

COMPOSITION AND ZOOGEOGRAPHICAL CHARACTERISTICS OF THE FENNOSCANDIAN MAYFLY FAUNA

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Fennoscandia represents geographically the European northern hemisphere including Norway, Sweden and Finland whereas Denmark belongs to continental Europe. During the maximal glaciation in the Pleistocene (until 10.000 years ago), the whole northern hemisphere and huge areas of central Europe were covered with a thick shield of ice and therefore free of Ephemeroptera. The width of the corridor between northern and Alpine ice shields amounted to only 280 miles. So, if colonization had taken place it could have been only by cold adapted Ephemeropteran fauna and this would have led to a complete intermixture of the Fennoscandian and the Alpine mayfly fauna, and consequently form a remarkable similarity between the fauna elements of these two groups. But, the relationship of the Fennoscandian mayfly fauna is closer to the Holarctic-tudral fauna than the relationships of the mayfly fauna elements inside Europe. Consequently, after glaciation the central European lowlands, the North Sea and the Baltic Sea became very quickly a barrier to distribution. This is demonstrated on family, genus and species level.

The present aquatic fauna of Scandinavia or better Fennoscandia, which means Norway, Sweden and Finland, was decisively influenced by the last ice age, called Pleistocene (Fig. 1). The ice age left even more definitive traces in Europe than in North America, because the mountain ranges in North America run in a north-south direction and in Europe they run east-west. Therefore, in North America flora and fauna could relatively easily retreat to the south and then return, while in Europe they were caught in between the main glaciers from the Alps.

During the maximal freezing the space between the two ice shields was only about 450 km as shown in Fig. 2 (KAHLKE, 1981). As a result most of the tertiary species in Europe died out, while they survived in North America. Therefore, in North America there are comparatively more genera, approximately four times the number of species as in Europe.

Without this knowledge it is not possible to understand the current situation of the European and Fennoscandian mayfly fauna. The number of species which died out during the ice age was quite large. Also because of the fact that the Fennoscandian ice shield had an enormous size and there had been three thrusts (in The Alps and in North America even four). The three Scandinavian glacial stages were named after the rivers they finally reached: Elster, Saale, Weichsel (Fig. 3).

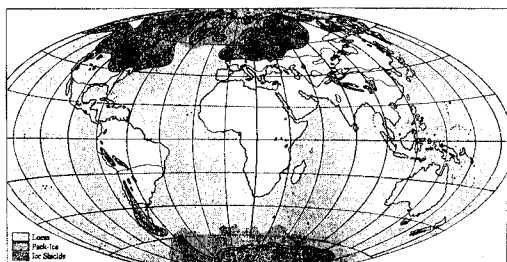


Fig. 1. Worldwide glaciation during the Pleistocene (according to KAHLKE, 1981).



Fig. 2. Glaciation in Europe (according to KAHLKE, 1981).

Table 1. Family and genus group taxa in Fennoscandia. Systematic mostly according to HUBBARD, 1990; Siphonuroidea according to KLUGE *et al.*, 1995. Abbreviations see text.

Family and genus group taxa in Fennoscandia	not present:	present:	not present:
Siphonuroidea:	not present:	Leptophlebiidae:	not present:
Siphonuridae		Leptophlebiidae	<i>Choroterpes</i> (med.-exp.)
<i>Siphonurus</i>		Atalophlebiinae	<i>Thraulus</i> (med.-exp.)
<i>Parameletus</i>		Leptophlebiinae	<i>Calliarctus</i> (atl.-med.)
Ameletidae		<i>Habrophlebia</i>	<i>Habroleptoidea</i> (alp.-exp., med.)
<i>Ameletus</i>	<i>Metreletus</i> (ponto-med.)	<i>Leptophlebia</i>	
Metretopodidae		<i>Paraleptophlebia</i>	
<i>Metretopus</i>	Ametropodidae (east. cont.-mer.)	Ephemeroidea:	Behmingiidae (east. cont.-mer.)
Baetoidea:		Ephemeridae	Palingeniidae (east. cont.-mer.)
Baetidae	<i>Baetopus</i> (east. cont.-mer.)	<i>Ephemera</i>	Polymitryidae (east. cont.)
<i>Acentrella</i>		Ephemeroidea:	Potamanthidae (palaeart.-mer.)
<i>Baetis</i>		Ephemerellidae	
<i>Centropitium</i>		<i>Ephemera</i>	
<i>Cloeon</i>	<i>Pseudocentropitiloides</i> (east. cont.-mer.)	Ephemeroidea:	<i>Drunella</i> (med., pont.)
<i>Procloeon</i>	<i>Pseudocentropitium</i> (med., east. cont.-mer.)	Ephemerellidae	<i>Torteya</i> (alp.-exp.)
Heptagenioidea:		<i>Ephemera</i>	
Arthropleidae	Oligoneuridae	<i>Serratella</i>	
<i>Arthroplea</i>	<i>Isonychinae</i> (east. cont.-mer.)	Timpanogae	
Heptageniidae	<i>Oligoneurinae</i> (med.-exp.)	<i>Eurylophella</i>	
	<i>Afronurus</i> (med.)	Caenoidea:	Neoephemeridae (east. cont.-mer.)
	<i>Cinygma</i> (circumtundral)	Caenidae	
	<i>Ecdyonurus</i> (alp.-exp.)	<i>Brachycercus</i>	
	<i>Electrogena</i> (alp.-exp., pont.-med.)	(east. cont.-mer.)	
	<i>Epeorus</i> (alp.-exp.)	<i>Caenis</i>	
<i>Heptagenia</i>	<i>Iron</i> (pont.-med., cauc.)		
<i>Nixe</i>	<i>Rhithrogena</i> (alp., pont.-med.)		
			Prosopistomatidae (east. cont.-mer.)

In discussing the present Fennoscandian mayfly fauna one must first mention the taxa which are not present in Fennoscandia, but occur in continental Europe (Table 1).

From the 18 European families 8 are absent and 2 other families are scarce. One of these (Polymitarciidae) just reached the border of south-eastern Fennoscandia and the other on (Prosopistomatidae) was found there only once, many years ago (ALM, 1918). The completely missing families show mostly a typical continental-meridional distribution in Europe or Eurasia.

As is to be expected most of the continental-meridional or mediterranean taxa are missing. But surprisingly, almost all of the taxa of alpine origin are missing, too.

As mentioned before, during the maximal glaciation the glaciers from Fennoscandia and from the Alps had approached up to 450 km. Because of the fact that the Fennoscandian and the Alpine fauna had been pushed towards each other by the glaciers moving, an exchange (or mixing) of the tundra and alpine fauna should have resulted. But exactly that did not happen, as demonstrated by the total absence of these typical, large alpine genera like *Ecdyonurus* and *Rhithrogena*.

This demonstrated that the North Sea, the lowlands and the Baltic Sea have proved themselves effective barriers to the migration of alpine mayflies. Compared with this, a few species of alpine origin or continental-merid-

Table 2. Alpine and transcontinental distributed species occurring in British Islands, but not present in Fennoscandia.

<u>alpine</u>	<u>transcontinental-meridional</u>
Heptageniidae: <i>Rhithrogena</i> <i>germanica</i> <i>semicolorata</i>	Baetidae: <i>Pseudocentropilum</i> <i>pennulatum</i>
<i>Electrogena</i> <i>lateralis</i>	Heptageniidae: <i>Heptagenia</i> <i>longicauda</i>
Ephemerellidae: <i>Torleya</i> <i>major</i>	Ephemeridae: <i>Ephemera</i> <i>lineata</i>
	Potamanthidae: <i>Potamanthus</i> <i>luteus</i>

ional distribution nevertheless occur in the British Islands (Table 2).

The species were able to reach Great Britain, because at the end of the last glacial stage the River Thames had been a tributary of the River Rhine (Fig. 4).

Table 3 is compiled out of old and recent authors, especially BAGGE, 1965; BENGTTSSON,

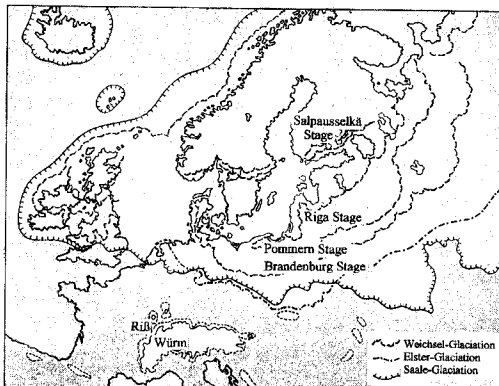


Fig. 3. Glacial stages in Europe (according to KAHLKE, 1981).

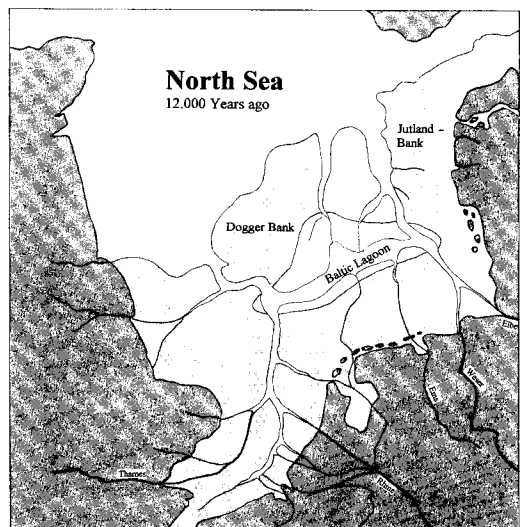


Fig. 4. Post-glacial coastline situation of the southern North Sea.

1909 ff*; BREKKE, 1940; ENGLOM *et al.*, 1993; HULDEN, 1984; HURU, 1984; ITÄMIS *et al.*, 1979; KLUGE, 1987; SAARISTO *et al.*, 1980 ff*; SAVOLAINEN *et al.*, 1980 ff*; SÖDERSTRÖM *et al.*, 1986; SOLDAN, 1981; TIENSUU, 1935 ff*; TSHERNOVA, 1941; ULMER, 1943 and for the holarctic distributed species BERNER, 1959; FLOWERS, 1986; MCCAFFERTY, 1985 and

MCCAFFERTY *et al.*, 1994 (*ff: means this and following published papers of the same author, which are cited in References).

Table 3 shows the mayfly species occurring in Fennoscandia. All species are immigrants, because during the ice age Fennoscandia was completely glaciated. Only a few summits were free from ice, but no water insect could live or

Table 3. Species occurring in Fennoscandia (N = Norway, S = Sweden, F = Finland) and arctic Russia (R).

Siphonuridae:					<i>fuscogrisea</i>	N	S	F	R	east. cont.-boreal	
<i>Siphonurus</i>					<i>orbiticola</i>		S	F	R	palaeart.-tundral	
<i>aestivalis</i>						N	S	F	R	boreal	
<i>alternatus</i>						N	S	F	R	holarct.-bor.	
<i>lacustris</i>						N	S	F	R	palaeart.	
<i>Parameletus</i>					<i>Nixe</i>						
<i>chelifer</i>						N	S	F	R	tundral	
<i>minor</i>					<i>joernensis</i>						
Ameletidae:					Leptophlebiidae:						
<i>Ameletus</i>					<i>Habrophlebia</i>						
<i>inopinatus</i>					<i>lauta</i>			F	R	east. cont.-boreal	
					<i>Leptophlebia</i>						
					<i>marginata</i>	N	S	F	R	palaeart.	
					<i>vespertina</i>	N	S	F	R	palaeart.	
Metretopodidae:					<i>Paraleptophlebia</i>						
<i>Metretopus</i>					<i>cincta</i>	N	S	F	R	transcont.	
<i>alter</i>					<i>strandii</i>	N	S	F	R	tundral	
<i>borealis</i>					<i>submarginata</i>	N	S	F	R	transcont.-boreal	
					<i>wernerii</i>	N	S	F		east. cont.-boreal	
Baetidae:					Ephemeridae:						
<i>Acentrella</i>					<i>Ephemer</i>						
<i>lapponica</i>					<i>danica</i>	N	S	F	R	transcont.	
<i>Baetis</i>					<i>vulgata</i>	N	S	F	R	transcont.	
<i>buceratus</i>						S				med.-exp.	
<i>digitatus</i>						S	F			east. cont.-mer.	
<i>fuscatus</i>						N	S	F	R	palaeart.	
<i>macani</i>						N	S	F		tundral	
<i>muticus</i>						N	S	F	R	palaeart.	
<i>niger</i>						N	S	F	R	palaeart.	
<i>rhodani</i>						N	S	F	R	palaeart.	
<i>scambus</i>						N	S	F	R		
<i>subalpinus</i>						N	S	F	R	tundral	
<i>vernus</i>						N	S	F	R	transcont.	
<i>Baetopus</i>											
<i>tenellus</i>								F		east. cont.-mer.	
<i>Centroptilum</i>											
<i>luteolum</i>						N	S	F	R	palaeart.	
<i>Cloeon</i>											
<i>dipterum</i>						N	S	F	R	holarct.	
<i>simile</i>						N	S	F	R	palaeart.	
<i>Proctoeon</i>											
<i>bifidum</i>						N	S	F	R	transcont.	
Arthropleidae:					Ephemerellidae:						
<i>Arthroplea</i>					<i>Ephemerella</i>						
<i>congener</i>					<i>aurivillii</i>	N	S	F	R	circumtundral	
					<i>mucronata</i>	N	S	F	R	palaeart.-boreal	
					<i>(Eurylophella</i>						
					<i>karelica</i>			R		boreal?)	
					<i>Serratella</i>						
					<i>ignita</i>	N	S	F	R	palaeart.	
Heptageniidae:					Caenidae:						
<i>(Cinygma lyriformis)</i>					<i>Brachycercus</i>						
<i>Heptagenica</i>					<i>harrisella</i>	N	S	F		east. cont.-boreal	
<i>dalecarlica</i>					<i>Caenis</i>						
					<i>horaria</i>	N	S	F	R	palaeart.	
					<i>lactea</i>	N	S	F	R	disj. boreo-montan	
					<i>luctuosa</i>	N	S	F		med.-exp.	
					<i>macrura</i>	N	S			transcont.	
					<i>rivulorum</i>	N	S	F			
					<i>robusta</i>		S	F	R	palaeart.	
Prosopistomatidae:					Prosopistomatidae:						
					<i>Prosopistoma</i>						
					<i>foliaceum</i>		S			east. cont.-mer.	

even survive on these «Nunatakker» (an Eskimo word from Greenland, where Nunatakkers still exist).

To characterize Fennoscandian mayfly fauna on species, you also need to explain first that most of the European species are missing in Fennoscandia. The present Fennoscandian mayfly fauna can be divided into three groups: The first group includes species which are widely spread throughout Europe. Their origin is not clearly recognizable (because mostly transcontinental or palaearctic or holarctic-meridional distributed). This is the biggest group of species.

To the second group belong species with boreal origin and a boreo-mountainous disjunction. Such a disjunction is clearly pronounced only for *Ameletus inopinatus* and less clearly for *Arthroplea congener*, *Ephemerella mucronata*, *Caenis lactea* and perhaps *Eurylophella karelica*. The third and most interesting group includes species with a strongly tundra distribution. In Europe these species appear only in Fennoscandia and/or in arctic Russia:

<i>Acentrella lapponica</i>	<i>Metretopus alter</i>
<i>Baetis macani</i>	<i>Heptagenia dalecarlica</i>
<i>Baetis subalpinus</i>	<i>Heptagenia orbiticola</i>
<i>Parameletus chelifera</i>	<i>Nixe joernensis</i>
<i>Parameletus minor</i>	<i>Paraleptophlebia strandii</i>
<i>Metretopus borealis</i>	<i>Ephemerella aurivillii</i>
	<i>Cinygma lyriformis</i>

Consequently the fennoscandian mayfly fauna is not only an impoverished fauna of continental Europe, but it includes also its own, particular tundra element with (an actual) evidence of 12 species. It would be interesting to find out if *Cinygma lyriformis* on its way from the Siberian glacial refuge to the west came to a standstill in the arctic Ural mountains and Petschora river basin or if it reached Fennoscandia.

REFERENCES

- ALM, G. 1918. Till k annedomen om *Prosopistoma foliaceum* FOURCR. Ent. Tidskr., Jg. 1918: 54-59.
- BAGGE, P. 1965. Observations on some mayfly and stonefly nymphs (Ephemeroptera and Plecoptera) in Utsjoki, Finnish Lapland. Ann. Ent. Fenn. 31(2): 102-108.
- BENGTSSON, S. 1909. Beitr age zur Kenntnis der pal arktischen Ephemeriden. Lunds Univ. Arsskr., N.F., Afd. 25 (4): 1-19.
- BENGTSSON, S. 1912. Neue Ephemeriden aus Schweden. Ent. Tidskr. 33: 107-117.
- BENGTSSON, S. 1912. An analysis of the Scandinavian species of Ephemerida described by older authors. Ark. Zool. 7(36): 1-21.
- BENGTSSON, S. 1917. Weitere Beitr age zur Kenntnis der nordischen Eintagsfliegen. Ent. Tidskr., 38: 174-194.
- BENGTSSON, S. 1930. Beitrag zur Kenntnis der Ephemeropteren des n rdlichen Norwegen. Troms  Mus. Arsh., Naturhist. Avd. Nr. 1, 51(2): 3-19.
- BENGTSSON, S. 1930. Kritische Bemerkungen  ber einige nordische Ephemeropteren, nebst Beschreibung neuer Larven. Lunds Univ. Arsskr., N.F. Avd. 2, 26(3): 3-27.
- BERNER, L. 1959. Newfoundland Mayflies (Ephemeroptera). Opusc. Ent. 24(3): 212-214.
- BREKKE, R. 1940. The Norwegian Mayflies. Norsk ent. Tidskr. 5: 55-73.
- ENGBLOM, E., LINGDELL, P.E., NILSSON, A.N. & SAVOLAINEN, E. 1993. The genus *Metretopus* (Ephemeroptera, Siphonuridae) in Fennoscandia - identification, faunistics and natural history. Entomol. Fennica 4: 213-222.
- FLOWERS, R.W. 1986. Holarctic distribution of three taxa of Heptageniidae (Ephemeroptera). Ent. News 97(5): 193-197.
- HUBBARD, M.D. 1990. Mayflies of the World. A Catalog of the Family and Genus Group Taxa; Flora & Fauna Handbook Nr. 8, Gainesville.
- HULDEN, L. 1984. A Checklist of the Finnish Insects Small Orders. Not. Ent. 64: 1-29.
- HURU, H. 1984. *Habrophlebia* (Eph., Leptophlebiidae) new to Norway. Fauna norv., Ser. B. 31: 107-108.
- IT MIES, J., KUUSILA, K. & SAVOLAINEN, E. 1979. *Brachycercus harrisella* (Ephemeroptera, Caenidae) found in Finland. Notulae Ent. 59: 89-90.
- KAHLKE, H.D. 1981. Das Eiszeitalter, 192 S., Urania Verlag Leipzig, Jena, Berlin.
- KLUGE, N.J. 1987. Podenki roda *Heptagenia* WALSH (Ephemeroptera, Heptageniidae) fauny SSSR. Ent. Obozr. 66: 302-320.
- KLUGE, N.J., STUEDEMANN, D., LANDOLT, P. & GONSER, T. 1995. A reclassification of Siphonuroidea (Ephemeroptera). Mitt. schweiz. Ent. Ges. 68: 103-132.
- MCCAFFERTY, W.P. 1985. The Ephemeroptera of Alaska. Proc. Ent. Soc. Wash. 87: 381-386.
- MCCAFFERTY, W.P., WIGLE, M.J. & WALTZ, R.D. 1994. Systematics and Biology of *Acentrella turbida* (MCDUNNOUGH) (Ephemeroptera: Baetidae). Pan-Pacific Ent. 70(4): 301-308.
- SAARISTO, M.I., ANDERS, N.N. & SAVOLAINEN, E. 1993. *Heptagenia orbiticola* KLUGE, a mayfly species new to Europe (Ephemeroptera, Heptageniidae). Ent. Tidskr. 114: 51-54.
- SAARISTO, M.I. & SAVOLAINEN, E. 1980. Suomen p iv nkorennot - Finlands dagsl ndor (Ephemeroptera). Notul. entomol. 60: 181-186.
- SAARISTO, M.I. & SAVOLAINEN, E. 1980. On the identity of *Heptagenia sulphurea* (M LLER, 1776) and *H. dalecarlica* BENGTSSON, 1912 (Ephemeroptera). Notulae entomol. 60: 187-193.
- SAVOLAINEN, E. 1980. First records of *Paraleptophlebia submarginata* (Ephemeroptera, Leptophlebiidae) within the present boundaries of Finland. Notulae entomol. 60: 105-106.

- SAVOLAINEN, E. & SAARISTO, M.I. 1981. Distribution of mayflies (Ephemeroptera) in the biological province of Kuusamo (Ks), Finland. *Notulae entomol.* 61: 23-29.
- SÖDERSTRÖM, O. & NILSSON, J. 1986. Redescription of *Parameletus chelifera* BENGSSON and *P. minor* (BENGSSON), with keys to nymphal and adult stages of the Fennoscandian species of Siphonuridae (Ephemeroptera). *Ent. scand.* 17: 107-117.
- SOLDAN, T. 1981. The mayflies (Ephemeroptera) of Utsjoki northernmost Finland. *Rep. Kevo Subarctic Res. Stat.* 17: 81-85.
- TIENSUU, L. 1935. On the Ephemeroptera-Fauna of Laatokan Karjala. *Suom. Hyönt. Aikak.* 1: 1-21.
- TIENSUU, L. 1937. Some records of Mayflies from Northern Norway. *Suom. Hyönt. Aikak.* 3: 44-45.
- TIENSUU, L. 1939. A survey of the distribution of Mayflies in Finland. *Suom. Hyönt. Aikak.* 5: 97-124.
- TSHERNOVA, O.A. 1941. Fauna podenok ewropejskogo sewera SSSR. *Zool. J.* 20: 213-236.
- ULMER, G. 1943. Die von Prof. A. THIENEMANN in der Umgebung von Absiko (Lappland) gesammelten Eintagsfliegen und ihre Larven. *Arch. Hydrobiol.* 40: 329-361, 5 Taf.