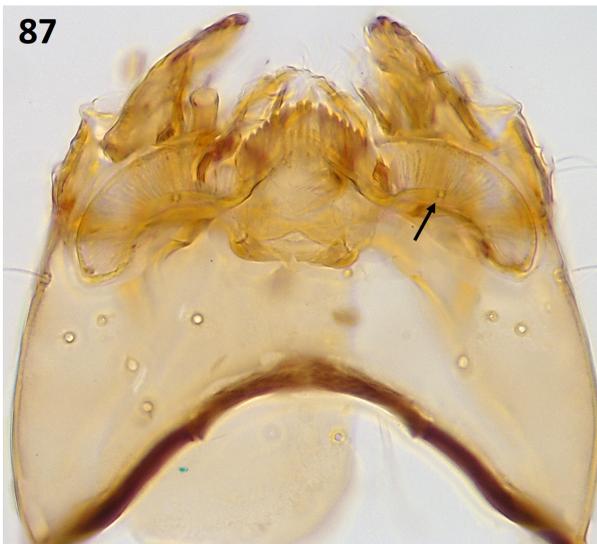
Subfossil remains were found in one dystrophic lake situated in forest zone, while data on occurrence of living immature stages in the Tatra Mts. lakes does not exist, yet. Only one species, *L. agrayloides* (Kieffer, 1911) is known from the Holarctic.

***Microtendipes* Kieffer (Fig. 86)**

Head capsule brownish with dark brown occipital margin. Antenna 6-segmented, Lauterborn organs alternate on segments 2 and 3. Premandible with 3 (*pedellus*-type) or 5 (*rydalensis*-type) teeth. Mandible with pale dorsal tooth, apical tooth and 3 inner teeth darkly pigmented. Median tooth of mentum trifid, pale or as dark as rest of mentum; central tooth either very small, so median tooth appears to consist of two teeth (*pedellus*-type), or about the same size as outer medians (*rydalensis*-type); 6 pairs of lateral teeth, while first and second laterals fused. Ventromental plates narrow and strongly curved and coarsely striated on upper half.

Remarks: The mentum with 3, usually pale, median teeth and mandible with 3 inner teeth are distinctive. Superficially similar genera *Omisus* and *Paratendipes* have 4 median mental teeth. In comparison with *Stictochironomus* the first lateral tooth of mentum is not lower than second.

Only *Microtendipes chloris* (Meigen, 1818), belonging to the *pedellus* species group is known from the Tatra Mts. lakes. Subfossil remains belonging to one morphotype were found in the lakes situated at lower altitude in sub-alpine zone.



FIGURES 85–90. *Lauterborniella*: 85—head capsule (arrow indicates ventromental plate). *Microtendipes pedellus*-type: 86—head capsule. *Pagastiella orophila*: 87—head capsule (arrow indicates position of seta submenti). *Phaenopsectra flavipes*-type: 88—head capsule, A—mandible. *Polypedilum nubeculosum*-type: 89—head capsule (arrow indicates two inner teeth of the mandible). *Polypedilum sordens*-type: 90—head capsule (arrow indicates three inner teeth of the mandible).

Microtendipes pedellus-type (Fig. 86)

Mentum with trifold, weakly pigmented median tooth (the central one is very small, almost invisible), premandible with 3 teeth.

***Pagastiella* Brundin (Fig. 87)**

Small pale head capsule with slightly darker occipital margin. Antenna 5-segmented. Premandible trifold, first and third longer and pointy, middle tooth shorter and broader. Mandible very slender with 2 dorsal and 5 inner teeth; all teeth pale. Mentum arched, weakly pigmented with four median teeth and 6 pairs of lateral teeth; outer pair of median teeth very small, first lateral tooth broad and the other laterals decreasing in size. Ventromental plates broad and largely arched, anterior margin finely crenulated.

Remarks: *Pagastiella* differs from *Nilothauma* by having unusual position of setae submenti on the ventromental plates (Fig. 87) and very small outer pair of median teeth, while in *Nilothauma* the central pair of median teeth is narrower.

The only Palaearctic species, *P. orophila* (Edwards, 1929), is also known from the Tatra Mts. lakes. Subfossil remains were found rarely and in low abundances in lakes of the forest zone.

***Phaenopsectra* Kieffer (Fig. 88)**

Head capsule medium sized, yellow, occipital margin dark brown. Antenna 5-segmented, premandible with 2 apical teeth and broad basal tooth. Mandible with relatively short dorsal tooth and 3 inner teeth; deep notch between basal inner tooth and mola can be present; all mandibular teeth dark brown. Mentum dark pigmented with four median teeth forming ventromentum (set forward of rest of mentum), inner median teeth are shorter than outer teeth; 5–6 pairs of lateral teeth, first lateral tooth much shorter than the second one and outermost pair of lateral teeth reduced. Ventromental plates as long as width of mentum, moderately curved and continuously striated.

Remarks: *Phaenopsectra* can be confused with genera that have clearly delineated ventromentum, i.e. *Sergentia*, *Endochironomus*/*Syndentodendipes*, *Tribelos* and *Stictochironomus*. In *Tribelos*, however, the line running from the anterior inner margin of ventromental plates meets the inner median tooth, while this line meets outer median tooth in other genera. *Sergentia* and *Syndentodendipes* have four inner teeth on the mandible, while *Stictochironomus* usually only two inner teeth. Ventromental plates in *Endochironomus*/*Syndentodendipes* are extended to a lobe and are longer as opposed to narrower and more curved plates in *Phaenopsectra*.

Subfossil remains belonging to *P. flavipes*-type (Brooks *et al.*, 2007) were found only in one dystrophic forest lake.

Phaenopsectra flavipes-type (Fig. 88)

Mentum strongly arched, with the central pair of median teeth shorter than outer pair, two outermost laterals reduced. Second inner mandibular tooth smaller than the other two; there is a deep gap between basal inner mandibular tooth and mola.

***Polypedilum* Kieffer (Figs 89, 90)**

Head capsule small to large, generally yellow, submentum may be darkly pigmented at different extent, usually just above the occipital margin. Occipital margin usually dark brown to black, sometimes pale. Antenna 5-segmented, one or more segments can be reduced in some species. Premandible with 2 apical teeth and broad basal tooth. Mandible usually with 1 dark dorsal tooth (absent in some species), and 2 (seldom 3) inner teeth. Mentum rather variable in shape, either “*Polypedilum*-like” with tall 2 median teeth, first of 6–7 lateral teeth small, second lateral as tall

as median teeth, followed by remainder of short laterals; or all mental teeth subequal, decreasing in size gradually. Ventromental plates variable in size and widely separated medially, striae continuous.

Remarks: Larvae of *Polypedilum* are very heterogeneous. Combination of 5-segmented antenna, 2 inner mandibular teeth and dark dorsal tooth together with the typical “*Polypedilum*-like” pattern of mentum (see above) may be sufficient to recognize *Polypedilum*. Species without “*Polypedilum*-like” menta will be distinguished from other genera by 16 subequal mental teeth.

There is only one evidence of the occurrence of *Polypedilum (Polypedilum) nubeculosum* (Meigen, 1804) in the Tatra Mts. lakes (see Bitušík 2004).

Small number of subfossils were found in the acid lakes of the forest zone.

Two morphotypes were identified following Brooks *et al.* (2007).

Polypedilum nubeculosum-type (Fig. 89)

Median teeth and first lateral tooth of various size, mandible with 2 inner teeth and 1 dorsal tooth.

Polypedilum sordens-type (Fig. 90)

Apex of mentum with teeth subequal in size, first laterals only slightly shorter than median teeth and second lateral teeth. Mandible with 3 inner teeth, dorsal tooth absent.

Sergentia Kieffer (Fig. 91)

Head capsule large, yellow. Antenna 5-segmented, premandible with 2–4 teeth. All mandibular teeth dull brown. One relatively short dorsal tooth and 4 inner teeth present. Mentum with 4 large, separated, equally broad and slightly elevated median teeth, central pair slightly lower than outer one, and with 6 pairs lateral teeth. Ventromental plates as wide as mentum, moderately curved and continuously striated, in *S. coracina*-type, however, with obvious paired striations along anterior margin.

Remarks: *Sergentia* is closely related to *Phaenopsectra* and the shape of mentum appearing as separated in three sections resembles some other genera (see remarks to *Phaenopsectra*). *Sergentia* may be recognized by the usual 4 inner mandibular teeth, 4 subequal median mental teeth, not reduced outermost lateral teeth, and paired striations conspicuous along anterior margin in *S. coracina*-type.

One species, *Sergentia coracina* (Zetterstedt, 1850), is documented from a few of the Tatra Mts. lakes, all situated in sub-alpine zone (Bitušík 2004).

The morphotype recognised was found in one lake only.

Sergentia coracina-type (Fig. 91)

Mandible with 4 dark inner teeth, premandibles with 2 apical teeth, mentum with 4 subequal median teeth, outermost lateral teeth not reduced, and distinct paired striations along anterior margin of ventromental plate (Fig. 91A).

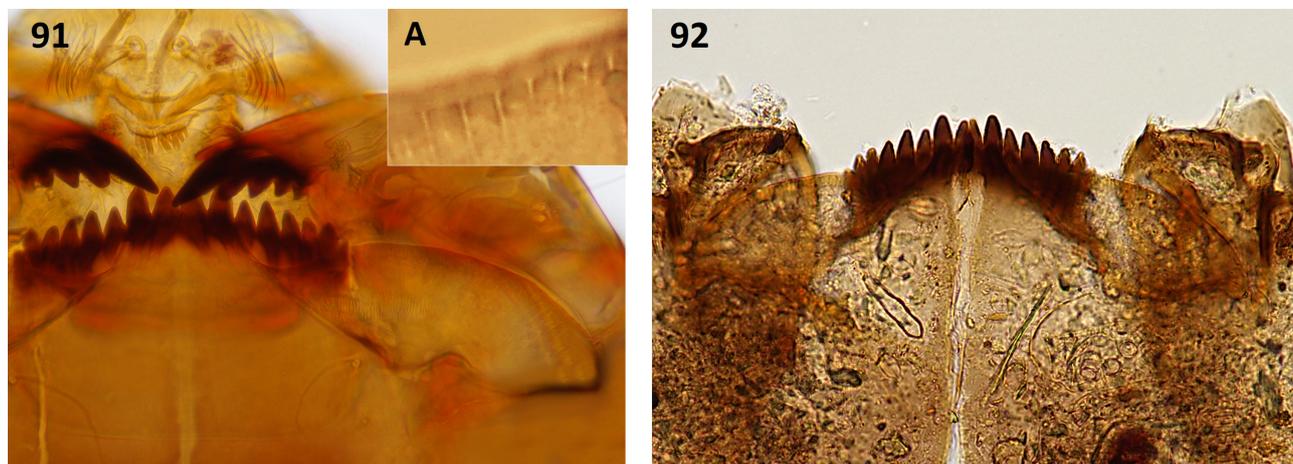
Stictochironomus Kieffer (Fig. 92)

Head capsule medium to large, yellow, posteriorly may be darkly pigmented, and dorsally may be distinct brown areas. Occipital margin mostly dark brown. Antenna 6-segmented, Lauterborn organs alternate on segment 2 and 3. Premandible with 2 apical teeth and broad basal tooth. Mandible basally broad and very slender distally, with 1 dorsal tooth and 2 inner teeth, all mandibular teeth dark. Mentum with 4 median teeth delineated from lateral regions;

central pair of median teeth lower and slender than outer pair; 6 pairs of lateral teeth; all teeth dark. Ventromental plates slightly wider than mentum, weakly curved, striations often indistinct, broad grey band on anterior margin.

Remarks: The shape of mentum with delineated ventromentum resembles some other genera (see comments to *Phaenopsectra*). However, the central pair of median teeth is thinner in *Stictochironomus*. Moreover, the 6-segmented antenna with alternate Lauterborn organs, 2 inner mandibular teeth and the grey band on the anterior margin on ventromental plates are also distinctive.

Immature stages of *Stictochironomus* were recorded from the Tatra Mts. lakes rarely (Bitušík 2004). Three subfossil remains of the same morphotype were found in one of the studied lakes.



FIGURES 91–92. *Sergentia coracina*-type: 91—head capsule, A—paired striations on the ventromental plate. *Stictochironomus* type B: 92—head capsule.

Stictochironomus type B (Fig. 92)

Our morphotype does not suit *Stictochironomus* type B described in Brooks *et al.* (2007) entirely, since our type has partly overlapping central median teeth (as opposed to separated in Brooks *et al.* 2007). However, we had limited amount of remains and this feature may be the consequence of their inferior condition.

Tanytarsini (Figs 7, 8)

Head capsule pale to brown. Occipital margin darkened, dark brown to black. Shape and degree of development of occipital plate, if present, is important for identification of subfossils. Antenna always 5-segmented arising on distinct elongate antennal base – pedestals distally often projecting into spur of different size, occasionally accessory multispined or palmate process is present. Lauterborn organs well-developed, usually mounted on segment 2 and often situated on short to long pedicels. Premandible with 2–5 teeth. Mandible with 2–3 inner teeth, one dorsal tooth (occasionally 2–3 dorsal teeth); 1–2 surficial teeth may be present on dorsal surface. Mentum with single median tooth (may be laterally notched) and mostly with 5 lateral teeth. Ventromental plates usually wide and slender, almost touching each other medially, in some genera narrow, separated medially by at least the width of the three median teeth.

***Micropsectra* Kieffer (Figs 93–98)**

Head capsule yellow to brown. Occipital margin usually with well-developed occipital plate. Antenna placed on elongate pedestal, often with apical tooth or spur. Lauterborn organs on long pedicels that extend beyond flagellum. Premandible bifid. Mandible with apical tooth, dorsal tooth and 3 inner teeth, all teeth brown. Mentum with the median tooth rounded, laterally notched to crenate, usually slightly paler than 5 lateral teeth. Ventromental plates close together medially, a little wider than mentum, with fine striation.

Remarks: *Micropsectra* head capsules closely resemble *Tanytarsus*. The best character for separating is the form of premandible (unfortunately often missing from subfossils), which is bifid in *Micropsectra*, while consisting 3–5 teeth in *Tanytarsus*. A projection on the antennal pedicel is characteristic for *Micropsectra*. However, some *Tanytarsus* species may also have a spur. On the other hand, spur is not always visible or is missing in some *Micropsectra* (very rarely though). The shape of spur can be also indicative, since it is sharp in *Micropsectra*, but always of different shape in *Tanytarsus* (e.g., long, broad and rounded apically) (Brooks *et al.* 2007). *Micropsectra* can be confused with *Paratanytarsus* as well, but *Paratanytarsus* has uniformly dark mentum, while in *Micropsectra* there is a pale area in the middle part of mentum.

Species of the genus *Micropsectra* are common inhabitants of the Tatra Mts. lakes. Up to now, 8 species were recorded: *Micropsectra apposita* (Walker, 1856), *M. atrofasciata* (Kieffer, 1911), *M. junci* (Meigen, 1818), *M. lindrothi* Goetghebuer, 1931, *M. notescens* (Walker, 1856), *M. radialis* Goetghebuer, 1939, *M. roseiventris* (Kieffer, 1909) and *M. sofiae* Stur & Ekrem, 2006 (Bitušik *et al.* 2006a; Gilka 2007; Novikmec *et al.* 2015).

Five morphotypes were identified in the subfossil material following Brooks *et al.* (2007).

Micropsectra contracta-type (Fig. 93)

Head capsule pale brown. Arch of occipital margin narrower. Spurs at antennae pedicels distinctive and noticeably point outwards.

Micropsectra insignilobus-type (Fig. 94)

Head capsule pale brown. Long antennae pedicels with short, pointed spurs. Occipital plate well-developed, arch of occipital margin relatively broad.

Micropsectra junci-type (Figs 95, 96)

Head capsule yellow. Similar to *M. insignilobus*-type, but first pair of lateral teeth of mentum clearly shorter than the second laterals.

Micropsectra radialis-type (Fig. 97)

Head capsule brown. Short rounded spurs present at relatively short (about as long as broad) antennae pedicel. Occipital plate strongly reduced. This morphotype was found most frequently with high abundance both in the lakes situated at higher altitude and in deep sub-alpine lakes.

Micropsectra type A (Fig. 98)

Head capsule yellow. Similar taxon to *M. insignilobus*-type, but occipital plate greatly enlarged and convex. The second most abundant morphotype in the surveyed lakes.

***Paratanytarsus* Thienemann & Bause (Figs 99–102)**

Head capsules yellow with dark brown occipital margin. Occipital arch is deeply incised, plate absent. Antenna placed on tall pedicel without any projections. Lauterborn organs sessile or on very short pedicels. Premandible bifid. Dorsal mandibular tooth, apical tooth and 2–3 inner teeth all dark brown. Median tooth of mentum usually rounded, occasionally notched laterally, 5 pairs of lateral teeth are present, all teeth uniform in colour, dark brown. Ventromental plates close together medially, each plate slightly longer than width of mentum.

Remarks: Subfossil head capsules of *Paratanytarsus* resembles *Micropsectra* and *Tanytarsus*, but *Paratanytarsus* can be distinguished from both by the combination of the deeply incised occipital arc, the short antennal pedicel and absence of tooth or spur on it. Another useful diagnostic feature is the uniformly coloured mentum with all teeth dark, compared to the paler median part of mentum in *Micropsectra* and *Tanytarsus*.

Currently, *Paratanytarsus austriacus* (Kieffer, 1924) and *P. laccophilus* (Edwards, 1929) are known from the Tatra Mts. lakes (Gilka 2007; Novikmec *et al.* 2015).

Two morphotypes were identified.

Paratanytarsus austriacus-type (Figs 99, 100)

Mandible with 3 inner teeth. Very common morphotype, recorded from lakes situated at altitude generally below 2000 m.

Paratanytarsus penicillatus-type (Figs 101, 102)

Mandible with 2 inner teeth. Rarely found in small number of the lakes situated mostly in forest zone (dystrophic).

***Tanytarsus van der Wulp* (Fig. 103–108)**

Head capsules yellow to brownish with dark brown to black occipital margin. Occipital plate present, well developed. Antenna placed on tall pedicel (2–3 times as long as broad), usually without distal tooth or spur (if present, it is of different shape as in *Micropsectra*, see Brooks *et al.* 2007). Lauterborn organs usually on long pedicels. Premandible with 3 (usually) to 5 apical teeth. Mandible with 2–3 inner teeth, 1–2 dorsal teeth and in some species/morphotypes 1–2 surficial teeth may be present additionally. Mentum with a single rounded or laterally notched median tooth and 5 pairs of lateral teeth. Ventromental plates narrowly separated medially, long, narrow and fine striated.

Remarks: As mentioned above, there are considerable difficulties to distinguish head capsules of *Tanytarsus* from *Micropsectra* and, to a lesser extent, from *Paratanytarsus* (see comments to *Micropsectra* and *Paratanytarsus*).

Five *Tanytarsus* species were confirmed in the Tatra Mts. lakes: *Tanytarsus bathophilus* Kieffer, 1911, *T. gibbosiceps* Kieffer, 1922, *T. gregarius* Kieffer, 1909, *T. nemorosus* Edwards, 1929 and *T. pallidicornis* (Walker, 1856) (Bitušik *et al.* 2006a; Gilka 2007).

Three morphotypes were distinguished following Brooks *et al.* (2007).

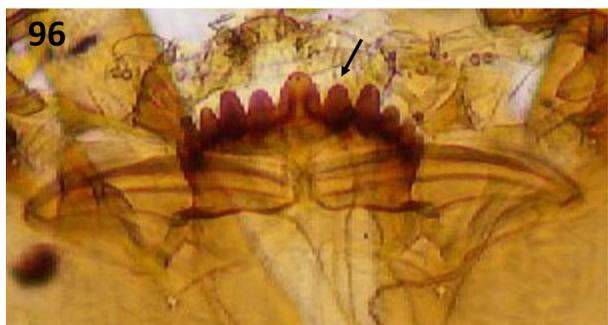
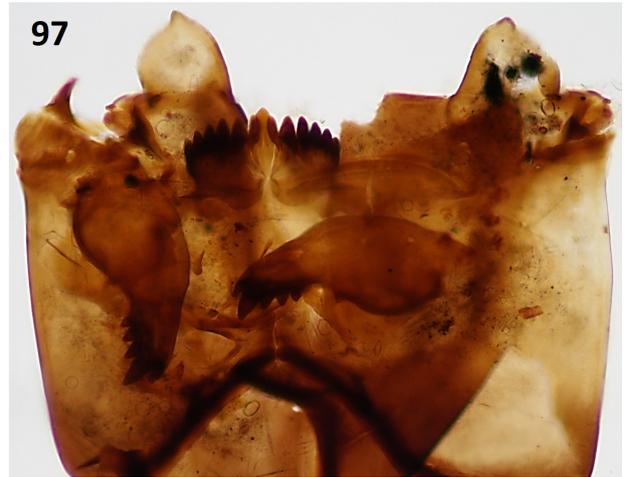
Tanytarsus lugens-type (Figs 103, 104)

Head capsule yellow with brown patch on submentum. Median tooth and first pair of lateral teeth are usually not at the same focal plane as the other laterals. Mandible with 3 inner teeth, 2 dorsal teeth and one surficial tooth, which is large and well visible (Fig. 104). Antennal pedicel is long without spur.

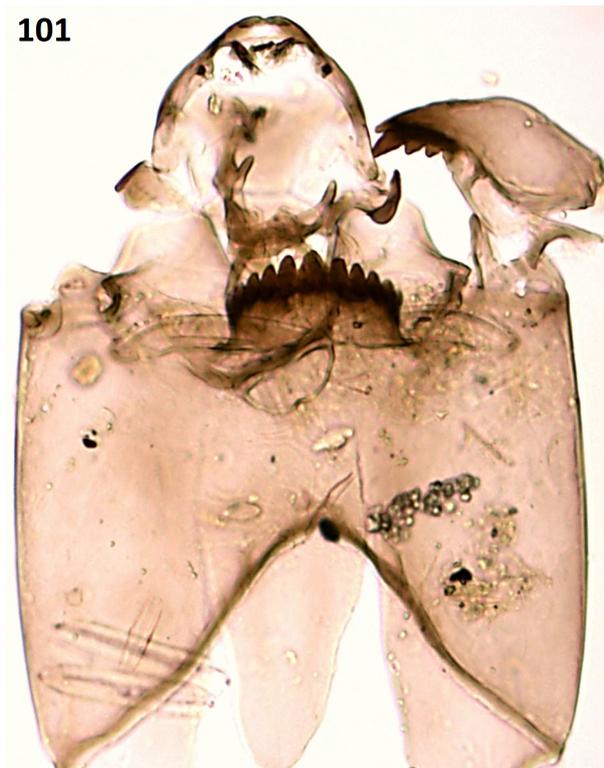
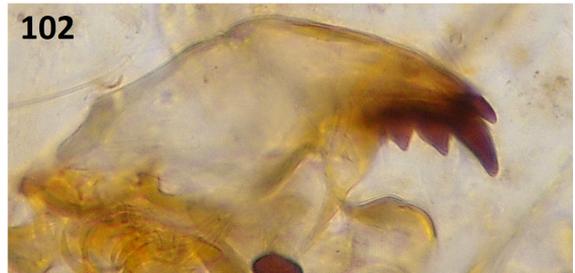
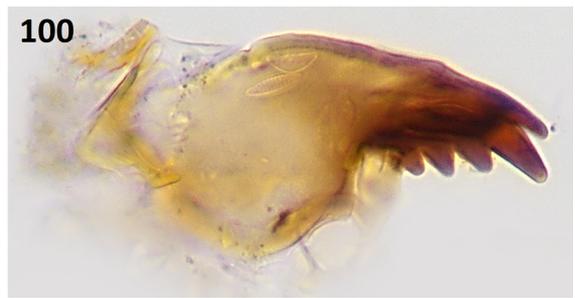
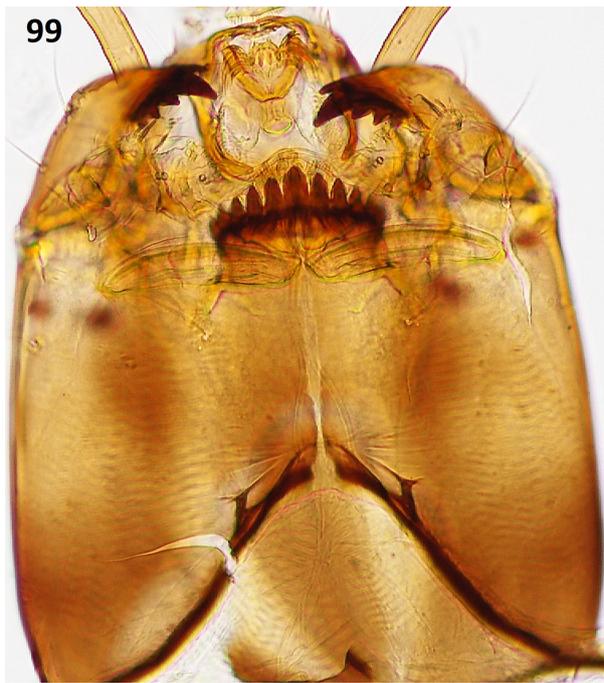
It belongs to the most common morphotypes in the Tatra Mts. lakes, usually absent in the coldest ones.

Tanytarsus mendax-type (Figs 105, 106)

All teeth of the mentum at the same focal plane. Median tooth laterally notched having a crown-like appearance. Mandible with 3 inner teeth and one dorsal tooth, surficial tooth absent. Antennae pedicel without spur. Occipital margin narrow, dark brown, post-occipital plate brown with slightly concave margin.



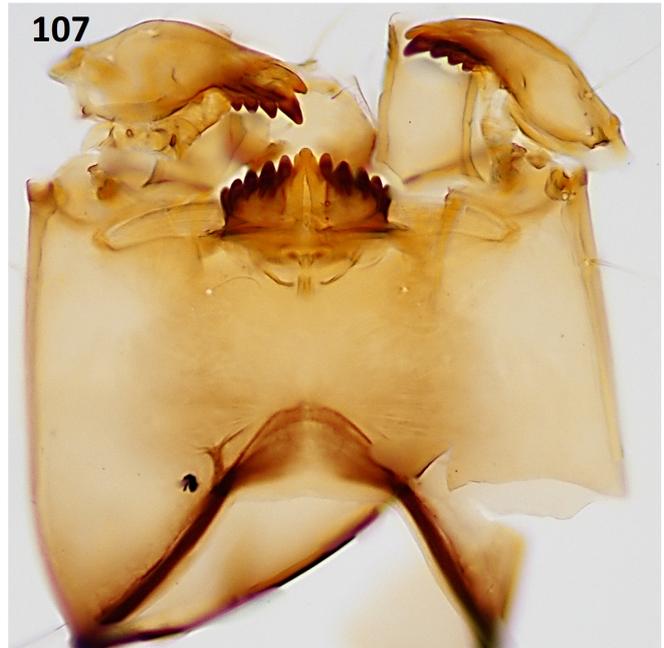
FIGURES 93–98. *Micropsectra contracta*-type: 93—head capsule (arrow indicates spur). *Micropsectra insignilobus*-type: 94—head capsule. *Micropsectra junci*-type: 95—head capsule. *M. junci*-type: 96—mentum (arrow indicates shorter first pair of laterals). *Micropsectra radialis*-type: 97—head capsule. *Micropsectra* type A: 98—head capsule (arrow indicates greatly enlarged and convex occipital plate).



FIGURES 99–104. *Paratanytarsus austriacus*-type: 99—head capsule. *P. austriacus*-type: 100—mandible. *Paratanytarsus penicillatus*-type: 101—head capsule. *P. penicillatus*-type: 102—mandible. *Tanytarsus lugens*-type: 103—head capsule. *T. lugens*-type: 104—mandible.

Tanytarsus pallidicornis-type (Figs 107, 108)

All teeth of the mentum at the same focal plane. Antennae pedestals with short, rounded spurs. Mandible with 3 inner teeth. Occipital margin broader than in *T. mendax*-type, dark brown top black, post-occipital plate brown with pale, straight margin.



FIGURES 105–109. *Tanytarsus mendax*-type: 105—head capsule. *T. mendax*-type: 106—mentum. *Tanytarsus pallidicornis*-type: 107—head capsule. *T. pallidicornis*-type: 108—antenna. Tanytarsini indet.: 109—head capsule.

Tanytarsini indet. (Fig. 109)

This is a new morphotype, not listed in Brooks *et al.* (2007).

Mandible with robust, blunt apical tooth, 2 inner teeth and 1 dorsal tooth, all brown; obvious hump present on the outer margin. Mentum strongly arched, with a tall and slender apical tooth and 5 lateral teeth, 1 to 4 subequal in size, outermost minute. Due to more structures, this morphotype was not associated to a certain genus, but its appearance indicates that it could be close to *Neozavrelia*, *Paratanytarsus* or *Sublettea*. The morphotype was present only in one lake.

DISCUSSION

In the present paper we describe and illustrate a total of 73 chironomid larval morphotypes from the surface sediments of the Tatra Mts. lakes. This is more than third of subfossil morphotypes Brooks *et al.* (2007) documented from all over the Palaearctic. Larocque-Tobler (2014) presented 104 morphotypes in the subfossil guide from 50 Polish lakes. However, the lakes surveyed were scattered all around Poland representing a particularly long environmental gradient. The Tatra Mts. training set comprises more lakes, but it is also more limited geographically and environmentally which is reflected in the lack of thermally plastic taxa and, as a consequence, in the lower overall taxonomic diversity.

The composition of subfossil chironomid assemblages is consistent with the existing paleo- (see Kubovčik 2012 and Stoklasa *et al.* 2017 for review) and recent publications (Bitušik 2004; Bitušik *et al.* 2006; Novikmec *et al.* 2015). Most morphotypes belonged to the Orthoclaadiinae subfamily (37), which is not surprising, since, together with Diamesinae, proportion of species of this subfamily increase with altitude (Boggero *et al.* 2006; Füreder *et al.* 2006; Hamerlík *et al.* 2017) as a result of their ecological preferences (Brodersen *et al.* 2004).

We describe 15 new morphotypes that are not recognised in the subfossil chironomid guide by Brooks *et al.* (2007), neither by Larocque-Tobler (2014). These morphotypes belong to three subfamilies, Diamesinae (*Diamesa* Tatra-type A, *D.* Tatra-type B, *Pseudodiamesa branickii*-type, *P. nivosa*-type, *Pseudokiefferiella parva*), Orthoclaadiinae (*Brillia bifida*-type, *Cricotopus (Paratrachocladus) skirwithensis*-type, *C. (Cricotopus) tremulus*-type, *Cricotopus/Orthocladus* I, *Eukiefferiella brevicealcar*-type, *E. claripennis*-type B, *Orthocladus (Orthocladus) dentifer*-type, *O. (Mesorthocladus) frigidus*, *O. (Euorthocladus) sp.*) and Chironominae (Tanytarsini indet.). Most of these morphotypes (or their associated species, e.g. *E. brevicealcar*, *C. skirwithensis*, *C. tremulus*), are common in the Palaearctic (Spies & Sæther 2013) and due to specific ecological features they represent their correct identification is important for precise and accurate palaeoreconstructions. This applies even more to morphotypes with distinct ecological requirements that are difficult to distinguish. For example, *Pseudodiamesa branickii*-type and *P. nivosa*-type occur in cold oligotrophic lakes, but while *P. branickii*-type is relatively plastic thermally, *P. nivosa*-type is stricter stenothermal, only present in the coldest Tatra lakes. The two morphotypes are extremely similar in appearance, but their correct separation could straighten the temperature reconstruction in mountain lakes, where these two types tend to alternate in the past (Ilyashuk *et al.* (2010). *Pseudokiefferiella parva* represents a morphotype of a genus which was distinguished in previous palaeo-guides. Larvae of *Pseudokiefferiella* are oligostenothermic inhabiting cold mountain streams and hygropetric zone and its correct identification may be important to represent past dynamics of inlet streams. *Zalutschia tatica* (member of the *mucronata*-type) is an acidotolerant taxa and as such it is important for reconstruction of past acidification events.

Other than subfossil characters, we are describing also the generic characteristics of recent larvae. This ensures that our illustrated manual can be used for identification not only of subfossil morphotypes but also of recent genera. We also believe that the effect our paper is not limited to the Tatra lakes but can be also used for lakes in the whole Carpathians and other European mountain ranges.

ACKNOWLEDGMENTS

We are grateful to all colleagues and students who helped us with sampling, especially the team of geologists under the leadership of Radovan Pipík, IES SAS, together with Milan Novikmec and Marek Svitok, Technical University

in Zvolen. Constructive comments of anonymous reviewers to the previous version of the manuscript are highly appreciated. The study was supported by projects APVV-15-0292 and VEGA 1/0341/18.

REFERENCES

- Andersen, T., Baranov, V., Hagenlund, L.K., Ivković, M., Kvifte, G.M. & Pavlek, M. (2016) Blind Flight? A New Troglolobitic Orthoclad (Diptera, Chironomidae) from the Lukina Jama—Trojama Cave in Croatia. *PLoS ONE*, 11 (4), e0152884. <https://doi.org/10.1371/journal.pone.0152884>
- Andersen, T., Cranston, P.S. & Epler, J.H. (2013a) The larvae of Chironomidae (Diptera) of the Holarctic Region. Keys and diagnoses. *Insect Systematics & Evolution*, 66, 1–571.
- Andersen, T., Sæther, O.A., Cranston, P.S. & Epler, J.H. (2013b) The larvae of Orthoclaadiinae (Diptera: Chironomidae) of the Holarctic Region—Keys and diagnoses. *In: Andersen, T., Sæther, O.A., Cranston, P.S. & Epler, J.H. (Eds.), Chironomidae of the Holarctic Region. Keys and diagnoses. Larvae. Insect Systematics & Evolution, Lund, Supplement*, pp. 189–386.
- Bitušik, P. (2000) *Príručka na určovanie lariev pakomárov (Diptera. Chironomidae) Slovenska. Časť I. Buchonomyinae, Diaminesinae, Prodiaminesinae a Orthoclaadiinae*. Vydavateľstvo Technickej Univerzity vo Zvolene, Zvolene, 133 pp. [in Slovak]
- Bitušik, P. (2004) Chironomids (Diptera. Chironomidae) of the mountain lakes in the Tatra Mts. (Slovakia). A review. *Dipterologica bohemoslovaca* 12, *Acta Facultatis Ecologiae, Zvolen*, 12 (1), 25–53.
- Bitušik, P. & Kubovčík, V. (1999) Sub-fossil chironomids (Diptera: Chironomidae) from the sediments of the Nižné Terianske pleso (High Tatra Mts., Slovakia). *Dipterologica Bohemoslovaca*, 9, 11–20.
- Bitušik, P., Svitok, M., Kološta, P. & Hubková, M. (2006a) Classification of the Tatra Mountains lakes (Slovakia) using chironomids (Diptera, Chironomidae). *Biologia*, 61 (18), 191–201. <https://doi.org/10.2478/s11756-006-0131-8>
- Bitušik, P., Kopáček, J., Stuchlík, E. & Šporka, F. (2006b) Limnology of Lakes in the Tatra Mountains. *Biologia*, 61 (18), 1–222. <https://doi.org/10.2478/s11756-006-0117-6>
- Bitušik, P., Trnková, K., Chamutiová, T., Sochuliaková, L., Stoklasa, J., Pipík, R., Szarłowicz, K., Szacilowski, G., Thomková, K., Šporka, F., Starek, D., Šurka, J., Milovský, R. & Hamerlík, L. (2018) Tracking human impact in a mining landscape using lake sediments: a multi-proxy palaeolimnological study. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 504, 23–33. <https://doi.org/10.1016/j.palaeo.2018.04.021>
- Boggero, A., Füreder, L., Lencioni, V., Simcic, T., Thaler, B., Ferrarese, U., Lotter, A.F. & Ettinger, R. (2006) Littoral chironomid communities of Alpine lakes in relation to environmental factors. *Hydrobiologia*, 562, 145–165. <https://doi.org/10.1007/s10750-005-1809-6>
- Brodersen, K.P., Pedersen, O., Lindegaard, C. & Hamburger, K. (2004) Chironomids (Diptera) and oxy-regulatory capacity: An experimental approach to paleolimnological interpretation. *Limnology and Oceanography*, 49, 1549–1559. <https://doi.org/10.4319/lo.2004.49.5.1549>
- Brodersen, K.P. & Quinlan, R. (2006) Midges as palaeoindicators of lake productivity, eutrophication and hypolimnetic oxygen. *Quaternary Science Reviews*, 25 (15–16), 1995–2012. <https://doi.org/10.1016/j.quascirev.2005.03.020>
- Brooks, S.J., Langdon, P.G. & Heiri, O. (2007) *The Identification and Use of Palaeartic Chironomidae Larvae in Palaeoecology. QRA Technical Guide No. 10*. QRA, London, 276 pp.
- Cranston, P.S. & Epler, J.H. (2013) The larvae of Tanypodinae (Diptera: Chironomidae) of the Holarctic region—Keys and diagnoses. *In: Andersen, T., Sæther, O.A., Cranston, P.S. & Epler, J.H. (Eds.), Chironomidae of the Holarctic Region. Keys and diagnoses. Larvae. Insects Systematics & Evolution, Supplements* 66, pp. 39–136.
- Cranston, P.S. & Krosch, M.N. (2015) DNA sequences and austral taxa indicate generic synonymy of *Paratrichocladus* Santos-Abreu with *Cricotopus* Wulp (Diptera: Chironomidae). *Systematic Entomology*, 40 (4), 719–732. <https://doi.org/10.1111/syen.12130>
- Cuppen, H.P.J.J. & Tempelman, D. (2018) Identification key for the 4th stage larvae of north west European species of *Cricotopus* (Diptera: Chironomidae: Orthoclaadiinae). *Lauterbornia*, 85, 69–90.
- Epler, J.H., Ekrem, T. & Cranston, P.S. (2013) 10. The larvae of Chironominae (Diptera: Chironomidae) of the Holarctic Region—Keys and diagnoses. *In: Andersen, T., Sæther, O.A., Cranston, P.S. & Epler, J.H. (Eds.), Chironomidae of the Holarctic Region. Keys and diagnoses. Larvae. Insect Systematics & Evolution, Lund, Supplement*, pp. 189–386.
- Ferrington, L.C. (2007) Global diversity of non-biting midges (Chironomidae; Insecta-Diptera) in freshwater. *Hydrobiologia*, 595, 447–455. <https://doi.org/10.1007/s10750-007-9130-1>
- Fittkau, E.J. & Roback, S.S. (1983) The larvae of Tanypodinae (Diptera: Chironomidae) of the Holarctic region—Keys and diagnoses. *In: Wiederholm, T. (Ed.), Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. Entomologica Scandinavica, Supplement* 19, pp. 33–110.

- Füreder, L., Ettinger, R., Boggero, A., Thaler, B. & Thies, H. (2006) Macroinvertebrate diversity in Alpine lakes: effects of altitude and catchment properties. *Hydrobiologia*, 562, 123–144.
<https://doi.org/10.1007/s10750-005-1808-7>
- Gąsiorowski, M. & Sienkiewicz, E. (2010) The Little Ice Age recorded in sediments of a small dystrophic mountain lake in southern Poland. *Journal of Paleolimnology*, 43, 475–487.
<https://doi.org/10.1007/s10933-009-9344-5>
- Giłka, W. (2007) Przegląd faunistyczny ochotkowatych z plemienia Tanytarsini (Diptera: Chironomidae) Tatrzańskiego Parku Narodowego. A faunistic review of chironomids of the tribe Tanytarsini (Diptera: Chironomidae) of the Tatra National Park. *Dipteron*, 23, 11–17. [in Polish]
- Gorek, A. & Kahan, Š. (1973) Prehľad geologického vývoja a stavby Vysokých Tatier [Review of the geological development and structure of the High Tatra Mountains]. *Zborník TANAP*, 15, 5–88. [in Slovak]
- Hamerlík, L. & Bitušík, P. (2008) Records of Chironomidae (Diptera) from a subalpine Tatra lake, new in Slovakia. *Lauterbornia*, 62, 131–133.
- Hamerlík, L., Dobříková, D., Szarłowicz, K., Reczynski, W., Kubica, B., Šporka, F. & Bitušík, P. (2016) Lake biota response to human impact and local climate during the last 200 years: A multi-proxy study of a subalpine lake (Tatra Mountains, W Carpathians). *Science of the Total Environment*, 545, 320–328.
<https://doi.org/10.1016/j.scitotenv.2015.12.049>
- Hamerlík, L., Svitok, M., Novikmec, M., Veselská, M. & Bitušík, P. (2017) Weak altitudinal pattern of overall chironomid richness is a result of contrasting trends of subfamilies in high-altitude ponds. *Hydrobiologia*, 793 (1), 67–81.
<https://doi.org/10.1007/s10750-016-2992-3>
- Ilyashuk, B.P., Ilyashuk, E.A., Makarchenko, E.A. & Heiri, O. (2010) Midges of the genus *Pseudodiamesa* Goetghebuer (Diptera, Chironomidae): current knowledge and palaeoecological perspective. *Journal of Paleolimnology*, 44 (2), 667–676.
<https://doi.org/10.1007/s10933-010-9446-0>
- Kowalyk, H.E. (1985) The larval cephalic setae in the Tanytarsini (Diptera: Chironomidae) and their importance in generic determinations. *The Canadian Entomologist*, 117, 67–106.
<https://doi.org/10.4039/Ent11767-1>
- Kownacki, A. (2010) Chironomidae (Diptera, Insecta) of the Tatra National Park: distribution, ecology, zoogeography. (Chironomidae (Diptera, Insecta) Tatrzańskiego Parku Narodowego rozmieszczenie, ekologia, zoogeografia). *Nauka a zarządzanie obszarem Tatr i ich otoczeniem*, 2, 113–118. [in Polish]
- Kownacki, A. (2011) Significance and conservation of Chironomidae (Diptera, Insecta) in aquatic ecosystems of Poland (Znaczenie i ochrona Chironomidae (Diptera, Insecta) w ekosystemach wodnych Polski). *Forum Faunistyczne*, 1 (1), 4–11. [in Polish with English Summary]
- Kubovčík, V. (2012) *Palaeoecology of Tatra Mts. lakes: Chironomids (Diptera: Chironomidae), climate change and acidification*. Technical University in Zvolen, Zvolen, 95 pp. [in Slovak]
- Langdon, P.G., Ruiz, Z.O.E., Wynne, S., Sayer, C.D. & Davidson, T.A. (2010) Ecological influences on larval chironomid communities in shallow lakes: implications for palaeolimnological interpretations. *Freshwater Biology*, 55 (3), 531–545.
<https://doi.org/10.1111/j.1365-2427.2009.02345.x>
- Larocque-Tobler, I. (2014) The Polish sub-fossil chironomids. *Palaeontologia Electronica*, 17 (1), 1–28.
- Matěna, J. & Frouz, J. (2000) Distribution and ecology of *Chironomus* Meigen species in the Czech Republic (Diptera, Chironomidae). In: Hoffrichter, O. (Ed.), *Late 20th Century Research on Chironomidae: An Anthology from the 13th International Symposium on Chironomidae*. Shaker Verlag, Aachen, pp. 543–548.
- Medeiros, A.S. & Quinlan, R. (2011) The distribution of the Chironomidae (Insecta: Diptera) along multiple environmental gradients in lakes and ponds of the eastern Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences*, 68 (9), 1511–1527.
<https://doi.org/10.1139/f2011-076>
- Michailova, P., Kownacki, A., Woznicka, O., White, K., Dean, A. & Szarek-Gwiazda, E. (2014) *Macropelopia nebulosa* group (Diptera, Chironomidae, Tanytarsini)—karyotype and morphology of larvae and pupae. *Zootaxa*, 3852, 83–100.
<https://doi.org/10.11646/zootaxa.3852.1.3>
- Moller Pillot, H.K.M. (2013) *Chironomidae Larvae of the Netherlands and Adjacent Lowlands. Biology and Ecology of the aquatic Orthoclaadiinae*. KNNV Publishing, Zeist, 312 pp.
- Moubayed-Breil, J. & Bitušík, P. (2019) Taxonomic notes on the genus *Chaetocladus* (*laminatus*-group) (Diptera: Chironomidae, Orthoclaadiinae) II. Descriptions of *C. bitusiki* sp. n. and *C. mantetensis* sp. n., two relict species inhabiting cold alpine springs and streams. *Biologia*, 74 (11), 1489–150.
<https://doi.org/10.2478/s11756-019-00253-8>
- Nicacio, G. & Juen, L. (2015) Chironomids as indicators in freshwater ecosystems: an assessment of the literature. *Insect Conservation and Diversity*, 8 (5), 393–403.
<https://doi.org/10.1111/icad.12123>
- Novikmec, M., Veselská, M., Bitušík, P., Hamerlík, L., Matúšová, Z., Klementová, B.R. & Svitok, M. (2015) Checklist of benthic macroinvertebrates of high altitude ponds of the Tatra Mountains (Central Europe) with new records of two species for Slovakia. *Check List*, 11 (1), 1522.
<https://doi.org/10.15560/11.1.1522>

- Oliver, D.R. & Roussel, M.E. (1983) Redescription of *Brillia* Kieffer (Diptera: Chironomidae) with descriptions of Nearctic species. *The Canadian Entomologist*, 115 (3), 257–279.
<https://doi.org/10.4039/Ent115257-3>
- Pinder, L.C.V. & Reiss, F. (1983) The larvae of Chironominae (Diptera: Chironomidae) of the Holarctic region—Keys and diagnoses. In: Wiederholm, T. (Ed.), Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. *Entomologica Scandinavica*, Supplement 19, pp. 149–294.
- Rieradevall, M. & Brooks, S.J. (2001) An identification guide to subfossil Tanypodinae larvae (Insecta: Diptera: Chironomidae) based on cephalic setation. *Journal of Paleolimnology*, 25, 81–99.
<https://doi.org/10.1023/A:1008185517959>
- Rossaro, B. & Lencioni, V. (2015) A key to larvae of *Diamesa* Meigen, 1835 (Diptera, Chironomidae), well known as adult males and pupae from Alps (Europe). *Journal of Entomological and Acarological Research*, 47, 123–138.
<https://doi.org/10.4081/jear.2015.5516>
- Ruse, L. (2010) Classification of nutrient impact on lakes using the chironomid pupal exuvial technique. *Ecological Indicators*, 10 (3), 594–601.
<https://doi.org/10.1016/j.ecolind.2009.10.002>
- Sæther, O.A. (1976) Revision of *Hydrobaenus*, *Trissocladius*, *Zalutschia*, *Paratrissocladius*, and some related genera (Diptera: Chironomidae). *Bulletin of the Fisheries Research Board of Canada*, 195, 1–287.
- Sæther, O.A., Ashe, P. & Murray, D.A. (2000) Family Chironomidae. In: Papp, L. & Darvas, B. (Eds.), *Contribution to a Manual of Palaearctic Diptera (with special reference to flies of economic importance)*. Appendix. Science Herald, Budapest, pp. 113–334.
- Sæther, O.A. & Andersen, T. (2013) 8. The larvae of Prodiamesinae (Diptera: Chironomidae) of the Holarctic Region—Keys and diagnoses. In: Andersen, T., Sæther, O.A., Cranston, P.S. & Epler, J.H. (Eds.), *Chironomidae of the Holarctic Region. Keys and diagnoses. Larvae*. Insect Systematics & Evolution, Supplement, Lund, pp. 189–386.
- Serra-Tosio, B. (1973) Ecologie et biogéographie des Diamesini d'Europe (Diptera, Chironomidae). *Travaux du Laboratoire d'Hydrobiologie et de Pisciculture de l'Université de Grenoble*, 63, 5–175.
- Schmid, P.E. (1993) A key to the larval Chironomidae and their instars from Austrian Danube Region streams and rivers. With particular reference to a numerical taxonomic approach. Part I. Diamesinae, Prodiamesinae and Orthoclaudiinae. *Wasser und Abwasser*, 3, 1–514.
- Silva, F.L. & Ekrem, T. (2016) Phylogenetic relationships of nonbiting midges in the subfamily Tanypodinae (Diptera: Chironomidae) inferred from morphology. *Systematic Entomology*, 41 (1), 73–92.
<https://doi.org/10.1111/syen.12141>
- Soponis, A. (1977) A revision of the Nearctic species of *Orthocladus* (*Orthocladus*) van der Wulp (Diptera: Chironomidae). *The Memoirs of the Entomological Society of Canada*, 102, 1–187.
<https://doi.org/10.4039/entm109102fv>
- Spies, M. & Sæther, O.A. (2013) Chironomidae. Fauna Europaea. In: Beuk, P. & Pape, T. (Eds.), *Fauna Europaea: Diptera, Nematocera*. *Fauna Europaea. Version 2.6*. Available from: <http://www.faunaeur.org> (accessed 10 November 2019)
- Stoklasa, J., Dobříková, D., Sochuliaková, L., Pipík, R. & Hamerlík, L. (2017) Identifying white spots on the roadmap of Late Pleistocene and Holocene palaeolimnology in Slovakia: Review and future directions. *Biologia*, 72 (11), 1229–1239.
<https://doi.org/10.1515/biolog-2017-0152>
- Štefková, E. & Šporka, F. (2001) Long-term ecological research of high mountain lakes in the High Tatras (Slovakia). *Ekologia*, 20 (2), 101–106.
- Vološčuk, I. (Ed.) (1994) *Tatranský národný park [Tatra National Park]*. Gradus, Martin, 551 pp. [in Slovak]
- Walker, I.R. (2001) Midges: Chironomidae and related Diptera. In: Smol, J.P., Birks, H.J.B. & Last, W.M. (Eds.), *Tracking environmental change using late sediments*. Vol. 4. Zoological Indicators, Kluwer Academic Publishers, Dordrecht, pp. 43–66.
https://doi.org/10.1007/0-306-47671-1_3