

Midges of the genus *Pseudodiamesa* Goetghebuer (Diptera, Chironomidae): current knowledge and palaeoecological perspective

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Abstract Larvae of the genus *Pseudodiamesa* Goetghebuer, which includes 12 described valid species and is divided by Makarchenko and Makarchenko (1999) into two species groups, *Pseudodiamesa branickii* group and *Pseudodiamesa nivosa* group, are widespread in lakes and running waters of cold, high-latitude and high-altitude areas of the Northern Hemisphere. Larval remains of the genus are often found in subfossil assemblages from these

cold regions, but intra-genus morphotypes usually are not distinguished by palaeoecologists. Current knowledge of the ecology of the species indicates that the *Pseudodiamesa nivosa* group is more cold-adapted than the *Pseudodiamesa branickii* group and, therefore, these two intra-genus morphotypes cannot be amalgamated into a larger taxonomic unit without losing substantial information. Here we present the morphological characters of head capsules of *Pseudodiamesa* larvae attributed to the different species-group morphotypes, which are clearly visible in subfossil specimens. The information summarized in this paper will help provide more reliable chironomid-based palaeoclimatic inferences from lake sediment records covering colder phases through the late Quaternary in the Northern Hemisphere.

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Introduction

Species of the genus *Pseudodiamesa* Goetghebuer, 1939 are relatively large chironomids (non-biting midges), which are recorded from all continents of the Northern Hemisphere (Pagast 1947). The taxonomy of this genus from the subfamily Diamesinae is based mainly on morphological characters of the adult males (Makarchenko 1985; Oliver 1989), but the larvae of the different *Pseudodiamesa* species are

morphologically similar and can be difficult to separate (Oliver 1983; Makarchenko and Makarchenko 1999; Makarchenko 2006). This genus was divided into two subgenera, *Pachydiamesa* Oliver, 1959 and *Pseudodiamesa* s. str. by Oliver (1959). The first subgenus is represented by only one Nearctic species, *Pseudodiamesa arctica* (Malloch), and the second subgenus includes all other known species of this genus, following the nomenclature of Oliver (1959, 1983). Makarchenko and Makarchenko (1999) suggested applying a species-group nomenclature to the *Pseudodiamesa* larvae and dividing the genus into two species groups, the *Pseudodiamesa branickii* group and the *Pseudodiamesa nivosa* group. According to the nomenclature of Makarchenko and Makarchenko (1999), the first species group is represented by two species, namely *Pseudodiamesa branickii* (Nowicki) and *Pseudodiamesa pertinax* (Garret), and the *Pseudodiamesa nivosa* group includes all other known species (Table 1). Hereafter, we use the species-group nomenclature to differentiate *Pseudodiamesa* larvae within the genus, as this nomenclature is based on different morphological characters of the larval head capsules and can be applied to chironomid subfossil material represented by larval remains.

The genus *Pseudodiamesa* is known as one of the cold-adapted chironomid taxa (Serra-Tosio 1976; Barley et al. 2006; Heiri and Lotter 2008). Larvae of both species groups are widespread in lakes and running waters of cold areas of the Holarctic and Oriental regions (Pagast 1947; Manca et al. 1998; Oliver et al. 1990; Makarchenko and Makarchenko 1999). Studies of fossil chironomid assemblages indicate that *Pseudodiamesa* was common in lakes during past cold climate phases of the late Quaternary (Ilyashuk et al. 2008; Kurek et al. 2009).

High-latitude and high-altitude regions are especially sensitive to the effects of recent climate warming (Ørbæk et al. 2004). In recent years, palaeoclimate studies in these remote regions have received increasing attention by the scientific community. Interest in chironomid-based palaeoclimate inferences has grown, especially over the past decade, driven largely by the potential for using chironomids to infer palaeotemperatures accurately and independently of other methods (Walker and Cwynar 2006). Larval remains of the genus *Pseudodiamesa* are quite often found in subfossil chironomid assemblages from

these cold regions, but intra-genus morphotypes are usually not distinguished by palaeoecologists (Larocque et al. 2001; Barley et al. 2006; Heiri and Lotter 2008). Previous studies in the European Alps (Pagast 1947; Serra-Tosio 1973, 1976; Rossaro et al. 2006) and the Nepalese Himalayas (Manca et al. 1998), however, have shown that the *Pseudodiamesa* species, which can be attributed to different species groups, but live together in these mountain areas, prefer different altitudes and/or temperature conditions within lakes and streams. As demonstrated by Brooks et al. (2007), many morphotypes within other genera show different distributions along environmental gradients than the genus as a whole, and therefore have the potential to be useful palaeoecological indicators. Thus, identification of *Pseudodiamesa* subfossil remains to a more precise taxonomic level would provide more reliable palaeoclimate inferences.

The aim of this work was to assess whether intra-genus morphotypes of *Pseudodiamesa* larvae can be differentiated reliably in subfossil material from surface and down-core samples. To achieve this objective, it is necessary to determine the morphological characters of head capsules of *Pseudodiamesa* larvae that are clearly visible in subfossil remains. Here we used subfossil specimens represented by both *Pseudodiamesa* species groups, which were collected in the European Alps and Northern Russia to examine several key morphological features described in the available literature for identification of contemporary *Pseudodiamesa* larvae. In addition, we provide a short summary of the zoogeography and ecology of *Pseudodiamesa* species, which will contribute to palaeoecological interpretation of subfossil records.

Zoogeography

At the end of the twentieth century, there were 11 valid *Pseudodiamesa* species known to science from the Holarctic and Oriental regions (Makarchenko and Makarchenko 1999). More recently, a twelfth species, *Pseudodiamesa sunabacedea* Tanaka and Sasa, was described from Japan (Tanaka and Sasa 2001) (Table 1).

At present, three *Pseudodiamesa* species are known from the Nearctic, where they are recorded only from western and northern areas (Oliver et al. 1990; Epler 2001). The *P. nivosa* group is represented

Table 1 Distribution of *Pseudodiamesa* species in the zoogeographic regions: (+) presence and (–) absence

Region	Nearctic ^a	Western Palaearctic			Eastern Palaearctic			Oriental ^b
		Northern Africa	Western Europe	Eastern Europe	Northern Asia	Central Asia	Japan	
<i>Pseudodiamesa branickii</i> group								
<i>P. branickii</i> (Nowicki 1873)	+	+	+	+	+	+	+	+
<i>P. pertinax</i> (Garret 1925)	+	–	–	–	–	–	–	–
<i>Pseudodiamesa nivosa</i> group								
<i>P. arctica</i> (Malloch 1919)	+	–	–	–	–	–	–	–
<i>P. nivosa</i> (Goetghebuer 1928)	–	+	+	+	+	+	–	–
<i>P. stackelbergi</i> (Goetghebuer 1933)	–	–	–	+	+	–	+	–
<i>P. nepalensis</i> Reiss, 1968	–	–	–	–	–	–	–	+
<i>P. gorodkovi</i> Makarchenko, 1983*	–	–	–	+	–	–	–	–
<i>P. venusta</i> Makarchenko, 1984	–	–	–	–	–	+	–	–
<i>P. latistyla</i> Makarchenko, 1989	–	–	–	–	+	–	–	–
<i>P. vetusta</i> Makarchenko, 1989*	–	–	–	–	–	+	–	–
<i>P. mongolzecea</i> Sasa and Suzuki, 1997*	–	–	–	–	–	+	–	–
<i>P. sunabacedea</i> Tanaka and Sasa, 2001*	–	–	–	–	–	–	+	–
References	1, 2	3, 4	5, 6	7–9	8, 10–12	11, 13	14, 15	16, 17

References: 1 Oliver et al. (1990), 2 Epler (2001), 3 Pagast (1947), 4 Kettani et al. (2001), 5 Sæther and Spies (2004), 6 Makarchenko (2009), 7 Goetghebuer (1933), 8 Pankratova (1970), 9 Makarchenko (1983), 10 Linevich (1989), 11 Makarchenko (1989), 12 Makarchenko (2006), 13 Hayford (2005), 14 Makarchenko (1993), 15 Tanaka and Sasa (2001), 16 Roback and Coffman (1987), 17 Manca et al. (1998)

* Immature stages are unknown

^a Are recorded only from western and northern areas

^b Only from the Nepalese Himalayas

there by *P. arctica*, and the *P. branickii* group is represented by two species, *P. branickii* and *P. pertinax*.

In the Palaearctic and Oriental regions, the *P. branickii* group is represented only by widespread *P. branickii*. The *P. nivosa* group is represented by one species, *Pseudodiamesa nepalensis* Reiss, in the Oriental region (Nepalese Himalayas; Manca et al. 1998) and by eight other species in the Palaearctic region. Among the Palaearctic *Pseudodiamesa* species belonging to the *P. nivosa* group, *Pseudodiamesa nivosa* (Goetghebuer) is the most widely distributed species known from both eastern and western areas of the Palaearctic (Table 1). Schnell and Willassen (1991) suggested that the Nearctic *P. arctica* and the Palaearctic *P. nivosa* are the same species and should be named *P. arctica*, as this is the older name (Sæther and Spies 2004). Makarchenko (2009), however, compared adult morphological characteristics of both

species and showed that they are two valid sister species.

Another of the widely distributed Palaearctic species from the *P. nivosa* group is *Pseudodiamesa stackelbergi* (Goetghebuer) known from both eastern and western areas. The other species are restricted to smaller areas of the Palaearctic. Furthermore, the immature stages of the four Palaearctic species are unknown (Table 1).

Ecology

Larvae of the genus *Pseudodiamesa* are detritus feeders that gather fine particulate organic matter, but can prey on smaller chironomids and other small aquatic invertebrates as well (Pagast 1947). The species are well adapted to harsh physical environments and can complete their life cycle where water temperatures never exceed 2°C (Milner et al. 2001).

On the other hand, the larvae can enter diapause during relatively long periods of low temperatures, when conditions are not suitable for activity. Usually, all instars develop during summer, enter diapause at the 4th instar, and emerge synchronously the next year during the springtime thaw period (Oliver 1959; Tátosová and Stuchlík 2006). Adults of *Pseudodiamesa* emerge through cracks in the ice cover at the onset of thawing, and can copulate on the snow cover at sub-zero temperatures (−1 to −2°C; Oliver 1964; Danks and Oliver 1972; Hågvar and Østbye 1973). Diapausal eggs of *Pseudodiamesa*, frozen and covered by snow, were also found in early spring near an Alpine glacial stream (Lencioni 2004). In contrast to the high degree of synchrony observed in mountain and Arctic lakes, stream studies suggest that emergence is not synchronized by diapause (Hayes and Murray 1987). Studies from North America and Europe indicated that the *Pseudodiamesa* species are usually univoltine (Oliver 1959; Tátosová and Stuchlík 2006). However, there is evidence that *P. branickii* exhibits bi- and trivoltinism under warmer conditions at lower altitudes and latitudes (Nolte and Hoffmann 1992).

Our knowledge of the ecology of the *Pseudodiamesa* species is still fragmentary. The most comprehensive studies of the ecology and distribution of the *Pseudodiamesa* species are from Western Europe, where the genus is represented by *P. branickii* and *P. nivosa*, i.e. every species group is represented by a single species. Both species are common and widespread taxa in the European Alps (Boggero et al. 2006; Rossaro et al. 2006), the Tatra Mountains (Bitušík et al. 2006; Krno et al. 2006), the Pyrenees (Rieradevall and Prat 1999), Arctic and sub-arctic regions of Fennoscandia (Paasivirta 2009) and Iceland (Langdon et al. 2008). In the European Alps, *P. branickii* prefers altitudes between 200 and 2,300 m asl, whereas *P. nivosa* dwells mainly at altitudes of 2,000–3,000 m asl (Pagast 1947; Serratosio 1973; Janecek 1998). Nevertheless *P. nivosa* can also colonize cold habitats of the periglacial zones at lower altitudes, 345–230 m asl (Siciński 1988).

Though both *Pseudodiamesa* species are known from lakes and running waters of Western Europe, *P. nivosa* prefers the cold profundal of Arctic and alpine lakes, where in some cases it displays very abundant populations (Nauwerck 1981; Lindegaard

1992; Tátosová and Stuchlík 2006). *P. branickii* is more common in running waters and the littoral zone of lakes (Bretschko 1974; Boggero et al. 2006; Rossaro et al. 2006). Previous studies of chironomids from European glacier-fed streams have shown that *P. nivosa* survives in the first 100 m from a glacier, where water temperature does not exceed 2°C. It colonises downstream habitats with maximum temperature <9°C, whereas *P. branickii* is associated with “non-glacial” conditions and can be very abundant further downstream in biotopes where the water temperature does not exceed 18°C (Janecek et al. 2002; Lods-Crozet et al. 2001; Lencioni and Rossaro 2005). According to Rossaro et al. (2006), who calculated water temperature optima for the chironomid taxa living in running waters in the Southern European Alps above 800–1,000 m asl, *P. branickii* is characterised by a higher temperature optimum than *P. nivosa* (4.90 and 4.45°C, respectively). In addition, the larvae of both species tolerate low pH and occur in acidified lakes and streams (Braukmann and Biss 2004; Bitušík et al. 2006).

The *Pseudodiamesa* species from Nearctic and Oriental regions demonstrate a similar difference in ecological preferences of the two species-group morphotypes. The Nearctic *P. arctica* and the Oriental *P. nepalensis*, both belonging to the *P. nivosa* group, prefer the cold profundal of lakes and, like their sister species *P. nivosa* in the Palaearctic region, often produce very abundant populations in large arctic lakes of North America (Oliver 1964, 1976) and in deep, high alpine lakes and glacial pools of the Nepalese Himalayas (Roback and Coffman 1987; Manca et al. 1998), respectively. Both species belonging to the *P. branickii* group from North America, *P. pertinax* and *P. branickii*, occupy similar warmer biotopes, namely the littoral zone of lakes and “non-glacial” habitats of springs and streams (Mackay 1969; Elgmork and Sæther 1970; Sæther 1970). Mackay (1969) found that the Nearctic *P. pertinax* is able to survive in the stream biotopes where the water temperature reaches 17.2°C. In high alpine lakes of the Oriental region, *P. branickii* is also restricted to habitats within the warmer littoral (Manca et al. 1998).

The information presented above suggests that the *P. nivosa* group is more cold-adapted than the *P. branickii* group, which occurs under more moderate conditions. Unfortunately, our knowledge of the

ecology of some Eastern Palaearctic species belonging to the *P. nivosa* group is poor. The distribution and ecology of the four species is restricted and comes only from the occurrence of the adult forms. It would be helpful to study the adults and immatures together, but this is not always practical. Current knowledge of the ecology of both species groups suggests that all the sister species forming the *P. nivosa* group have similar environmental preferences within different zoogeographic regions.

Materials and methods

Subfossil material from surface and down-core samples gathered in the European Alps and Northern Russia was used in this study. Material including *Pseudodiamesa nivosa* species-group subfossils was taken from sediment sequences (core tops and lower parts) retrieved from three sites: (1) Nikolay Lake, a large Arctic lake situated in northeast Russia (73°20'N, 124°12'E; ~1 m asl); (2) Schwarzsee ob Sölden, a high alpine lake located at 2,796 m asl in the Ötztaler Alps, Austria (46°58'N, 10°57'E); and a palaeo-lake near the Maloja Pass, Central Alps, Switzerland (46°24'N, 9°41'E; 1,865 m asl). Cores were collected at all three sites to produce late Quaternary palaeoclimate reconstructions (Andreev et al. 2004; Ilyashuk et al. 2008, 2009). Material including *Pseudodiamesa branickii* species-group subfossils was taken from surface and down-core sediment samples that were collected from Lake Golcovoe, a subarctic lake situated on the Kola Peninsula, northwest Russia (67°50'N 33°40'E; 208 m asl), and from surface sediment samples collected at Weißenbach, a first-order tributary of the Inn River, Austria (47°17'N, 11°31'E; 605 m asl). In addition, material including subfossils of both the *Pseudodiamesa* species groups was taken from surface sediment samples collected at Matscherjochsee, a high alpine lake located 3,188 m asl in the Italian Alps (46°47'N, 10°41'E). At least 40 *Pseudodiamesa* head capsules from every site were examined.

The *Pseudodiamesa* head capsules were picked from the fresh sediment in a Bogorov counting tray at 40–50× magnification under a stereomicroscope. After dehydration they were mounted on glass slides in Euparal® mounting medium for microscopic identification. Taxonomic identification of the

Pseudodiamesa intra-genus morphotypes was accomplished using different key morphological characters of the larval head capsules described in Oliver (1959, 1983), Makarchenko (1985, 2006), Schmid (1993), Janecek (1998), Makarchenko and Makarchenko (1999), and Epler (2001). Morphological terminology is consistent with that of Sæther (1980).

Results

Key morphological characters: contemporary versus subfossil material

The *Pseudodiamesa* larvae belonging to the different species groups are separable by several morphological characters, namely by antennal ratio, pecten epipharyngis, mandibular seta interna, and mentum, following Makarchenko and Makarchenko (1999). Morphological features of the larval head capsules described in the identification keys to the contemporary *Pseudodiamesa* larvae, and summarised in Table 2, were used to identify subfossil specimens.

Labral lamellae and labral setae SI

The larvae of *P. arctica* can be separated from all other *Pseudodiamesa* species by having labral lamellae (Oliver 1959, 1983). The larvae of *P. arctica* and *P. pertinax* belonging to the *P. nivosa* group and the *P. branickii* group, respectively, are separable from all other *Pseudodiamesa* species by the shape of labral setae SI. *P. arctica* has simple seta-like SI and *P. pertinax* has apically bifid SI, whereas all known larvae of other *Pseudodiamesa* species are characterized by lamelliform SI (Oliver 1983). Unfortunately, labral lamellae and labral setae SI are rarely preserved in subfossil specimens and these characters thus cannot be used to distinguish chironomid taxa in subfossil material.

Mandibular seta interna

Mandibular setae interna of the *P. nivosa* group consist of 14–24 branches according to Makarchenko (1985, 2006) and Makarchenko and Makarchenko (1999), and 18–23 branches according to Schmid (1993), whereas mandibular setae interna of the *P. branickii* group consist of 9–15 branches (10–15

Table 2 Morphological characters of the *Pseudodiamesa* larval head capsules for identification of the species-group morphotypes within contemporary and subfossil material

Characters	<i>P. branickii</i> group	<i>P. nivosa</i> group	References	Applicability to subfossils
Labral lamellae	Absent	Present* or absent	1, 2	–
Setae SI	Apically bifid** or lamelliform	Simple* or lamelliform	1, 2, personal observation	+
Mandibular seta interna	With 9–15 branches	With 14–24 branches	3–6, personal observation	+
Antennal ratio	<2.5	≥2.5	3–7, personal observation (Fig. 1a, b)	++
Pecten epipharyngis	Single median scale and 3 pairs of lateral scales	Two median scales and 2–3 pairs of lateral scales	3, 5, 6, 8, personal observation (Fig. 1c–f)	++
Mentum	Median tooth as dark as lateral teeth	Median tooth lighter than lateral teeth	3, 5, 6, personal observation (Fig. 1g–j)	+++

References: 1 Oliver (1959), 2 Oliver (1983), 3 Makarchenko (1985), 4 Schmid (1993), 5 Makarchenko and Makarchenko (1999), 6 Makarchenko (2006), 7 Janecek (1998), 8 Epler (2001). Applicability within subfossils: non-applicable (–) and applicable within < 5% (+), ≤ 30% (++), or ≤ 100% (+++) of subfossils

* Only *P. arctica*

** Only *P. pertinax*

branches according to Schmid (1993) and 9–13 according to Makarchenko (1985, 2006) and Makarchenko and Makarchenko (1999). Unfortunately, the mandibular setae interna are rarely preserved and usually absent in subfossil specimens (Table 2).

Antennal ratio and pecten epipharyngis

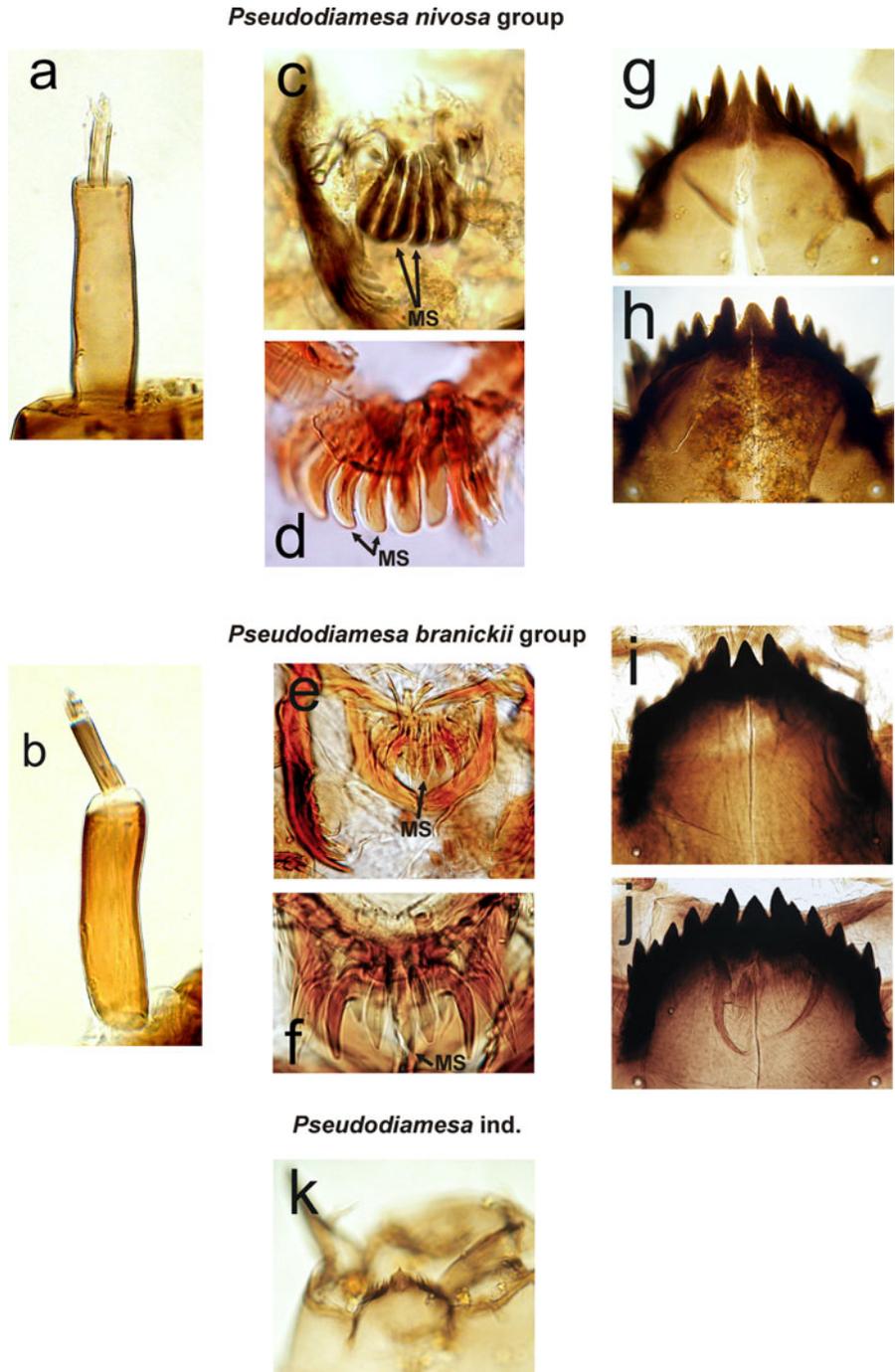
Other key morphological features for the separation of the *Pseudodiamesa* species-group morphotypes are the antennal ratio and pecten epipharyngis, which are often preserved in subfossil specimens (up to 30% of subfossils; Table 2) (Fig. 1a–f). The antenna of the *P. nivosa*-group larvae is characterized by an antennal ratio ≥ 2.5 , whereas the antennal ratio of the *P. branickii* group is < 2.5 (Makarchenko 1985, 2006; Schmid 1993; Janecek 1998; Makarchenko and Makarchenko 1999). The pecten epipharyngis of the *P. nivosa*-group larvae consists of an even number, namely 3–4 pairs, of broad, elongate, apically blunt scales (Fig. 1c, d), but that of the *P. branickii*-group larvae is characterized by an odd number, namely seven scales (Fig. 1e, f) (Makarchenko 1985, 2006; Makarchenko and Makarchenko 1999; Epler 2001) (Fig. 1e, f). Our inspection of the subfossils showed that the pecten epipharyngis of the species *P. branickii* consists of seven very weakly sclerotized scales

(Fig. 1e, f), whereas that of the species *P. nivosa* consists of six strongly sclerotized scales (Fig. 1c, d). The pecten epipharyngis consisting of seven scales was assigned mistakenly to the species *P. nivosa* by Schmid (1993) and Janecek (1998), and to all the *Pseudodiamesa* species in Oliver (1983), whereas the species *P. arctica* has a pecten epipharyngis consisting of eight scales (E. Makarchenko, personal observation). In both species groups, two outer pairs of scales often overlap the chaetulae laterales and are difficult to see. Median scales, having paired or unpaired character, can however, be used for the separation of the *Pseudodiamesa* species-groups (Makarchenko and Makarchenko 1999; Makarchenko 2006) (Table 2).

Mentum

The mentum is a well-preserved structure in subfossil specimens and can be one of the best morphological characters for differentiating *Pseudodiamesa* species-group morphotypes in subfossil material. All teeth of the mentum of the *P. branickii*-group are similar in colour, whereas the *P. nivosa* group has a mentum with a lighter median tooth than the lateral black teeth (Makarchenko 1985, 2006; Makarchenko and Makarchenko 1999) (Fig. 1g–j). In addition, lateral

Fig. 1 *Pseudodiamesa*: antenna (a, b); labro-epipharyngeal region and median scales (MS) of pecten epipharyngis (c, e); pecten epipharyngis and median scales (MS) (d, f); unflattened mentum of 3rd (g), 4th (h, i), and 2nd (k) instars; flattened mentum of 4th instar (j). *Pseudodiamesa nivosa* (Goetghebuer) (a, c, d, g, h); *Pseudodiamesa branickii* (Nowicki) (b, e, f, i, j); *Pseudodiamesa* ind. (k)



teeth are more visible in the unflattened mentum of the *P. nivosa* group than in that of the *P. branickii*-group (Makarchenko 1985) (Fig. 1h, i). Finally, the 1st and 2nd instars of both subgenera have an identical mentum, with a broad median tooth that is lighter than the lateral blackish teeth (Fig. 1k).

Conclusions

We concluded that the species-group morphotypes of *Pseudodiamesa* larvae can be differentiated within the subfossil material from surface and down-core samples using a combination of morphological

characters, namely the mentum, pecten epipharyngis, and antennal ratio (Table 2). The *Pseudodiamesa* species groups from different zoogeographic regions demonstrate similar ecological preferences. Thus, more precise taxonomic identification and splitting of the genus into two intra-genus morphotypes could improve existing chironomid-temperature transfer functions and provide better palaeoclimate reconstructions and palaeolimnological interpretation of subfossil chironomid records.

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