

Geographical distribution of the small mussels (Sphaeriidae) in North Europe (Denmark, Faroes, Finland, Iceland, Norway and Sweden)

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Distribution maps of 23 species of Sphaeriidae occurring in North Europe are presented, based on more than 11 000 revised samples from ten zoological museums or other institutions (Bergen, Copenhagen, Göteborg, Helsinki, Joensuu, Lund, Oslo, Stockholm, Tromsø, Trondheim). Denmark has 17 sphaeriid species, the Faroes 9, Finland 21, Iceland 11, Norway 20 and Sweden 22. Moreover, one subfossil species (*Pisidium stewarti* Preston = *P. vincentianum* Woodward) is known from Denmark and Sweden. Of the 22 species found today, 15 are holarctic (4 circumpolaric included) and 7 palearctic. Iceland is the westernmost outpost of 3 palearctic species viz., *Pisidium hibernicum* Westerlund, *P. personatum* Malm, *P. pulchellum* Jenyns.

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1. Introduction

North Europe (Denmark, the Faroes, Finland, Iceland, Norway, Sweden) is, notwithstanding its vastness, faunistically one of the best explored regions for Sphaeriidae. For more than a century, many field workers, either within the framework of their investigations or incidentally, have sampled these small freshwater molluscs. A great deal of the material has eventually been lodged in public collections for future study. Several North European taxonomists, limnologists and ecologists have published papers on Sphaeriidae, but our knowledge of their geographical distribution has been stilled, mainly due to identification problems and to a consequent lack of homogeneity in taxonomy and nomenclature.

A turning point, in this respect, came some years ago when Jan and Karen Anna Økland, within the scope of their limnological research, sampled Sphaeriidae in hundreds of water bodies, mainly

lakes, throughout Norway. One of the results of this project was distributional maps of the twenty species of small bivalves living in Norway (Økland & Kuiper 1980, 1982).

During the Ninth International Malacological Congress, held in Edinburgh in 1986, four malacologists from North Europe, viz. J. Knudsen, Copenhagen, K. A. Økland, Oslo, T. von Proschwitz, Göteborg and I. Valovirta, Helsinki, decided to collaborate on a mapping project covering all of northern Europe west of the Soviet Union. Of course, from a zoogeographical point of view, it would have been preferable to include the northern part of Russia, but time is not yet ripe for this, at least not taxonomically. J. G. J. Kuiper, Paris, who since 1962 had been working on sphaeriid public collections in Denmark, Norway and Sweden, and partially also in Finland, was invited to participate. Later, L. Koli also joined the project.

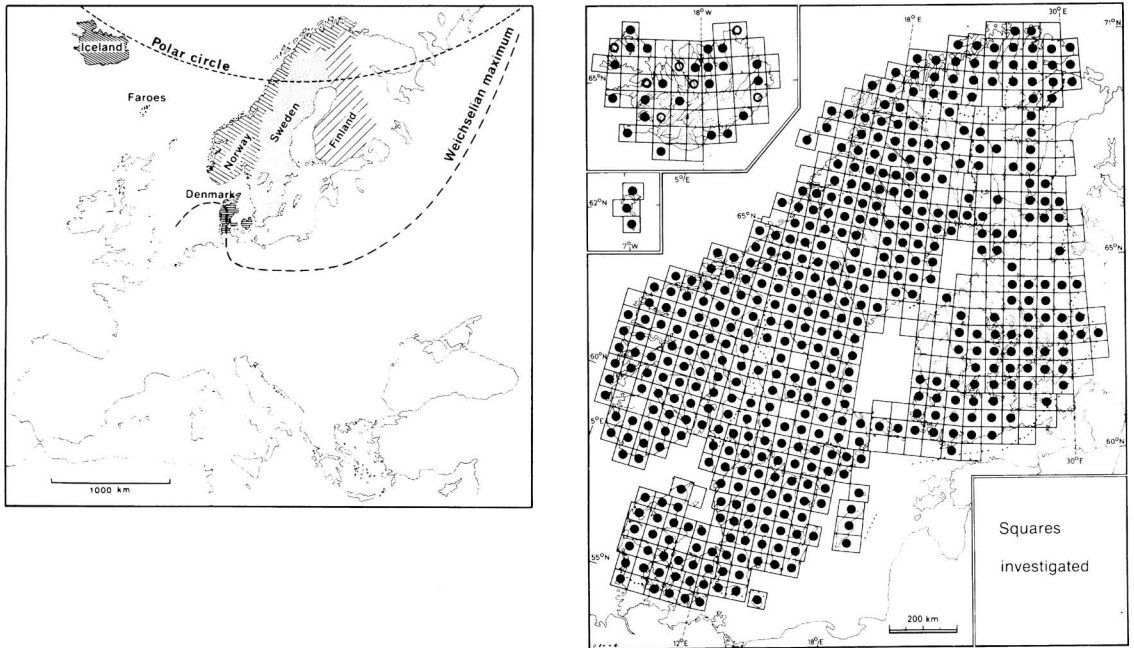


Fig. 1. North Europe and the 50 km square grid (646 squares).

- — squares where one or more species of small mussels have been found (investigated squares).
- — squares where the only records are those listed by Mandahl-Barth (1938) in Iceland.

2. Material and methods

The mapping project is based mainly on information taken from collection labels. In this paper no literature is cited unless documentary evidence is available. This rigorous rule was necessary in order to guarantee some homogeneity in taxonomy and nomenclature. In this regard, especially Kuiper has revised or identified the complete museum collections of Bergen, Copenhagen, Göteborg, Lund, Oslo, Stockholm, Tromsø and Trondheim and partially also that of Helsinki. The Finnish records of Sphaeriidae have mainly been checked by L. Koli.

A total of 23 species of Sphaeriidae have been identified from North Europe (Table 1, p. 99). The new E.I.S. (European Invertebrate Survey) map with the 50 km grid (Økland & Økland 1986) has been used. This grid has proved to be useful for zoogeographical studies on a continental scale. North Europe comprises a total of 646 squares (Fig. 1). At present, no sphaerid samples have been reported from 153 squares (24%). The largest numbers of blank squares are in Iceland and in Central Finland.

The absence of records from most of these squares can probably be attributed to a lack of investigations, or to unfavorable ecological conditions. Denmark, Norway and Sweden together have a coverage of 90% (42 blank squares). It goes without saying that the total number of records (at least 11 000)

is much more than the total number of dots on the maps, and often numerous records exist within the limits of one square.

Information on elevation above sea level in North Europe is from Økland & Kuiper (1980) and Økland (in press). The data are from the central high mountain areas in Norway.

Lists with selected localities chosen to represent each specific square are being kept by T. von Proschwitz for Sweden, and by K. A. Økland for Norway, Iceland, the Faroes and Denmark (the mapping of Denmark is performed by J. G. J. Kuiper for *Pisidium* and by J. Knudsen for *Sphaerium* and *Musculium*).

The samples on which the maps are based are preserved in the following public collections in North Europe:

- Bg — Bergen, Zoologisk Museum, Universitetet i Bergen
- Kh — Copenhagen, Universitetets Zoologiske Museum
- Gb — Göteborg, Naturhistoriska Museet
- He — Helsinki, Zoological Museum of the University
- Jn — Joensuu, University of Joensuu, Department of Biology
- Lu — Lund, Zoologiska Museet, Lunds Universitet
- Os — Oslo, Zoologisk Museum, Universitetet i Oslo
- St — Stockholm, Naturhistoriska Riksmuseet
- Tr — Trondheim, Det Kongelige Norske Videnskabers Selskab, Museet
- Tø — Tromsø Museum, Universitetet i Tromsø

A small number of samples collected in the mapped area by non-Scandinavian malacologists are lodged in the following museums:

- RML — Leiden, The Netherlands, Rijksmuseum van Natuurlijke Historie
 SMF — Frankfurt/Main, Federal Republic of Germany, Senckenberg Museum
 ZIW — Vienna, Austria, 1. Zoologisches Institut der Universität Wien
 ZMA/K — Amsterdam, The Netherlands, Instituut voor Taxonomische Zoölogie & Zoölogisch Museum, Collectie Kuiper
 ZMM — Ann Arbor, U.S.A., Museum of Zoology, The University of Michigan
 HZ — private collection of Dr. Werner Hinz, Duisburg, Federal Republic of Germany

The realisation of this mapping project has been made possible by the contributions of the total of about 300 field workers in North Europe, since 1860. A list of these persons, as well as of working groups, is deposited at the Instituut voor Taxonomische Zoölogie & Zoölogisch Museum, Collectie Kuiper, Amsterdam, The Netherlands.

A complete list of all the Norwegian records of Sphaeriidae, as well as a list of the field workers, is deposited at the Biological Institute, Division of Limnology, P.O.Box 1027 Blindern, N-0315 Oslo 3, Norway, to be published in the near future.

3. Comments on the material

The question has arisen as to whether the *Pisidia* collected by Hans Schlesch (1891–1962) in Iceland should be mapped or not. As a pharmacist, Schlesch practised for some years in East Iceland. He took the opportunity to collect land and freshwater molluscs. He submitted the *Pisidia* for identification to A. W. Stelfox, Dublin, and published the faunistic results (Schlesch 1921), listing as many as eight species of *Pisidium*, several of which he considered new to Iceland. In the next number of the *Journal of Conchology* appeared the text of a letter to the editor, signed by the three well known specialists in this matter, A. W. Stelfox, R. A. Phillips and Charles Oldham. The following is a quote from this letter: "It is true that the specimens upon which the records are founded have passed through our hands, but the appearance¹ of

some of them at any rate did not suggest shells from a northern latitude, and it occurs to us that Herr Schlesch may have sent us shells from some continental locality under the impression that they were really the ones he had collected in East Iceland. We wish to make it clear, therefore, that except as regards *P. casertanum*, which is a well-known Icelandic species, Herr Schlesch is solely responsible for the statement that these *Pisidia* occur in the localities cited in his paper."

It is probable that this letter would not have been written if Stelfox, Phillips and Oldham had previously examined the samples collected earlier in Iceland by O. Davidsson, A. Feddersen, A. C. Johansen, B. Saemundsson, F. H. Sikes, J. Steenstrup and T. Thoroddsen, and preserved in the museums of Copenhagen and Stockholm, and that Mandahl-Barth (1938) would have modified his text on this subject accordingly.

Based on the current revision of these samples, it may be concluded that:

- 1) eight species of *Pisidium* had already been collected in Iceland before Schlesch's stay there;
- 2) the appearance of these specimens is not different from those collected later by Schlesch;
- 3) there is, conchologically, no reason to presume a continental origin of Schlesch's samples.

Therefore, Stelfox's scientific objections do not stand.

Kuiper has examined Schlesch's entire Icelandic collection of *Pisidium* preserved in the museum in Stockholm, the samples contained in Stelfox's collection in the Museum of Zoology, Ann Arbor, Michigan, U.S.A., and the series of *Pisidium* collected in Iceland by P. Einarsson, B. Fristrup, J. H. Hallgrímsson, P. Hólm, I. J. Holopainen, S. Jónhson, N. McMillan, J. B. Sigurdsson, F. Starmühlner and F. Sveinbjörnsson. The revision of these materials yielded no less than eleven species of *Pisidium* in Iceland, two of them (*P. amnicum* and *P. henslowanum*) having been recorded, until now, by Schlesch only. Therefore Schlesch's Icelandic records are included in the distributional maps.

In Schlesch's collection of Danish Sphaeriidae, there are about 150 records, a great number of which have been confirmed by later records from other malacologists. For this reason we do not adhere to Jespersen's (1945:171) categorical rejection of all Schlesch's records.

¹Replying to Kuiper's (1988a) paper on this matter, Dr. Nora McMillan, who knew Stelfox very well, was kind enough as to write a letter to the author explaining that in particular the absence of well-marked "winter rings" was meant here, indicating cessation of growth in the cold winter and a sudden outburst of growth in the summer, a phenomenon in which Stelfox has always been interested.

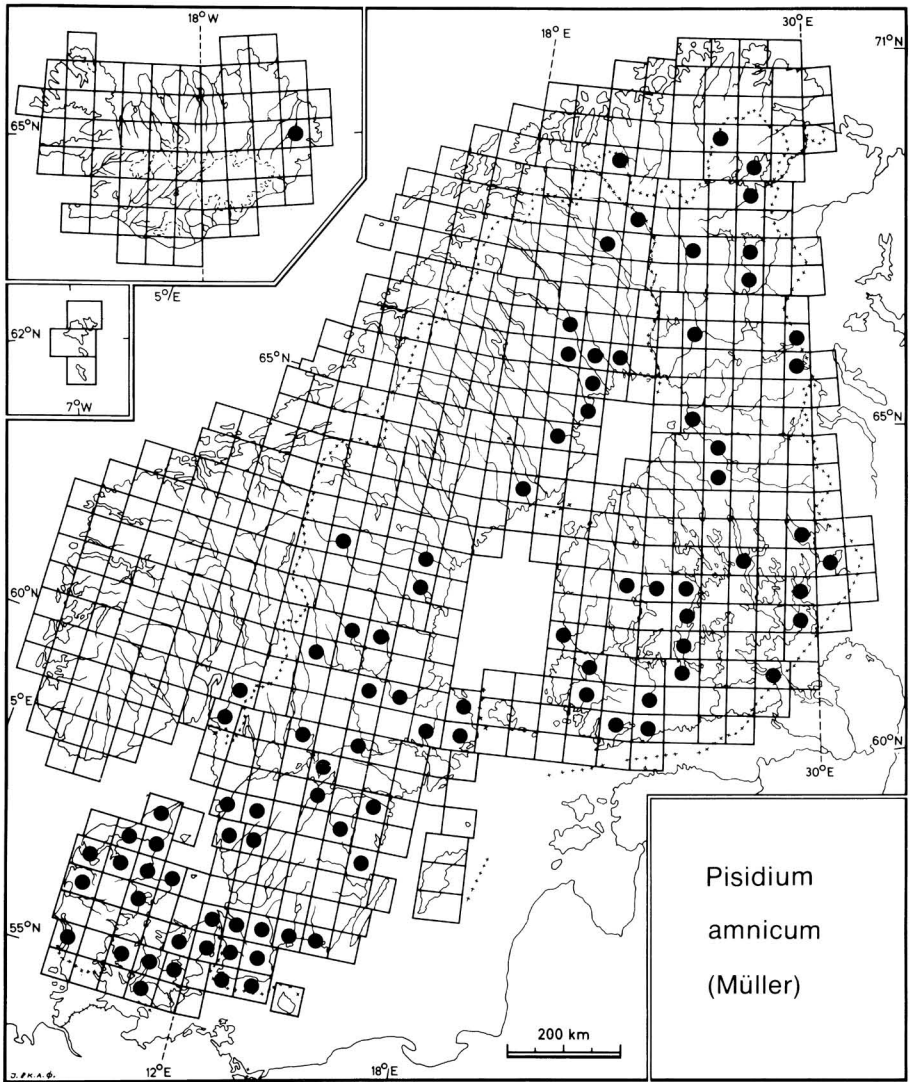


Fig. 2. Distribution of *Pisidium amnicum* in North Europe.

4. Results

Pisidium amnicum (Müller, 1774)

This species is recorded in 91 squares (Fig. 2). General distribution: palearctic and a small part of northeastern America. In all of Europe, but sporadic in the Mediterranean area. In Iceland just one record, by Schlesch (1921): Fljótssdal in E. Iceland. *P. amnicum* exists far to the north in the Baltic region, but is absent from the western and southern parts of Nor-

way. The species shares this typical pattern of distribution with *P. henslowanum*, *P. moitessierianum* and *P. pseudosphaerium*. Three other species, viz. *P. pulchellum*, *Sphaerium corneum* and *Musculium lacustre*, have the same pattern, but with a few records further west. *P. amnicum* inhabits streams and the shallow regions of lowland rivers; in Finland it occurs in lakes too. In Central Europe it rarely occurs in habitats above 500 m elevation, hence the absence of this species from the high mountains of the Scandinavian Peninsula.

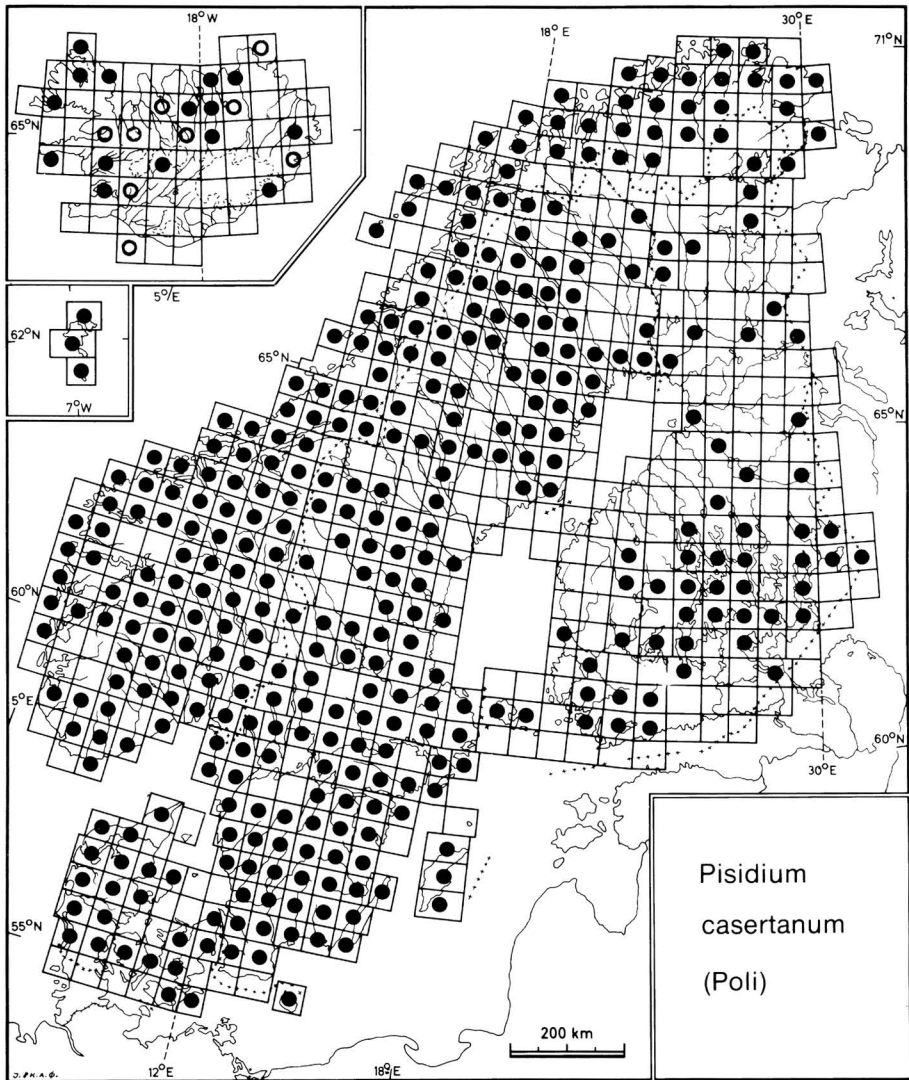


Fig. 3. Distribution of *Pisidium casertanum* in North Europe. ○ — records by Mandahl-Barth (1938) in Iceland.

Pisidium casertanum (Poli, 1791)

The species is recorded in 393 squares (Fig. 3). General distribution: cosmopolitan, but in the tropics in mountains only. This is the most common species in North Europe, found up to 1400 m above sea level. The thick-shelled form (f. *ponderosa* Stelfox) has often been collected in South Sweden, South Finland, and Denmark. *P. casertanum* is the only species of the genus which has been recorded, (Økland & Kuiper 1980) in some strongly acidified lakes. Only a very few specimens could then be found, and the shell was often nearly completely decalcified.

P. casertanum is a polymorphous and, taxonomically, sometimes a puzzling species, especially in the North. Several forms have been published as distinct species, but in most cases they are probably merely ecological forms. Rather frequent in the North is a poorly defined form with a narrow and relatively short hinge. It is common in the Storeskarvatn in Hemsedal, Norway and in many other lakes, and merits further taxonomic study. The form, *globularis* Clessin, is very swollen and in extreme cases the diameter of the shell is equal to its height.

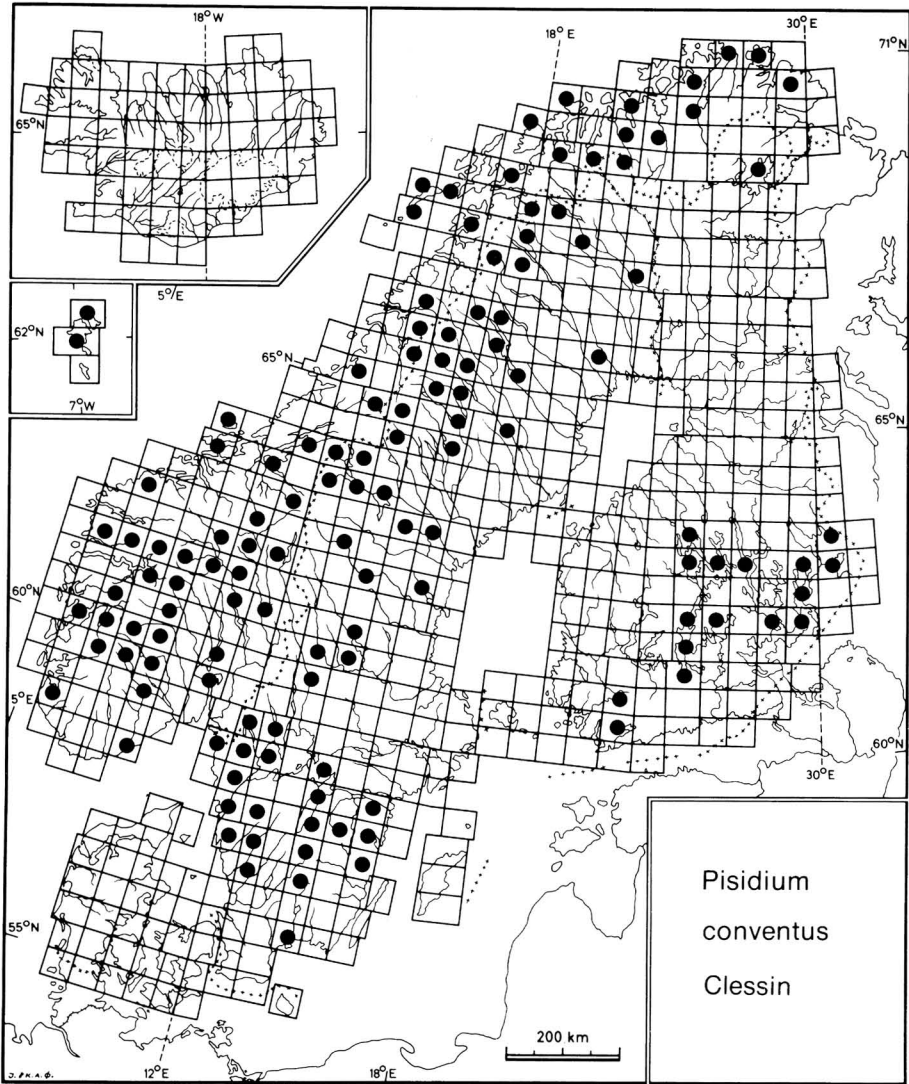


Fig. 4. Distribution of *Pisidium conventus* in North Europe.

Pisidium conventus Clessin, 1877

The species is recorded in 133 squares (Fig. 4). General distribution: holarctic. North Europe is currently the main distributional subarea in Europe. The species occurs in the profundal zone of many deep pre-alpine lakes, as well as in some moraine lakes on the north German and Baltic plains, and in mountain tarns in Scotland, Wales and Ireland (Kuiper 1974b:32, 33), where it has been found at altitudes of from 800 m to 2000 m above sea level. In North Europe the species has been found up to 1373 m. The presence of *P. conventus* in the lake with the highest

elevation in North Europe (1837 m) Gjuvatn, as well as at 1408 m Fantesteinvatn, (Brundin 1956) seems probable, although the samples have not been checked by Kuiper. In North Norway, *P. conventus* also occurs in the littoral zone of lakes, at a depth of 1–1 1/2 m. Odhner (1923:6) assumes that "*P. conventus* is a true arctic species, having its most favorable conditions in N. Norway. In the southern districts it is a relic from the late-glacial epoch which has been able to survive until the present time by finding refuge in the cold regions of the deep lakes." This relic concept is adamantly rejected by L. Koli, who stresses the

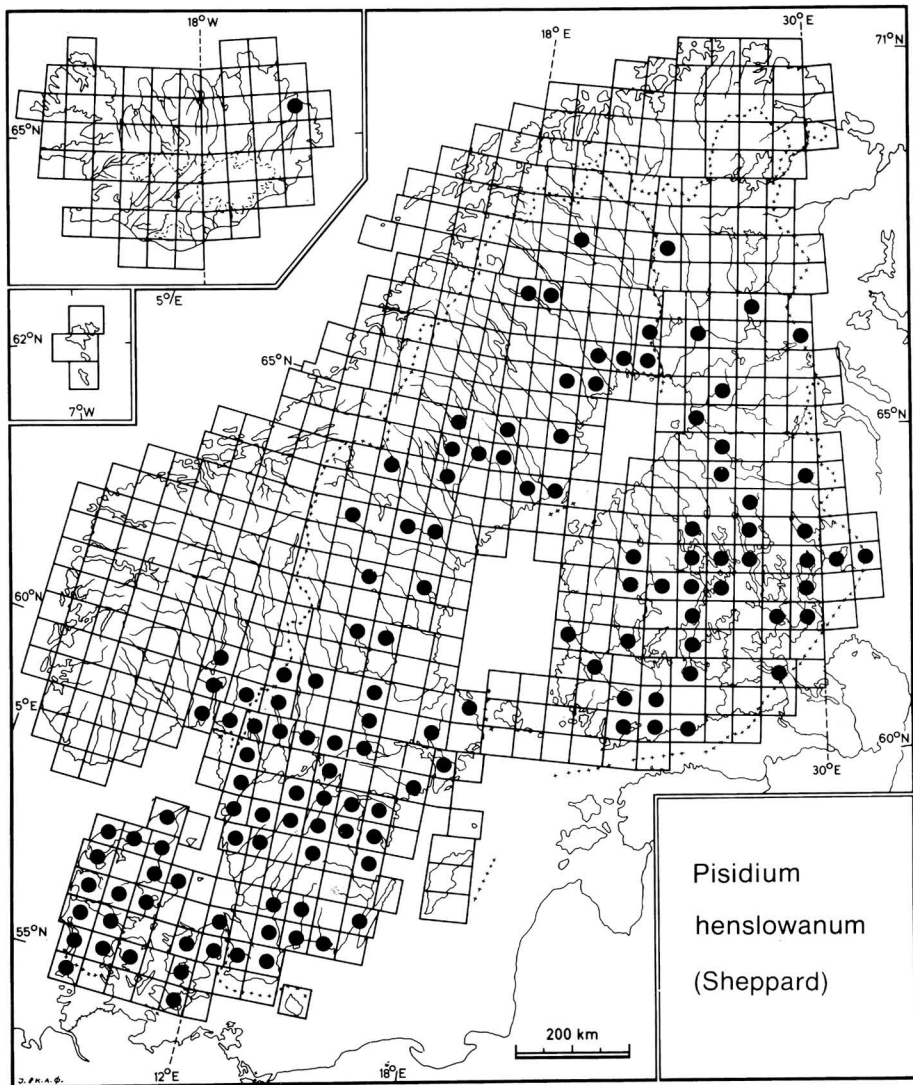


Fig. 5. Distribution of *Pisidium henslowanum* in North Europe.

cold-stenothermic character of *P. conventus*. In this connection, it should be kept in mind that this species is very rare in Pleistocene deposits elsewhere in Europe. Up to now only three fossil records from Western and Central Europe have been published (Kuiper 1974b). Favre (1935:373) points out that *P. conventus* colonized Lake Geneva not earlier than after the retreat of the Rhône Glacier, and that this species, based on many core samples has never lived in the littoral zone of the lake. Consequently, *P. conventus* must have been dispersed to the lake postglacially, undoubtedly by migrating birds. *P. conventus* may have

postglacially immigrated into North Europe from the south, or mainly from the east, like *P. waldeni*, *P. hinzi*, *P. subtilestriatum* and *Sphaerium nitidum*.

Pisidium henslowanum (Sheppard, 1823)

The species is recorded in 131 squares (Fig. 5). General distribution: palearctic as well as a small part of northeast America. The species has often been considered to be a recent immigrant there, but Harris (1973:86), who cites some new records in western

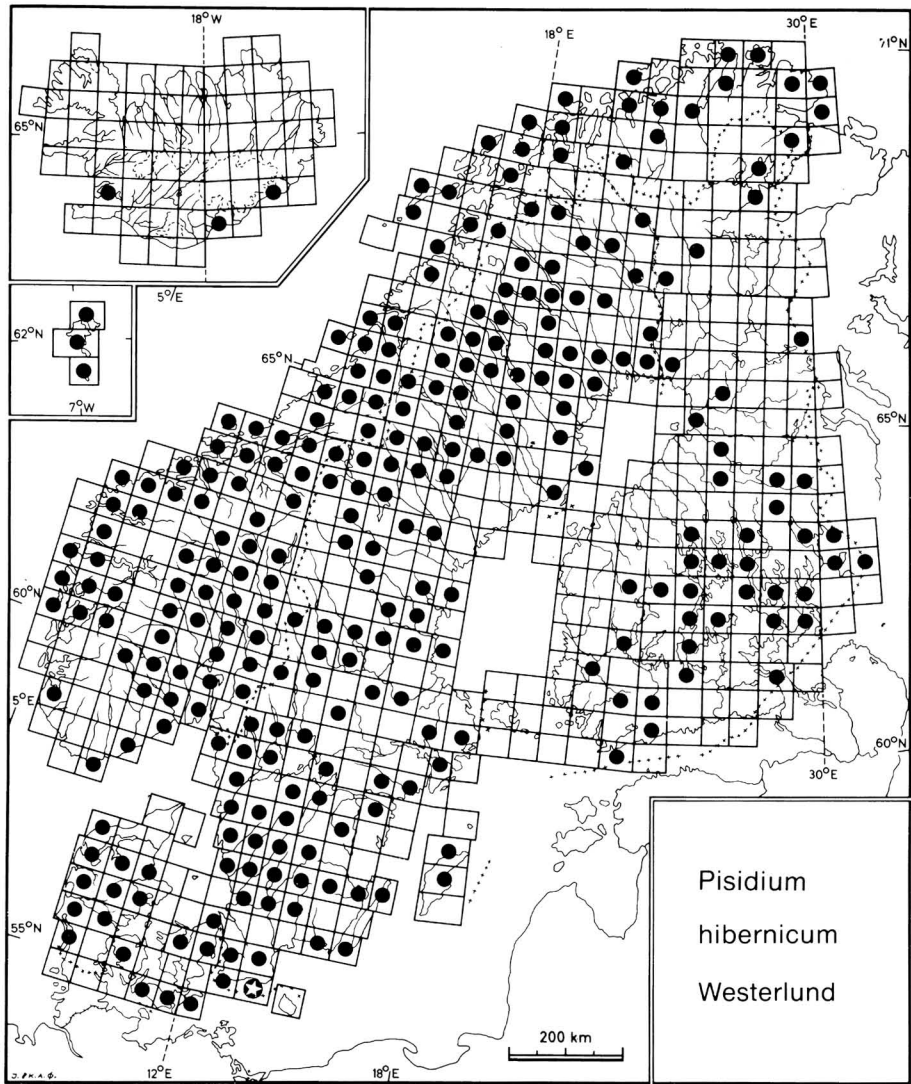


Fig. 6. Distribution of *Pisidium hibernicum* in North Europe. ● — subfossil records only.

and central Canada, draws attention to subfossil records in postglacial alluvial deposits over 7000 years old. The habitat of *P. henslowanum* is about the same as *P. amnicum*, which has a similar distribution in North Europe. A form without an appendiculum on the beaks, f. *inappendiculata* auctorum non Moquin-Tandon (Kuiper 1987b), occurs in populations of the normal form. The inappendiculate form is very common in Jylland where it has the aspect of a geographical subspecies. Many of the samples of *P. henslowanum* collected by Teilmann Friis on the island

of Mors, Denmark, consist entirely of the inappendiculate form. This phenomenon merits further study within the framework of 5 or 10 km grid maps of Denmark.

Pisidium hibernicum Westerlund, 1894

The species is recorded in 281 squares (Fig. 6). General distribution: Palearctic. Very common in North Europe, up to 1300 m above sea level. In the

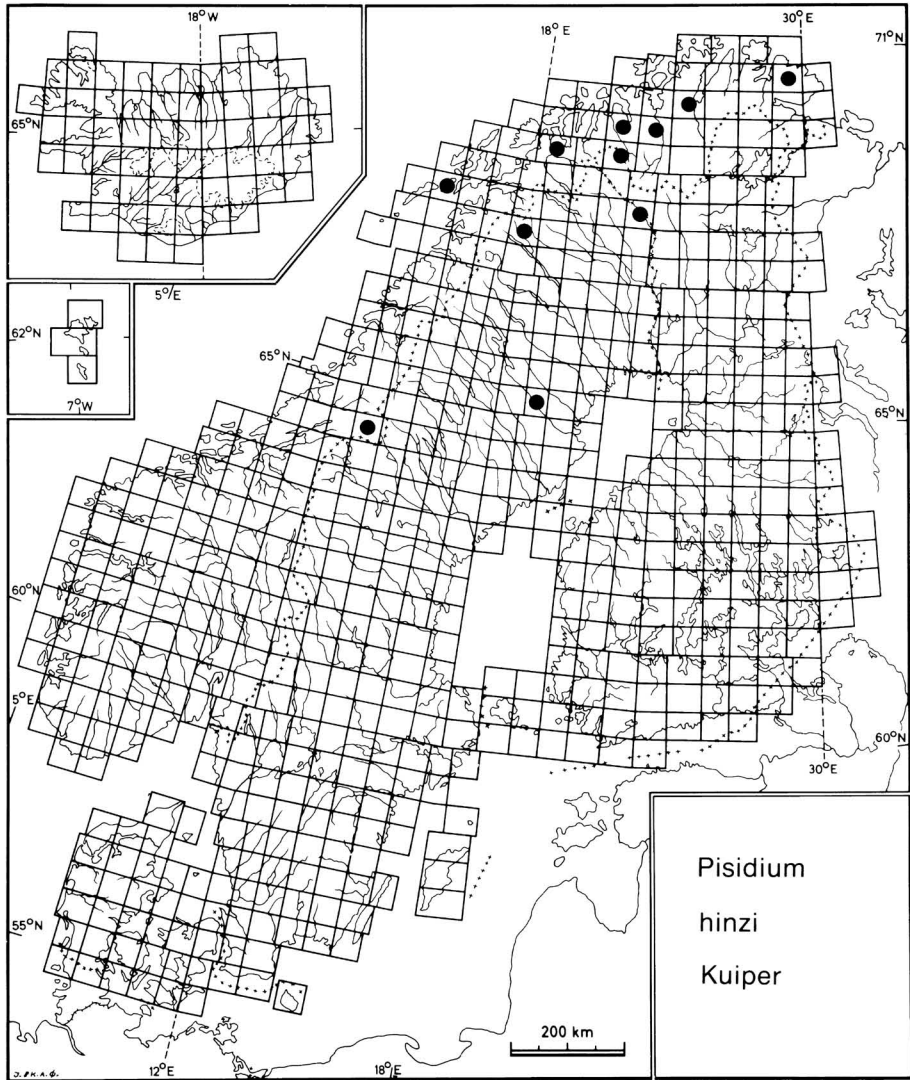


Fig. 7. Distribution of *Pisidium hinzi* in North Europe.

Nearctic a closely allied species occurs, *P. ferrugineum* Prime. Some authors (Herrington 1954:133; 1962, Boettger 1961:242) treated both species as synonyms. Kuiper (1966) pointed out that *P. hibernicum* and *P. ferrugineum* are geographical vicariants and distinct species. The form, *gigas*, with a shell length of 5 mm or more and known from several localities in the Alps and in the Pyrenees, is not known from Scandinavia. Boettger (1961:243) regarded *P. parvulum* Clessin 1873 as a senior synonym of *P. hibernicum* Westerlund 1894. Kuiper (1965), after examination of all series of *P. parvulum* Clessin, labelled by Westerlund, concluded that *P. parvulum* is a

composite species and that this name has to be included in the synonymy of *P. obtusale* (Lamarck).

Pisidium hinzi Kuiper, 1975

The species is recorded in 11 squares (Fig. 7). General distribution: probably holarctic-circumpolar. The Swedish Vega Expedition 1878–1879 collected this species near Port Clarence, Alaska. Like *P. waldeni*, *P. conventus* and *Sphaerium nitidum*, it is a lacustrine, cold-water species. It has been found only twice south of the Arctic Circle in Scandinavia.

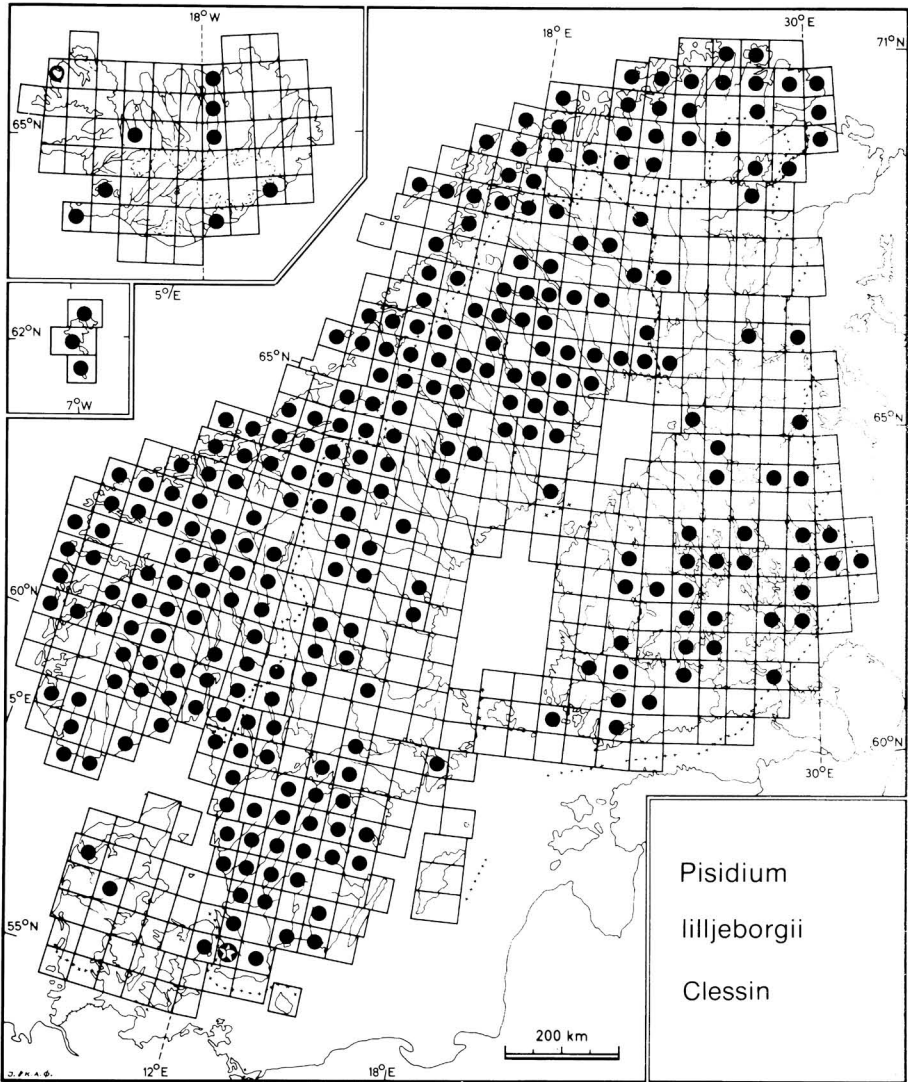


Fig. 8. Distribution of *Pisidium lilljeborgii* in North Europe.

○ — records by Mandahl-Barth (1938) in Iceland; ● — subfossil records only.

Pisidium lilljeborgii Clessin 1886 (in Esmark & Hoyer 1886)

The species is recorded in 285 squares (Fig. 8). General distribution: holarctic, mostly in the littoral zone of lakes. With *P. casertanum*, *P. hibernicum* and *P. obtusale* the commonest species of *Pisidium* in North Europe (Table 1). It is found up to 1230 m above sea level. In Denmark, *P. lilljeborgii* is very rare. These four species are the most tolerant of the Sphaeriidae to acid waters (Økland & Kuiper 1980).

Its distribution elsewhere in Europe is discontinuous. This species is also very common in late Pleistocene deposits of the former periglacial zones in western Europe. The form *cristata* Sterki, with an appendiculum on the beaks, quite like *P. henslowanum* (Shepherd), occurs on the islands of Strømø and Østerø, Faroes (Fog 1971:4), and has been dredged from Lake Tyrifjorden, Norway, by W. Hinz (1976a) as well as from lakes in Hälsingeland, Sweden (Kh). *P. lilljeborgii* has been collected from lakes on the island of Sealand, Denmark, and from some small lakes in

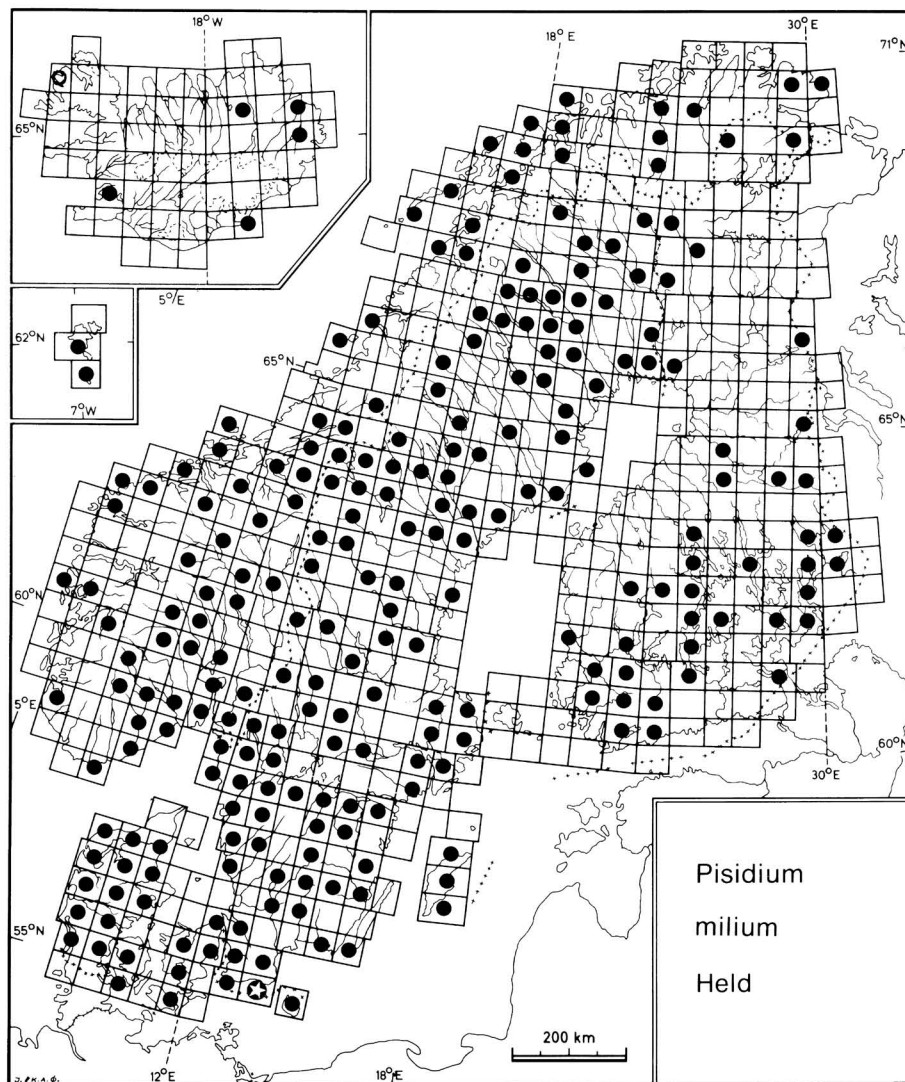


Fig. 9. Distribution of *Pisidium milium* in North Europe.

○ — records by Mandahl-Barth (1938) in Iceland; ☆ — subfossil records only.

Jylland. Its presence on the small island of Taasinge, Funen Archipelago, Denmark (Jespersen 1945:212) has not been confirmed. It is certainly an identification error. Piechocki (1985: 485) states that the Pleistocene and Early Holocene distribution of *P. lilljeborgii* "was considerably wider than the present one", a view which is now plainly contradicted by the Fennoscandinavian facts:

Pisidium milium Held, 1836

This species is recorded in 246 squares (Fig. 9). General distribution: holarctic. It is common in Europe and has been recorded in the Alps at 2000 m above sea level. Widely distributed in North Europe, the highest elevation recorded being 1180 m. The form *unioides* Westerlund, with an elongated, relatively low and swollen shell and a straight ventral margin, is found in the north of Scandinavia. The form occurs as a subfossil in periglacial facies of Pleistocene deposits in western Europe.

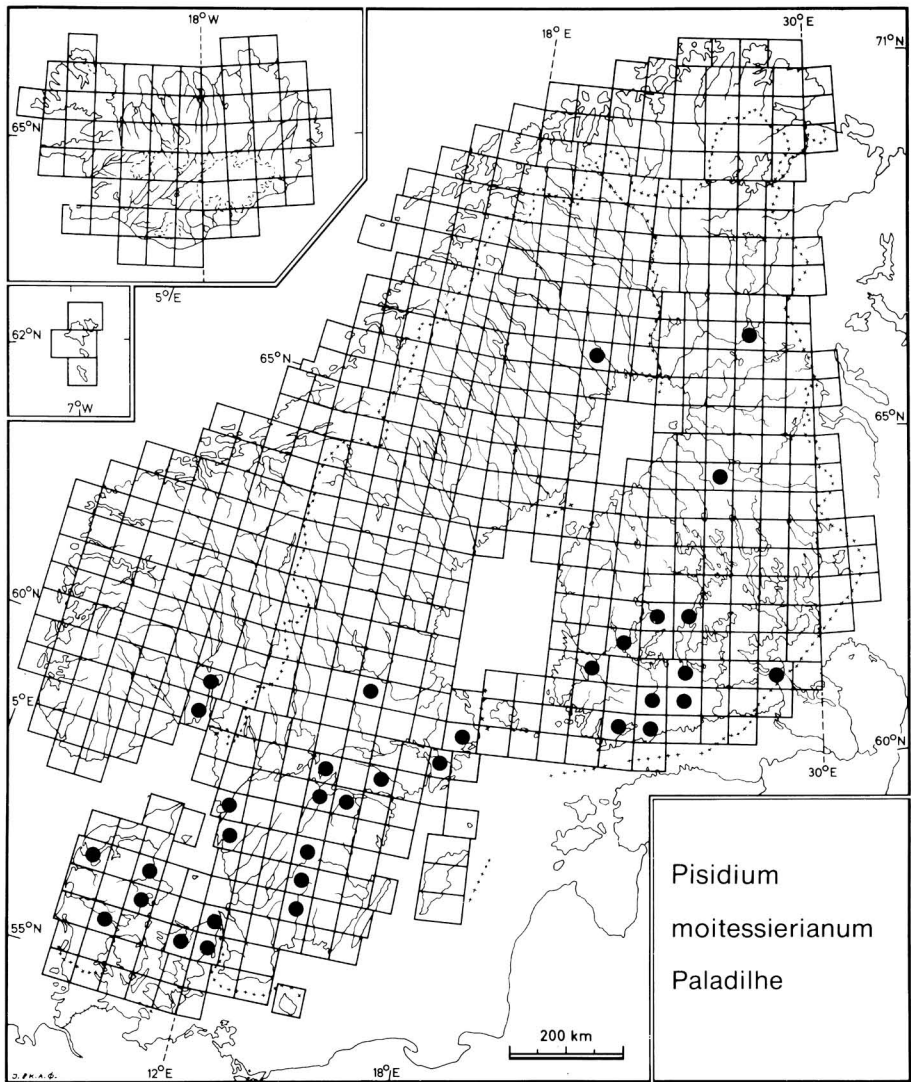


Fig. 10. Distribution of *Pisidium moitessierianum* in North Europe.

Pisidium moitessierianum Paladilhe, 1866

The species is recorded in 34 squares (Fig. 10). General distribution: (western) palearctic. Present in all of Europe, but more common north of the Alps than in the Mediterranean region. Absent in the west part of the Scandinavian Peninsula. Habitat: lowland rivers and streams, and the littoral of lakes, often in association with *P. henslowianum* and *P. amnicum*. Formerly, *P. moitessierianum* was often overlooked and classified as juvenile *P. supinum*.

Pisidium nitidum Jenyns, 1832

This species is recorded in 247 squares (Fig. 11). General distribution: holarctic, all Europe. In the Alps the species is found up to 2500 m above sea level; in northern Europe the maximum elevation is 1230 m. A common sphaeriid, living in running as well as in stagnant water. Common in North Europe but absent from the most acidic lakes. In streams, on sandy bottoms, is a regularly ribbed form, f. *arenicola* Stelfox, resembling *P. pulchellum*. The thick-shelled

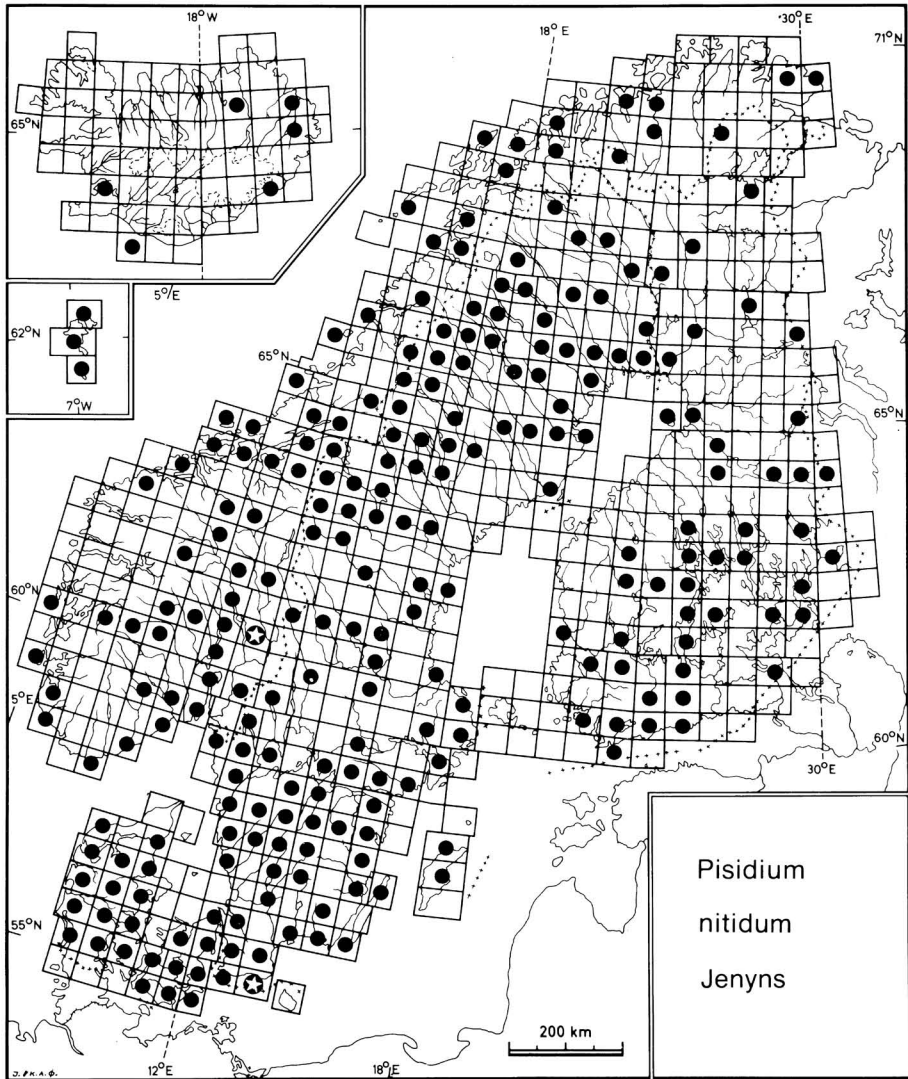


Fig. 11. Distribution of *Pisidium nitidum* in North Europe. ● — subfossil records only.

form with a heavy hinge, f. *crassa* Stelfox, is not known from North Europe.

Pisidium obtusale (Lamarck, 1818)

The species is recorded in 349 squares (Fig. 12). General distribution: holarctic. Over all of Europe, though sporadic in the Mediterranean area. One of the most common species in North Europe, occurring up to about 1230 m above sea level. It is considered

identical with the North American *P. rotundatum* Prime, but specifically distinct from the North American *P. ventricosum* Prime, which has erroneously been synonymized with *P. obtusale* (Herrington 1962:64, Kuiper 1987a). The arctic form *lapponica* Clessin, 1873, with swollen and broad beaks and a shell length equal to its height and diameter, may be considered a geographical subspecies. However, intermediates with the normal form may occur in the same population, whereas the phenomenon of

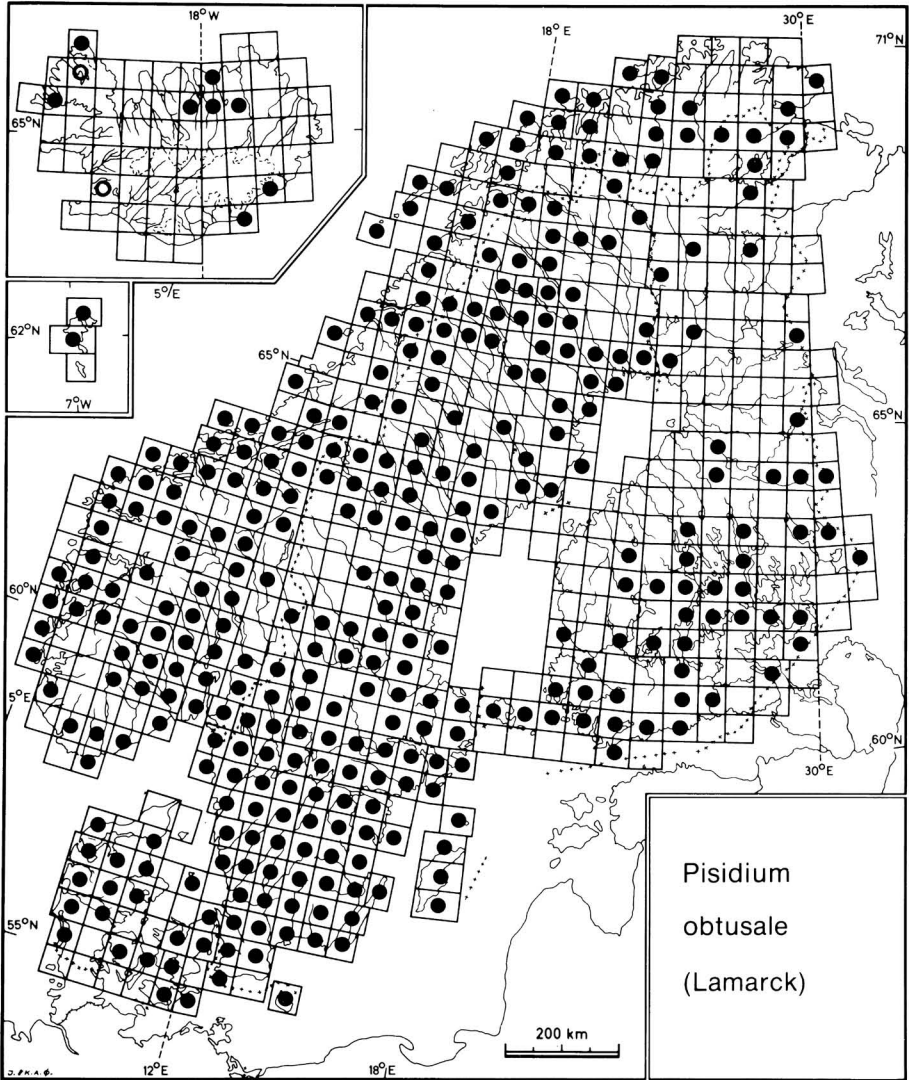


Fig. 12. Distribution of *Pisidium obtusale* in North Europe. ○ — records by Mandahl-Barth (1938) in Iceland.

very swollen beaks and extreme convexity is also observed with other species at high latitudes, e.g. *P. casertanum* f. *globularis* Clessin, *P. lilljeborgii* f. *transversalis* Clessin, as well as unnamed forms of *P. hibernicum* and *P. milium*. The form *lapponica* is a subfossil, characteristic of the periglacial facies of Late Glacial deposits in western and central Europe. The typical habitats of *P. obtusale* are small bodies of water with stagnant acidic water, and bogs and swamps.

Pisidium personatum Malm, 1855

The species is recorded in 115 squares (Fig. 13). General distribution: (western) palearctic. In all of Europe, often numerous in cold springs and in other water bodies, rivulets and ditches, fed with spring-water. It is absent in the littoral zone of lakes, but often numerous in the profundal zone of deep pre-alpine lakes, together with the only other *Pisidium* species living there, *P. conventus* (Kuiper 1974a: 23). L. Koli states that *P. personatum* in Finland has also been collected in rivers and lakes. In the Alps, the

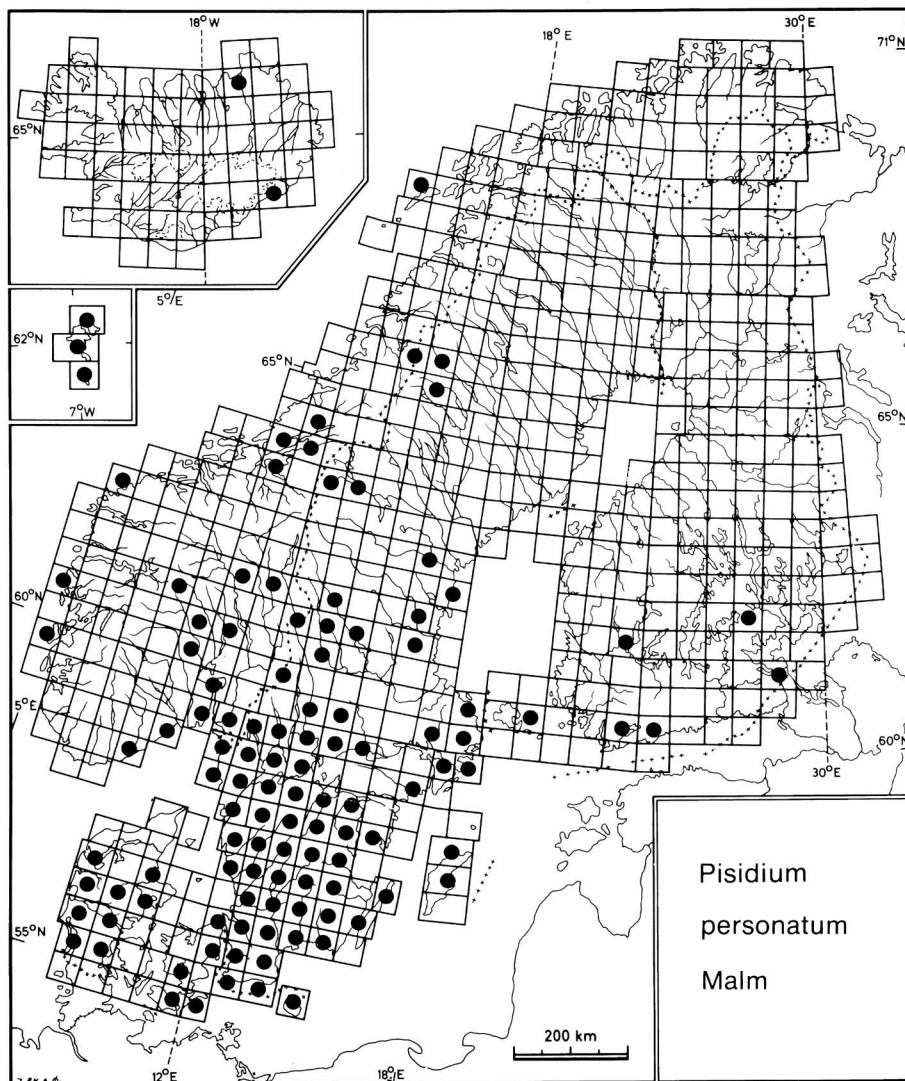


Fig. 13. Distribution of *Pisidium personatum* in North Europe.

species is found up to 2800 m above sea level and in Norway up to 1000 m. Of the all-European species, *P. personatum* is the only one to reach further to the north in Norway than in the Baltic region. The absence of the species from the northern parts of Norway, Sweden and Finland has still to be explained.

***Pisidium pseudosphaerium* Schlesch, 1947**

The species is recorded in 35 squares (Fig. 14). General distribution: European, discontinuously distributed between 44°N (Toulouse) and 63°N (Jämtland), and 7°W (Dublin) and 31°E (Leningrad). The species is rare in North Europe, occurring mostly in the southern part. Habitat: marshes and other densely vegetated bodies of water, rarely in habitats above 300 m elevation (Kuiper 1972). Mostly associated with *P. obtusale*, *P. milium*, and *Sphaerium corneum* f. *nucleus* Studer.

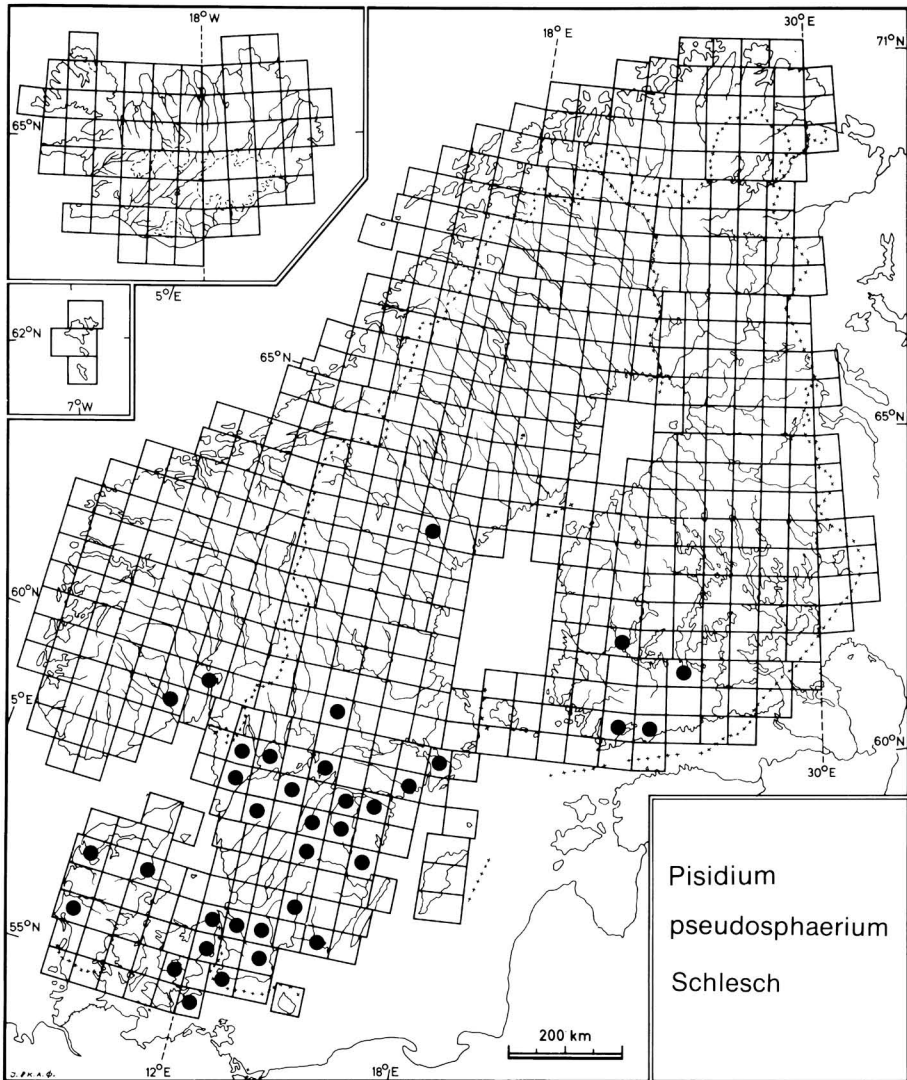


Fig. 14. Distribution of *Pisidium pseudosphaerium* in North Europe.

Pisidium pulchellum Jenyns, 1832

The species is recorded in 104 squares (Fig. 15). General distribution: palearctic, from the westernmost localities in Iceland to the easternmost known locality on the island of Sachalin; discontinuous in Siberia. Jónsson (1971) reports three records in Iceland, but unfortunately, we have not had the op-

portunity to verify the identifications. His illustrations are clear but are copied from Mandahl-Barth (1949), after Danish specimens. In the 19th century European literature, *P. pulchellum* is often misidentified with a striate form of *P. casertanum* (Kuiper 1986). Already Westerlund (1873:546 and Clessin 1879:24) drew attention to this error. This discrep-

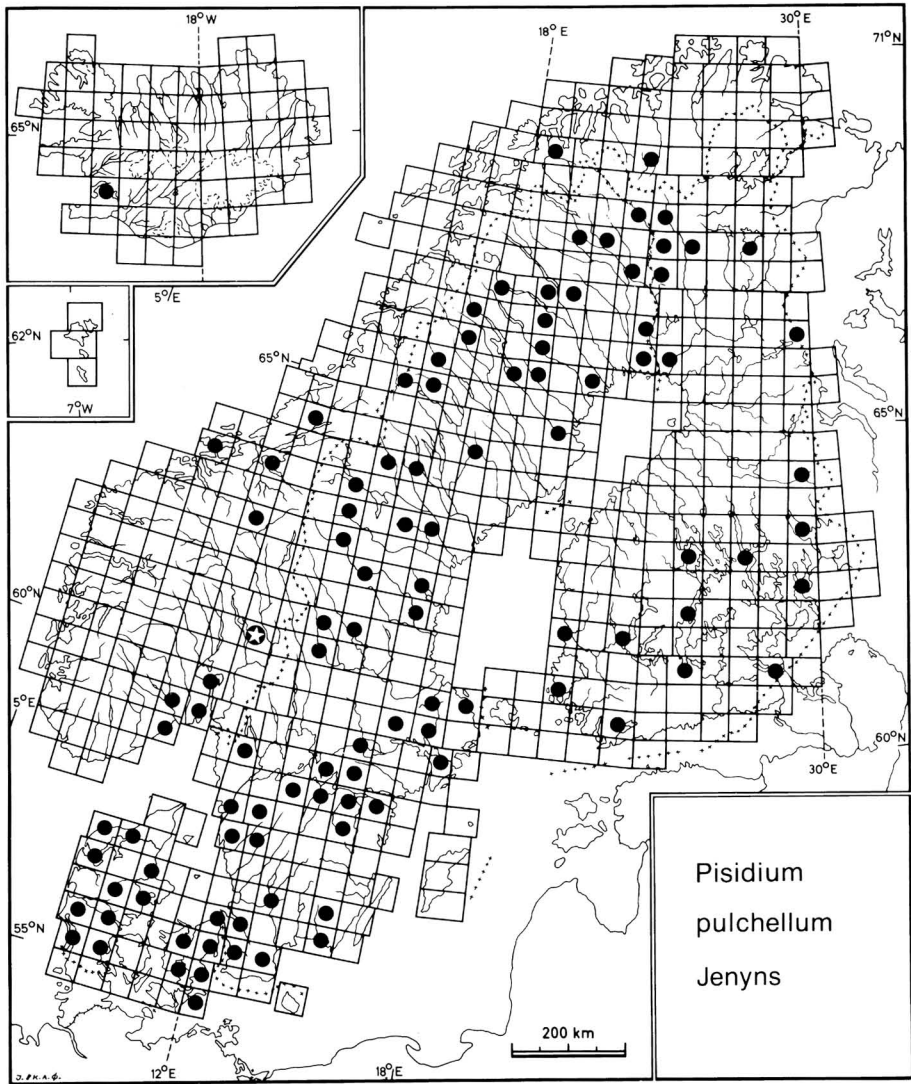


Fig. 15. Distribution of *Pisidium pulchellum* in North Europe. ● — subfossil records only.

ancy has been perpetuated for a long time (Germain 1931:707), and as a result, *P. pulchellum* has been reported more widely distributed than it really is.

Jaekel (1962:218) defines *P. pulchellum* as a "stark zurückgehende Art", a declining species. This statement is contradicted by the facts. Since the Pleistocene, *P. pulchellum* has considerably enlarged

its range towards the north. It settled in southern Norway, as long ago as the beginning of the Holocene (Økland & Kuiper 1980), 9000 years ago. Since then, it has colonized nearly the entire Peninsula, and even reached Iceland, which indicates more of a dynamic than a declining tendency.

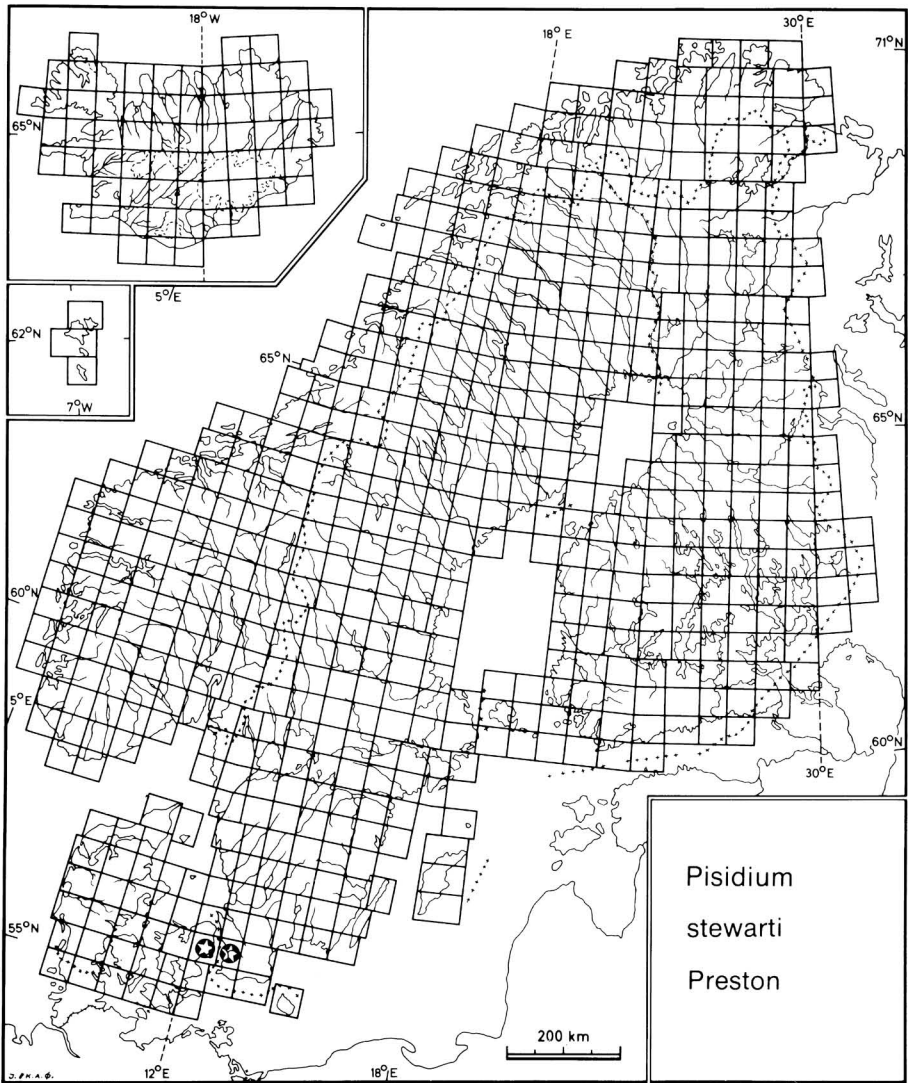


Fig. 16. Distribution of *Pisidium stewarti* in North Europe. ● — subfossil records only.

Pisidium stewarti Preston, 1909 (syn. *vincentianum* Woodward)

The species is recorded as subfossils in 2 squares (Fig. 16). General distribution: Asia, north of the Himalayas. During the Pleistocene, this species went through a distributional expansion westwards as far as Ireland. It lived at that time in the periglacial climate, often associated with *P. lilljeborgii*, *P. obtusale*

lapponicum and *P. hibernicum*. *P. stewarti* followed the retreating Weichselian ice wall northwards to nearly 56°N (Copenhagen, Denmark, and Landskrona, Sweden), then disappeared from Europe at the beginning of the Holocene (Kuiper 1968:36).

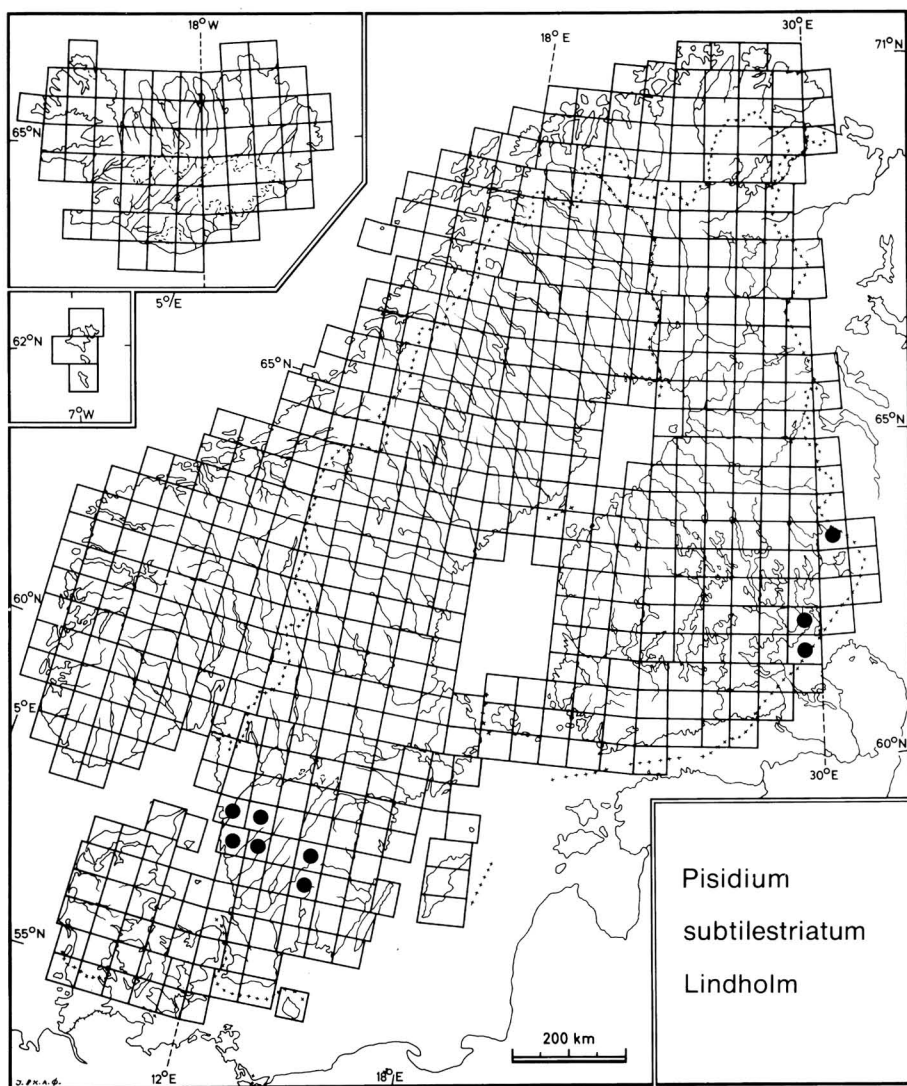


Fig. 17. Distribution of *Pisidium subtilestriatum* in North Europe.

***Pisidium subtilestriatum* Lindholm, 1909**

The species is recorded in 9 squares (Fig. 17). General distribution: palearctic with a very discontinuous area. Apparently rare in South Sweden and East Finland. In North Europe it is undoubtedly a post-glacial immigrant from Asia. The North American *P. idahoense* Roper is its nearctic counterpart. Both species live at great depths of large lakes.

***Pisidium subtruncatum* Malm, 1855**

The species is recorded in 243 squares (Fig. 18). General distribution: holarctic. In Europe it is one of the more common species of the genus, but it is rare in West Norway. Habitat: all kinds of water bodies, but not in the profundal zone of lakes, and not found in the most acidic waters. In the Pyrenees it occurs up to 2400 m above sea level. In North Europe its highest elevation is 1230 m.

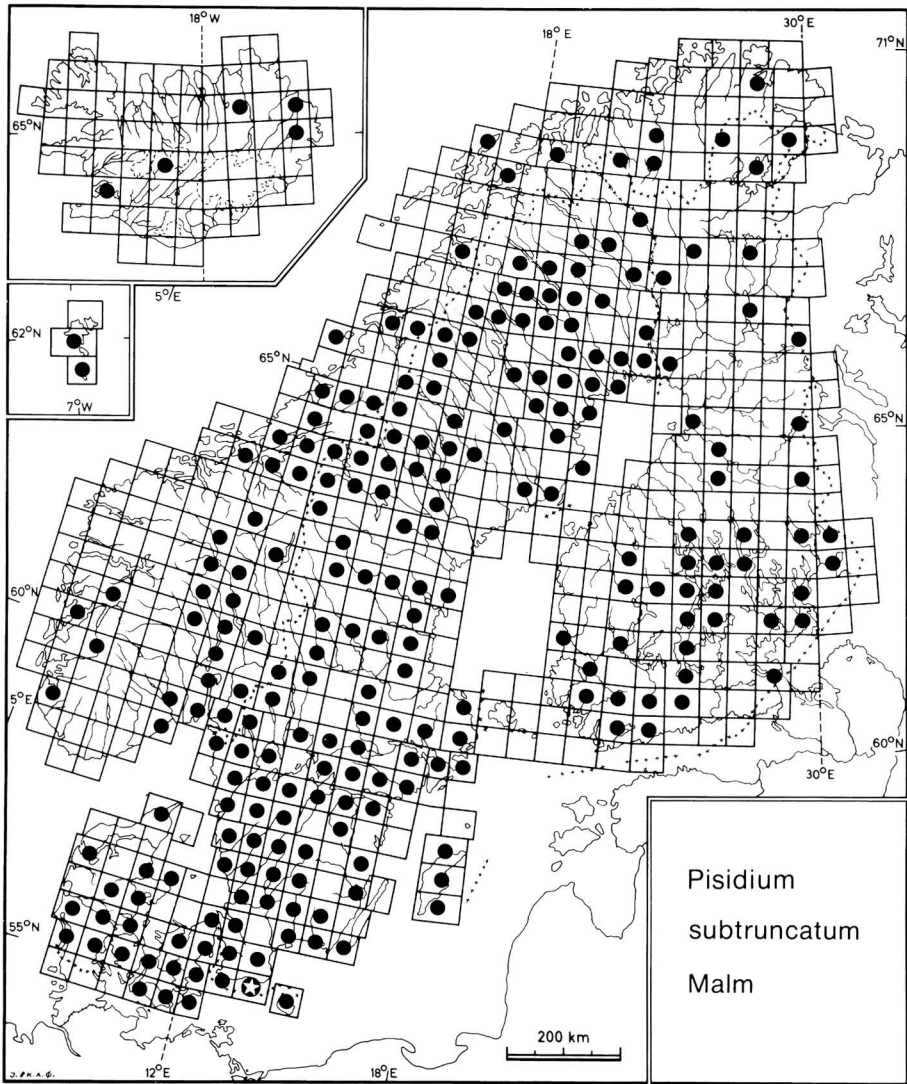


Fig. 18. Distribution of *Pisidium subtruncatum* in North Europe. ☆ — subfossil records only.

Until the beginning of the 20th century *P. subtruncatum* remained unknown as a distinct species. Well known authors, like S. Clessin, O. Goldfuss, A. Locard, A. Moquin-Tandon and others, regarded this species as being rare, or did not mention it at all. As a matter of fact, many authors labelled *P. subtruncatum* as an inappendiculate form of *P. henslowanum*.

Pisidium supinum Schmidt, 1851

The species is recorded in 9 squares (Fig. 19). General distribution: palearctic, central latitudes, as well as in NE America. It is said to have been collected from Upper-Pliocene and Lower Pleistocene deposits in Idaho, U.S.A. (Clarke 1981:416). This species typically lives in rivers. *P. supinum* is sometimes considered to be a thick-shelled, trigonal form of *P. henslowanum*, analogous to *P. casertanum* f.

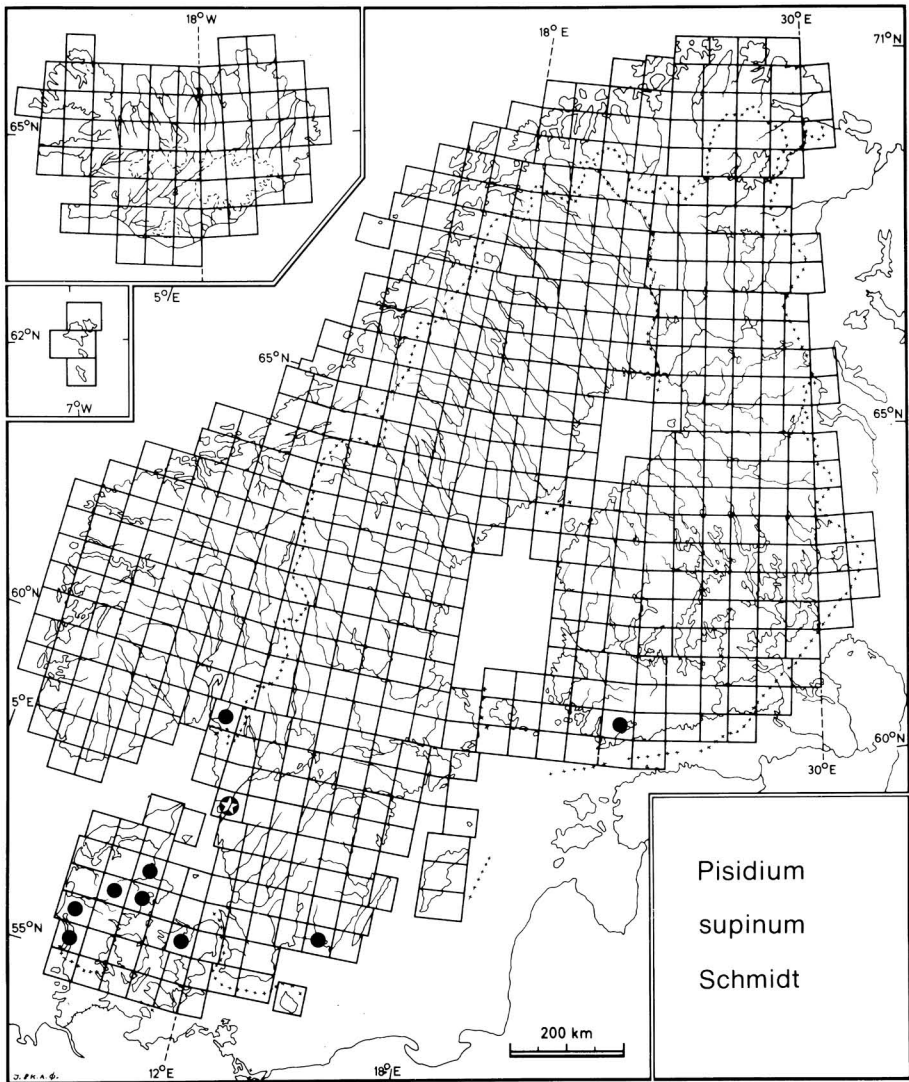


Fig. 19. Distribution of *Pisidium supinum* in North Europe. ● — subfossil records only.

ponderosa, *P. nitidum* f. *crassa*, *P. subtruncatum* f. *incrassata*, etc. As a matter of fact, especially in subfossil deposits, the conchological distinction between *P. henslowanum* and *P. supinum* is not sharp and their identification is often very subjective. Although intermediate forms are common, there are arguments to maintain the specific distinctness of *P. supinum* (Kuiper 1977). The occurrence of *P. supinum* in Iceland (Clarke 1981:416) needs confirmation.

The difference in distribution of *P. henslowanum* and *P. supinum* in North Europe is striking (Figs. 5 and 18).

Pisidium tenuilineatum Stelfox, 1918

The species is recorded in 4 squares (Fig. 20). General distribution: (western) palearctic. It occurs throughout Europe but is rarely collected in large

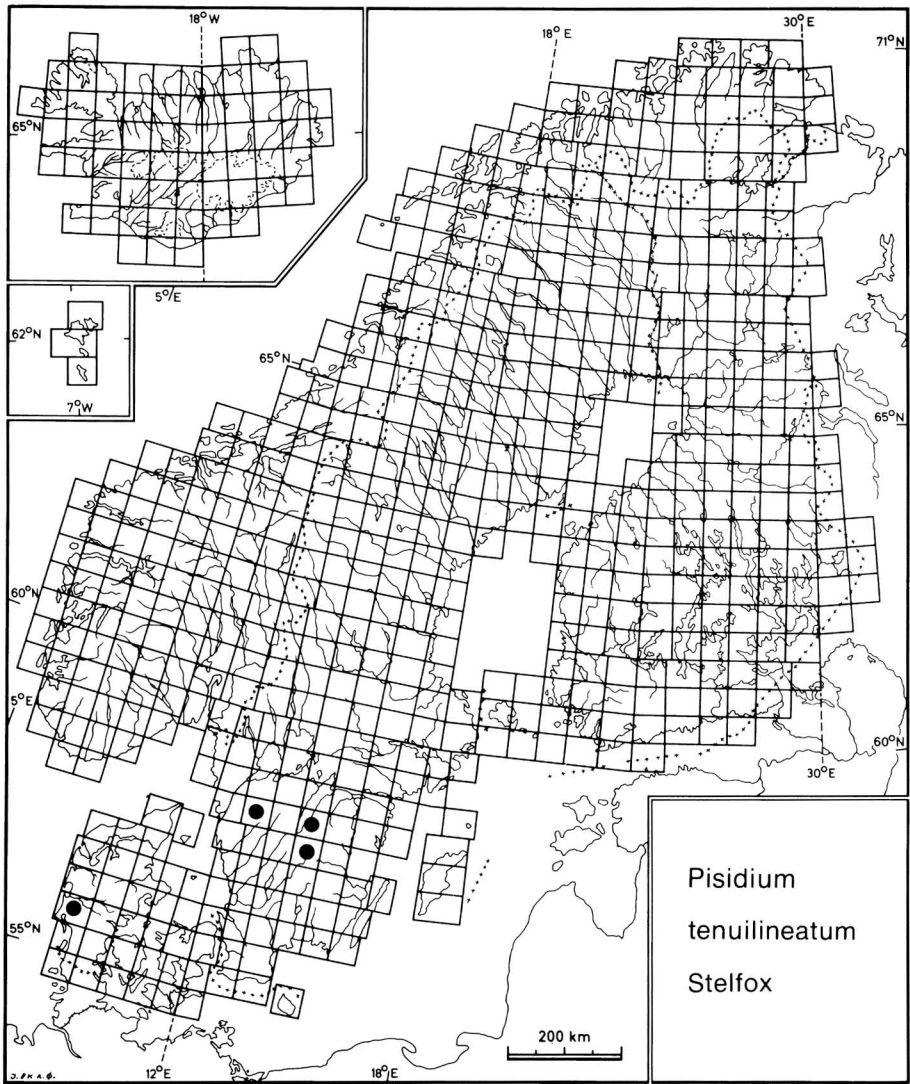


Fig. 20. Distribution of *Pisidium tenuilineatum* in North Europe.

numbers. It prefers clear, small streams on the plains, and the littoral zone of lakes, rarely above 500 m elevation. In Sweden, only three localities are known: Stensjön in Småland (Odhner 1940:9–12), Nossan, at Herrljunga in Västergötland, leg. Hubendick 1945 (St), and Vättern, leg. Widegren (St). In Denmark just one locality is known: Skjern Å, Jylland, leg. Steenberg, 1916 (Kh).

Pisidium waldeni Kuiper, 1975

The species is recorded in 36 squares (Fig. 21). General distribution: northern holarctic. Like *Sphaerium nitidum*, this cold-stenothermal species is most common in mountain lakes up to 1300 m above sea level, but it is also found in the profundal zone of lowland lakes in southern Scandinavia. The specimen figured by Odhner (1939: pl. 6, fig.4), from Unimak

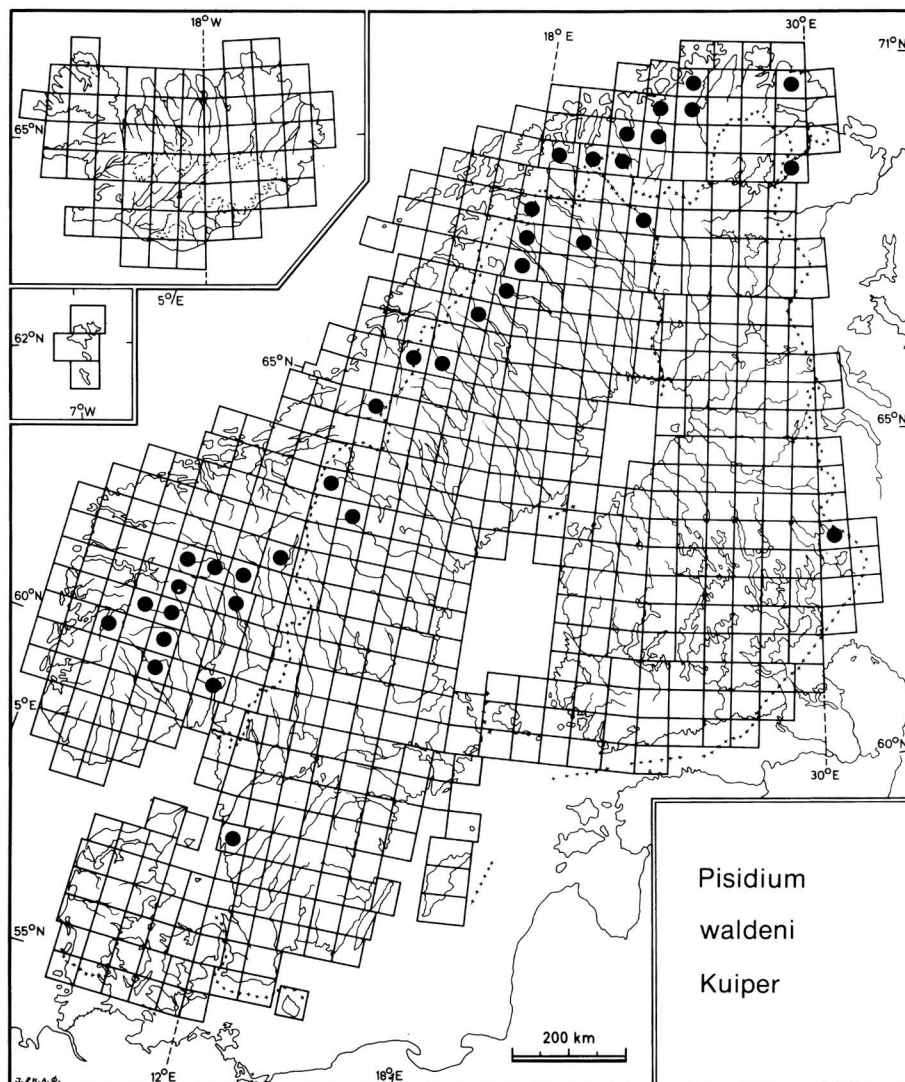


Fig. 21. Distribution of *Pisidium waldeni* in North Europe.

Island, Aleutian Archipelago, is not *P. lilljeborgii*, but *P. waldeni*.

Sphaerium corneum (Linné, 1758), *S. nitidum* Clessin, (in Westerlund 1877), and *Musculium lacustre* (Müller, 1774)

All these species have a holarctic distribution (Figs. 22–24). *S. corneum* is a common lowland

species; *S. nitidum*, on the other hand, is more of a mountain dweller, living in cold lakes, but both species have often been collected together. *M. lacustre* lives in lowlands, in marshes, pools and ditches, often together with *Pisidium obtusale*, *P. milium*, *P. casertanum* and *P. personatum*. So far, neither *Sphaerium* nor *Musculium* have been recorded from Iceland or the Faroes.

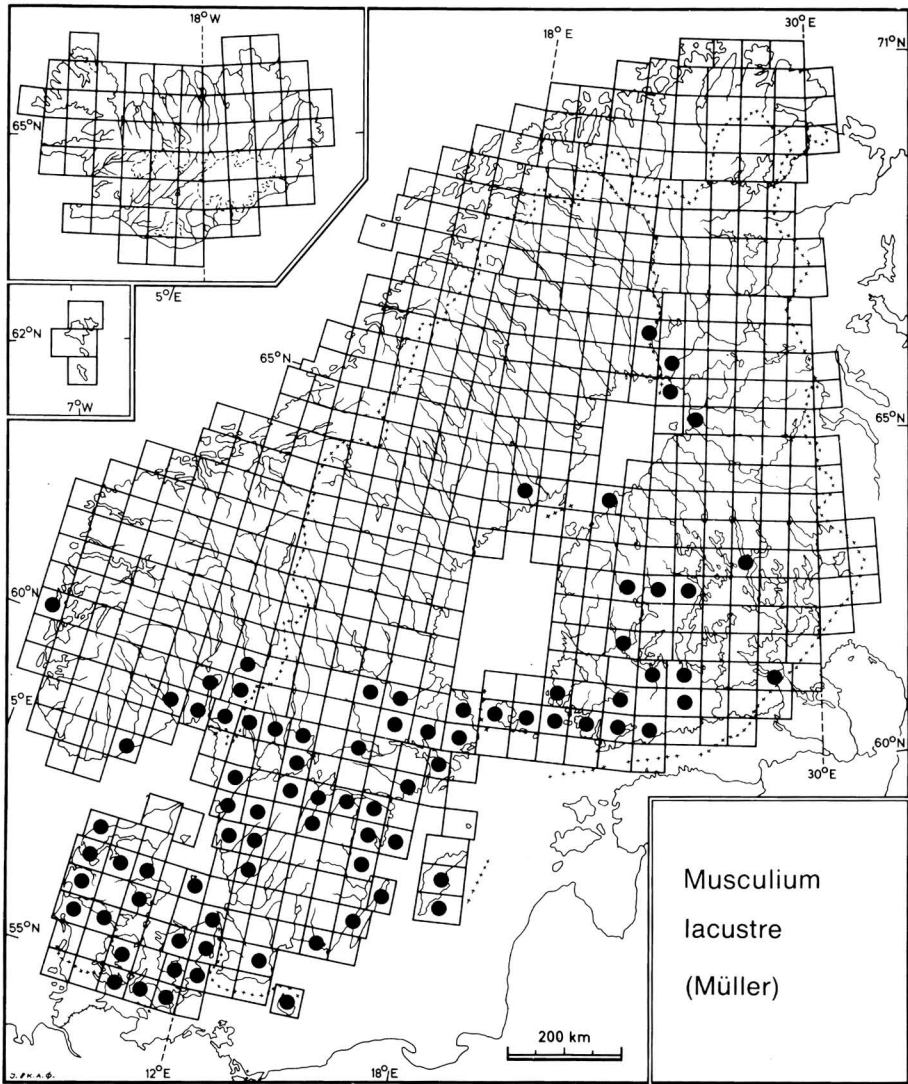


Fig. 22. Distribution of *Musculium lacustre* in North Europe.

5. Discussion

Of the 23 species of small mussels occurring in North Europe one is represented only by subfossil records. All species have been found in Sweden. Three of the southern species are absent from Norway, and the four northern species do not inhabit Denmark (Table 1). The number of species decreases in the Faroes and Iceland.

The four most common species, occurring in 57–80% of the investigated squares, are *Pisidium casertanum*, *P. hibernicum*, *P. lilljeborgii* and *P. ob-*

tusale (Table 1). Another group of species (*P. milium*, *P. nitidum*, *P. subtruncatum* and *Sphaerium corneum*) are found in about half of the investigated squares. The remaining species occur in less than 27% of the squares.

From a historical point of view the sphaeriid distribution ranges are far from being static. On the contrary, species' ranges have often been considerably modified by climatic fluctuations. North Europe offers striking examples of this. During the Weich-

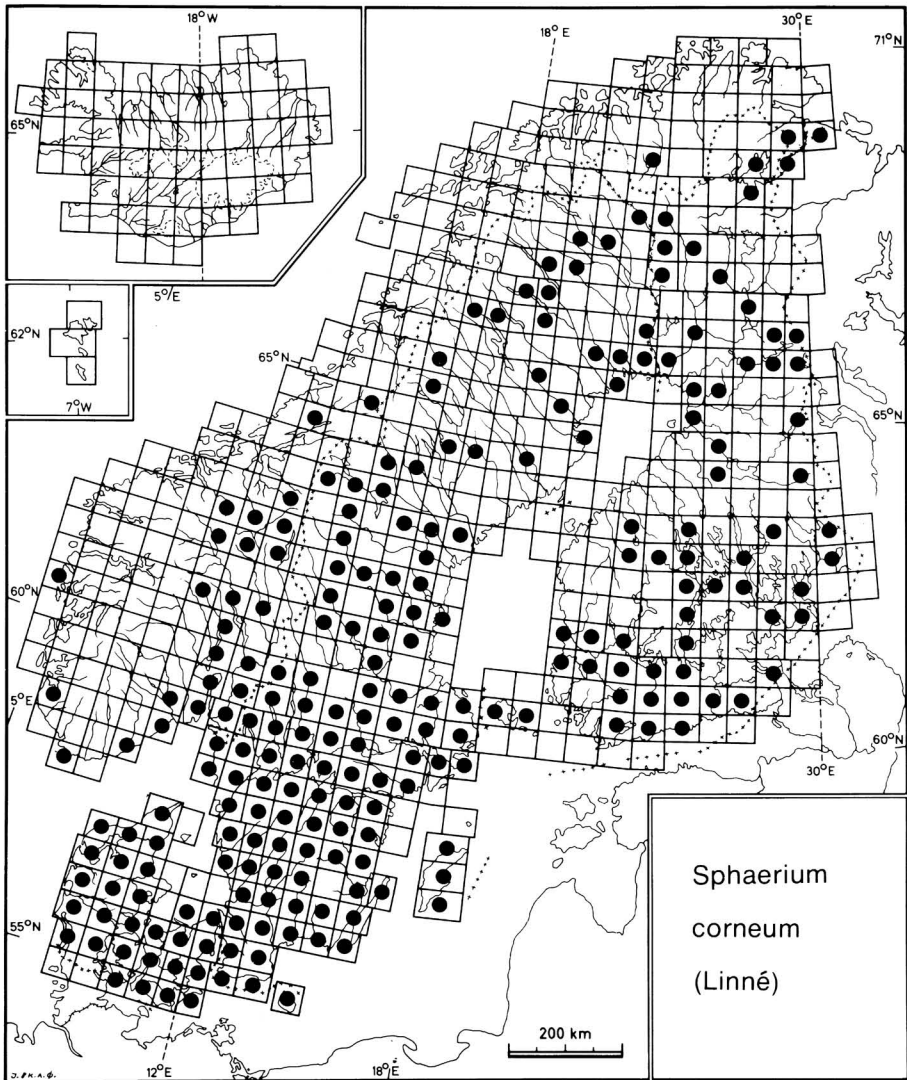


Fig. 23. Distribution of *Sphaerium corneum* in North Europe.

selian glaciation North Europe was, with the exception of western Denmark, covered by ice, and was uninhabitable for Sphaeriidae. With the improvement of climate and the gradual retreat of the glaciers, many sphaeriid species of western and central Europe extended their range northward. This has been the case with *Pisidium amnicum*, *P. casertanum*, *P. henslowanum*, *P. hibernicum*, *P. milium*, *P. moitessierianum*, *P. nitidum*, *P. obtusale*, *P. personatum*, *P. pseudosphaerium*, *P. pulchellum*, *P. sub-*

truncatum, and to a lesser degree, with *P. supinum* and *P. tenuilineatum*. It is probable that a large fresh-water basin some 8000 years ago, the *Ancylus* lake, has favoured the dispersal of typical lacustrine and fluvial species, like *P. amnicum*, *P. henslowanum* and *P. moitessierianum*, as well as *P. casertanum*, *P. nitidum* and *P. subtruncatum*.

One of the most common species in Pleistocene periglacial deposits, *P. lilljeborgii*, has disappeared from the western European plains. Since the begin-

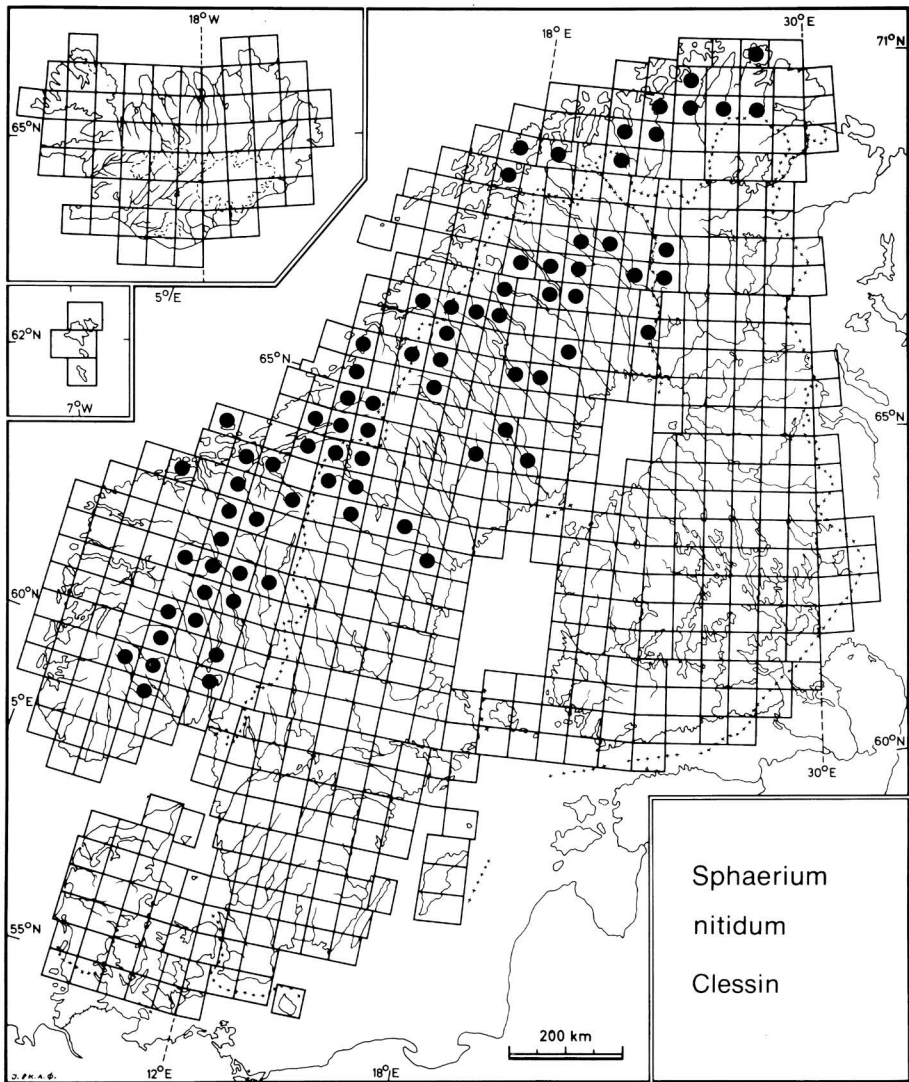


Fig. 24. Distribution of *Sphaerium nitidum* in North Europe.

ning of the Holocene this species took refuge in the littoral zone of pre-alpine and some mountain lakes. Its main European area of distribution now lies in Scandinavia. An analogous case is *P. conventus*, but this species also lives in the depths of several central European lakes.

The northern Asian *P. stewarti* extended its range westwards during the Pleistocene. Beside being found in Sweden and Denmark this easily recognizable species is known from Ireland, England, France, Belgium, The Netherlands, Switzerland, West and

East Germany, Poland, Czechoslovakia and Austria. It no longer belongs to the living fauna of Europe, but still occurs in Siberia. A closely allied species, *P. anandalei* Prasad, which was synonymised with *P. vincentianum*, and of which fossil records are known from late Miocene deposits in Bavaria and from Miocene and Pliocene deposits in Turkey, still occurs in southern Italy and in Greece. Its general distribution includes southern Asia as far as Japan, Hongkong and the Philippines.

Table 1. Distribution of the species of *Pisidium*, *Musculium* and *Sphaerium* in North Europe (with the number of squares with records including the records listed by Mandahl-Barth 1938 and proportion of total number of investigated squares), the Nearctic and the Palearctic regions.

circ = circumpolar, cosm = cosmopolitan, D = Denmark, Fa = Faroes, Fi = Finland, I = Iceland, N = Norway, NE = northeast, s = subfossil, S = Sweden.

	North Europe							Squares	%	Nearctic Region	Palearctic Region
	I	Fa	N	S	Fi	D					
<i>P. amnicum</i>	+	-	+	+	+	+	91	18	+NE	+	
<i>P. casertanum</i>	+	+	+	+	+	+	393	80	+ cosm	+	
<i>P. conventus</i>	-	+	+	+	+	-	133	27	+ circ	+	
<i>P. henslowanum</i>	+	-	+	+	+	+	131	27	+	+	
<i>P. hibernicum</i>	+	+	+	+	+	+	281	57	-	+	
<i>P. hinzi</i>	-	-	+	+	+	-	11	2	+ circ	+	
<i>P. lilljeborgii</i>	+	+	+	+	+	+	285	58	+	+	
<i>P. milium</i>	+	+	+	+	+	+	246	50	+	+	
<i>P. moitessierianum</i>	-	-	+	+	+	+	34	7	-	+ West	
<i>P. nitidum</i>	+	+	+	+	+	+	247	50	+	+	
<i>P. obtusale</i>	+	+	+	+	+	+	349	71	+	+	
<i>P. personatum</i>	+	+	+	+	+	+	115	23	-	+ West	
<i>P. pseudosphaerium</i>	-	-	+	+	+	+	35	7	-	+ West	
<i>P. pulchellum</i>	+	-	+	+	+	+	104	21	-	+	
<i>P. stewarti</i>	-	-	-	s	-	s	2	-	-	+ N Asian	
<i>P. subtilestriatum</i>	-	-	-	+	+	-	9	2	-	+	
<i>P. subtruncatum</i>	+	+	+	+	+	+	243	49	+	+	
<i>P. supinum</i>	-	-	+	+	+	+	9	2	+ NE	+	
<i>P. tenuilineatum</i>	-	-	-	+	-	+	4	<1	-	+ West	
<i>P. waldeni</i>	-	-	+	+	+	-	36	7	+ circ	+	
<i>M. lacustre</i>	-	-	+	+	+	+	83	17	+	+	
<i>S. corneum</i>	-	-	+	+	+	+	234	47	+	+	
<i>S. nitidum</i>	-	-	+	+	+	-	76	15	+ circ	+	
Number of species	11	9	20	23	21	18					

Since there is no fossil evidence of *Pisidium waldeni*, *P. hinzi* and *P. subtilestriatum* in western and central Europe, it is reasonable to conclude that these species have migrated postglacially from east to west. *Sphaerium nitidum* is also an Asian immigrant. It has never been recorded as a subfossil elsewhere in Europe.

Whereas *Sphaerium corneum* and *Musculium lacustre* are presently widespread in North Europe, two other European species of *Sphaerium*, viz. *S. rivicola* (Lamarck) and *S. solidum* Normand, both living mainly in rivers, are absent. A taxonomic problem is still the little known *S. subsolidum* Clessin 1888, a postglacial subfossil from Skåne, Sweden. It is also known from late Weichselian deposits in the Netherlands. Living specimens have been found in the Ladoga region (Odhner 1937:268). *S. subsolidum* has been identified with *S. solidum*, but there are zoogeographical, morphological and ecological objections

against this view (Kuiper 1988). The taxonomic solution to this problem has to wait until more material has been collected. Noteworthy is the fact that neither *Sphaerium* nor *Musculium* have been recorded from either Iceland or the Faroes.

The fact that Iceland constitutes the westernmost outpost of widespread species like *P. pulchellum*, *P. personatum* and *P. hibernicum*, and that no nearctic species have found their way to Iceland, underlines the importance of the Greenland area as a zoogeographical, i.e. climatic and dispersal, barrier. Only three sphaeriid species, viz. *P. casertanum*, *P. lilljeborgii* and *P. obtusale*, have up to now been recorded from Greenland.

Acknowledgements. The assistance of Dr. Gísli Már Gíslason, Reykjavik, in locating some geographic names on the map of Iceland, is kindly acknowledged.

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