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ON THE ORIGIN OF THE CASPIAN AND BAIKAL SEALS AND THE PALEOCLIMATOLOGICAL IMPLICATION*

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ABSTRACT. The Caspian and Baikal seals, closely related to the ringed seal of the Arctic seas, are usually held to have arrived as a result of Pleistocene events. However, evidence suggests that they are relicts of late Miocene connections with the Arctic basin. The three species are more differentiated than is generally supposed. More important, some of the fossils from the upper Miocene of southern Russia and Hungary (and perhaps elsewhere) belong to the same subgenus (*Pusa*), and remains of the present Caspian seal are found in lower Pleistocene deposits, formed before the putative glacial entry of seals.

The fossils most readily diagnosed as belonging to the ringed seal group are an anterior fragment of a skull attributed to *Phoca pontica* by Alekseev and part of a lower jaw named *Praepusa pannonica* by Kretzoi. Some of the syntypes of *Phoca pontica* Eichwald (1853) also belong to this group and a lectotype is accordingly chosen here to prevent further confusion of the name. Much confusion has resulted from the identification by Simionescu as *Phoca pontica* of a form with a peculiar, distally expanded femur; this species is named *Pontophoca sarmatica* (Alekseev) n. comb. The synonymies of other forms which have been involved with the status of *Phoca pontica* are reviewed and lectotypes chosen when necessary.

The northern seals (subfamily Phocinae) are relatively cold stenothermic and probably entered the Sarmatian basin by direct connections to the north. The pups of living Phocinae have white coats as an adaptation to birth on ice, and this is almost certainly of common ancestry; the three species of the subgenus *Pusa*, within this subfamily, even more probably retain this adaptation from a common ancestor. Thus, if the ancestors of the Caspian seal were present in late Miocene times, ice almost certainly formed then, at least in the Arctic basin, and probably in the innermost reaches of the Sarmatian Sea.

INTRODUCTION

The presence in two great Asian lakes of seals closely related to the ringed seal of the Arctic seas has naturally excited much speculation. This note is prompted by certain Russian and eastern European papers which present views on the subject which are not widely recognized. Basically two theories have been put forward to explain the origin of these seals. The first presumes that they arrived as a result of Pleistocene events, and this is the only theory to be found in the zoogeographical literature of western Europe and America, as far as the author is aware. The second theory supposes that the Caspian seal and probably the Baikal seal are relicts of older, Tertiary connections with the northern seas. This paper attempts to show that the latter is the correct view.

The seals involved are members of the subfamily Phocinae of the hair seal group (family Phocidae). The systematics of the subfamily have been reviewed recently by Chapsky (1955a), whose views are substantially adopted by Scheffer (1958).

Many seals produce and nurture their pups on ice, but only the living members of the subfamily Phocinae (except for the specialized and probably early-separated bearded seal, *Erignathus*) are apparently derived from a single ice-breeding common ancestor. They are all related on anatomical grounds, of course, but more significantly their pups all have a white natal

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coat (lanugo). One, the harbor seal (*Phoca vitulina*) of the Atlantic and eastern Pacific, now breeds on land and the pup sheds the white coat *in utero*. The gray seal (*Halichoerus*) has turned to land-breeding in parts of its range, surely recently, for the pup retains the white coat. In all others the pup is produced on ice, where the functional value of the white coat is obvious in protective coloration and perhaps thermoregulation. It is improbable that this adaptation developed independently in seven species of the same subfamily. In the Antarctic, where predation (until man came) was not a factor, the white coat is not found in the five species of hair seal which may pup on ice. In the north Atlantic, the hooded seal (subfamily Cystophorinae) and the bearded seal (mentioned above) have failed to develop this feature. The importance of these considerations will become apparent.

The ringed, Caspian, and Baikal seals are members of the genus *Phoca*. Their subgenus, *Pusa*, has recently been raised to generic rank by Scheffer (1958), but reference to *Phoca* is preferred as it implies a relationship to the harbor seal group (*Phoca vitulina*) rather than to the other members of the subfamily Phocinae (the more specialized *Pagophilus*, *Histriophoca*, and *Halichoerus*). This follows the recommendation of Chapsky (1955a).

The Caspian seal (*Phoca caspica*) and the Baikal seal (*P. sibirica*) were described in 1788 by Gmelin, who thought them to be varieties of the harbor seal (*P. vitulina*). However, it became apparent that they were allied to the ringed seal (*P. hispida*), their affinities being discussed in detail by Nordqvist (1899), who relegated them to subspecific status. Seals have even recently (Mohr, 1952) been listed as possibly living in the Asian lakes Oron, Aral, and Kuku-nor, but this apparently is a mistake, for no seals are found in these lakes today (Ognev, 1935; apparently not noted by Mohr).

The possibility of Pleistocene origin will be discussed first. It will not be elaborated here in detail, since its refutation depends on confirmation of the opposing theory.

THE THEORY OF PLEISTOCENE ORIGIN

To account for the presence of Arctic elements, including the seal, a fish, and several Crustacea, in the Caspian Sea, Högbom (1917) assumed that a late glacial emigration from the Baltic region had occurred. The mechanism involved damming by glacial ice of northern lakes with the appropriate relict fauna, causing them to overflow into the Volga drainage and thence into the Caspian basin. Two of the relicts (the fish *Stenodus*, and the amphipod *Gammaracanthus*) are unknown from the Baltic or its relict lakes, and this led Pirozhnikov (1937) to propose that the northern fauna had been sent southwards from ice-dammed lakes formed by the west Siberian ice sheet.

Davies (1958a), who recently treated pinniped zoogeography as a whole, has accepted Pirozhnikov's theory and has attempted to elaborate and date the sequence of events. He supposes that during the third glaciation, which was the most extensive, the ice sheet formed first on the highlands of Novaya Zemlya and the Taimur Peninsula, spread southward to dam up the Ob and Yenesei Rivers, and picked up the seals from the gulfs of these rivers. The seals thus became inhabitants of the lake formed along the southern margin of

the Siberian ice sheet. There is geological evidence for a lake or lakes, which were controlled by a spillway at the head of the Tobol River and discharged into a route leading to the Aralo-Caspian basin (Flint, 1957). There is no evidence, however, for a lake as extensive as that which Davies has drawn (his figure 7, 1958a), incorporating the Caspian and Aral Seas and extending to the Central Siberian Highland. Lake Baikal drains into the Yenesei River, but is at present 300 meters above any possible ice-dammed lake. Davies cites evidence for considerable epeirogenetic uplift during the Pleistocene, and supposes that Lake Baikal would have been more accessible during the third glacial advance.

THE EVIDENCE FOR TERTIARY ORIGIN

The other opinion, that the Baikal and Caspian seals are relicts of pre-Quaternary connections of these waters with the northern seas, is not new. It was first put forward in the last century (by Andrussov, 1888; cited by Chapsky, 1955b), but only recently has the idea been given the full attention it merits by Chapsky, whose views form the basis for much of the argument presented here.

First of all, the degree of differentiation of the two lake-dwelling seals must be clarified. Nordqvist (1899) considered them to be subspecies, thus expressing their greater difference from the northern ringed seal than found in the "varieties" inhabiting the Baltic lakes Ladoga and Saima, which were obviously of recent, post-glacial origin. Subspecific status is still commonly accorded to them in the literature of northern Europe (Mohr, 1952; Eckman, 1953; Segerstråle, 1957) and this status would accord with a presumption of their Pleistocene origin. However, most recent authors concerned with their systematic position have given them specific status, if only because of their isolation.

The ringed seal of the Arctic and north-boreal seas is quite variable, and has been divided into a number of subspecies. Doubtless Scheffer (1958) is correct in presuming that most of these are invalid. At any rate, probably none can stand as defined, for the descriptions fail to account for differences imposed by age and sex (Chapsky, 1952) and for ecotypical differences in size related to ice conditions and latitude (McLaren, 1958). The differences between the ringed, Caspian and Baikal seals are not of this order at all and have been underemphasized. Chapsky (1955a; 1955b) redescribes each species thoroughly, but all their characteristics cannot be repeated here. There are consistent, age-independent differences in the skulls of the species. The pelt of the ringed seal throughout its wide range is "ringed" or marbled, that of the Baikal seal is spotted, while the skin of the Caspian seal is an unmarked gray. There are differences in parasites and feeding habits. There is a pronounced difference in the reproductive ecology of the Caspian seal, which breeds gregariously on ice floes, whereas the other two construct solitary pupping-lairs in the snow overlying land-fast ice.

The Caspian seal appears rather more differentiated from the ringed seal type, although the two lake seals have some features in common not found in the ringed seal. Taliev (cited by Brooks, 1950) found the Baikal seal serologi-

cally closer to the Arctic ringed seal than to the seals of Lake Ladoga or the Caspian Sea. However, this result cannot be significant of relationships, for there is no doubt that the Ladoga seal is merely a recently isolated and little differentiated ringed seal.

Taken as a whole, these differences imply an earlier separation than if we dismiss the inland seals as being mere subspecies of the ringed seal. Now an argument based on degree of differentiation alone would not suffice to overcome the argument for Pleistocene origin. The latter theory could claim that the populations were, at least on arrival, very small, and that this combined with the isolation in new surroundings would certainly result in more rapid evolution. However, the evidence for a pre-Quaternary origin of the Caspian seal, at least, rests on the fossil record, which must supersede any theory based on the Recent forms alone.

Pre-Pleistocene fossils.—The Sarmatian and Pontian basins of the late Miocene and early Pliocene[1] have provided a surprising number of fossils of marine mammals. Among the more important papers describing these fossils are those of Alekseev (1924a; 1924b), Kretzoi (1941), Macarovici and Oescu (1941), Macarovici (1942), and Simionescu (1926). Kellogg (1922) gives a very thorough review of all earlier finds, and Friant (1947) lists and discusses most species described to that date. Seals of the tropical-Antarctic group (subfamily Monachinae) and the northern group (subfamily Phocinae) are represented.

One of the first species described was *Phoca pontica* Eichwald (1853) from the Sarmatian of Bessarabia and from two localities on the Kerch Peninsula, both listed as Pontian (e.g., Kellogg, 1922), but apparently Sarmatian (Alekseev, 1924a). The name has become badly confused, for the original description was based on material of more than one species, and the name has since been applied to still other forms. Since the identification and relationships of *Phoca pontica* are important to the argument, it is necessary first to discuss misapplications and dubious changes of the name, and to divest it of fossils which are unrelated to Eichwald's type material. After this we may redefine the species from the original description by choosing a lectotype and then discussing its relationships. There are other problems of relationships and synonymy among the Sarmatian species, but these are beyond the scope of the present paper.

The fossils named *Phoca pontica* from Bessarabia were shown by Nordmann (1860) to be from a much larger species, which Nordmann renamed *Phoca maeotica*. There is complete agreement among the several authors on the identification of at least the femur (fig. 1e) of this large form, although it has been removed from the genus *Phoca* by some. Trouessart (1897) recognized that it belonged to the tropical-Antarctic group and renamed it *Monatherium maeoticum* (the spelling *Monotherium* has priority; see Kellogg.

[1] There is controversy over the correlations involved, but Russian workers (e.g., Neiman, 1957) believe that the Pontian stage and some of the top of the Sarmatian stage are to be considered as Pliocene. Some of the Sarmatian fossils have been listed as middle Miocene, but this cannot be maintained. It is sufficient for the argument and for wider correlation to suppose that the events described here took place near the Miocene-Pliocene transition. Reference has been made to the Lexique Stratigraphique International for correlation with western Europe.

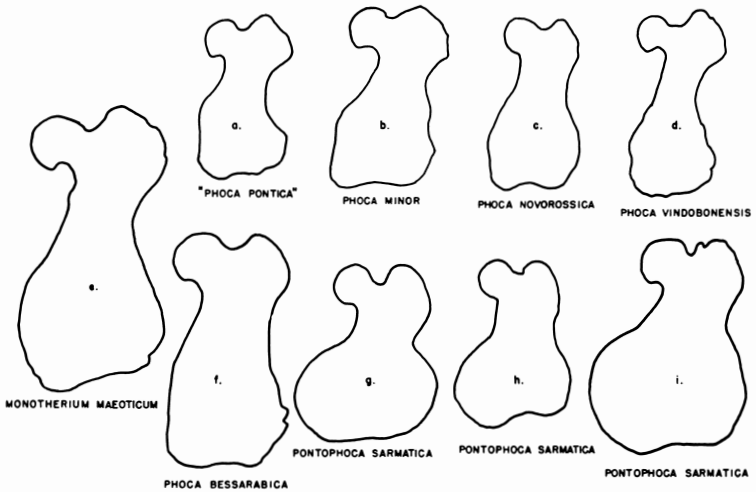

Fig. 1. Femurs from fossil seals. All to same scale (×1/3). Some reversed from originals for purposes of composition. (b and d from Friant, 1947; h from Simionescu, 1926; i from Macarovici and Oescu, 1941; others from type illustrations, as discussed in text.).

1922). The work of Nordmann should have resulted in the restriction of the name *Phoca pontica* to fossils from the small species of *Phoca* which formed important parts of the collection described, without designation of a holotype, by Eichwald.

Peters (1867) attributed seal fossils from the upper Miocene of the Vienna basin to *Phoca pontica*, without illustrating his material. Toula (1898) believed that these and more extensive remains were referable to a new species, *Phoca vindobonensis*.

Alekseev (1924a) described and figured from middle Sarmatian deposits of Kishinev the facial part of a skull and a fragment of a lower jaw, apparently from the same individual. These were from a small seal of the subfamily Phocinae and matched very well the small braincase from the Kerch Peninsula illustrated by Eichwald (1853) for *Phoca pontica*. Alekseev found skeletal material as well, which he neither described nor figured, but which he also referred to *Phoca pontica*.

Other bones, of which the femur seems to have been the source of most confusion, have been used to define the Sarmatian species. The femur (fig. 1a) considered to be part of the type of *Phoca pontica* by Eichwald was very small (65 mm. long) and resembles quite closely the femora of other species of *Phoca*, particularly *Phoca minor* (fig. 1b) from the Pliocene of Belgium, as illustrated by Friant (1947).

A grossly different form of femur (fig. 1h), with a very much expanded distal portion, was attributed to *Phoca pontica* by Simionescu (1926). Later Macarovici and Oescu (1941), following Simionescu, described a similar but larger femur (fig. 1i) under the same name. These are without doubt the same type of femur (fig. 1g) which had been defined earlier by Alekseev (1924b)

under the then new name *Phoca sarmatica*. Macarovici (1942), having newly discovered Alekseev's work, recognized this relationship and felt that the form described by Alekseev should be considered a variety, *Phoca pontica* var. *sarmatica*. Macarovici realized that these femora (fig. 1g, h, i) by no means matched the original illustration of the femur (fig. 1a) of *Phoca pontica*, but claimed that they fitted Eichwald's description of this bone. Actually, Eichwald's description agrees with his illustration quite adequately, and the measurements given in his text are exactly those of the illustrated femur. In the meanwhile Kretzoi (1941), who had not seen Alekseev's (1924b) work, recognized that the "*Phoca pontica*" of Simionescu (fig. 1h) had peculiarities which demanded its removal from the genus *Phoca*, and accordingly he renamed it *Pontophoca simionescui*. Friant (1947) had at hand an illustration of this peculiar femur which, following Simionescu, she believed to be representative of *Phoca pontica* Eichwald. Although apparently unaware of Kretzoi's work, she too recognized that this femur did not belong to the genus *Phoca*, and considered it to be allied to the modern tropical seal. Thus *Phoca pontica* Eichwald was termed *Monachus ponticus* (Eichwald) by Friant. In fact, this femur seems to bear little resemblance to that of the modern genus *Monachus*, or any other Recent genus. It is generically distinct and under the rules of priority it should retain the generic name given it by Kretzoi (1941) and the specific name given it earlier by Alekseev (1924b). It is therefore now designated *Pontophoca sarmatica* (Alekseev) McLaren n. comb. It is just possible that there are two types of seals involved under this name, in view of the wide range of size shown by the femora (fig. 1h, i), but the point to be made here is that they are not representative of, nor even related to the type material of *Phoca pontica*.

Macarovici (1942) also attempted to clear up confusion surrounding three other species of seals: *Phoca novorossica* Alekseev (1924b), *P. bessarabica* Simionescu (1926), and *P. vindobonensis* Toula (1898). In doing so, he reduced the second to synonymy with the first, on the basis of supposed resemblances of their femora and pelves. However, Alekseev stated emphatically that his *Phoca novorossica* was a small species, comparable in size with *Phoca vindobonensis* of the Vienna basin. *Phoca bessarabica*, as described by Simionescu and later by Macarovici and Oescu (1941), was a much larger form comparable in size with *Monotherium maeoticum*. The femora (fig. 1c, f) of the two forms that Macarovici considered synonymous actually bear little resemblance to one another and are respectively ca. 65 and 94 mm long. The pelves are more alike in appearance but show the same disparity of size. One might accept Macarovici's contention that size alone is not sufficient to separate these species, but at this point the status of *Phoca pontica* becomes involved. Since Macarovici had decided that the "real" *Phoca pontica* was represented by the peculiar femur discussed above (*Pontophoca sarmatica*), he concluded that the femur (fig. 1a) illustrated by Eichwald belonged to the species *Phoca novorossica* (fig. 1c), with which he considered *P. bessarabica* (fig. 1f) to be synonymous. There seems to be no justification for this identification of the femur originally described among the type material of *Phoca pontica*.

Kretzoi (1941) was unsatisfied with the supposed affinities of the femur and humerus illustrated by Eichwald as *Phoca pontica* and believed that they were referable to the Monachinae. He therefore proposed a new genus for the species and called it *Monachopsis pontica*, without designating a lectotype. No other worker seems to have considered this possibility, which appears unlikely as regards the femur at least, considering the small size of the bone and its resemblance to femora of other species of *Phoca*. The humerus is rather shorter and thicker than comparable bones from Recent *Phoca*, but these differences do not seem to be a sufficient basis for Kretzoi's new generic name.

Bogachov (1927) described a humerus from Sarmatian deposits near Baku on the Caspian Sea which was almost identical with that described by Eichwald among the type material of *Phoca pontica*.

Finally, Calvert and Neumayr (1880) have listed a few remains from Turkey which they believed were identifiable as *Phoca pontica*. Unfortunately, they gave neither measurements nor illustrations which would perhaps demonstrate the affinities of their finds, for at that time they seemed unaware of the possible existence of more than one species of seal in Sarmatian deposits.

There remains, then, the problem of redefining *Phoca pontica*, which has been cleared of some unrelated material, but which probably contained more than one species as described. For these reasons we must choose a lectotype from the type material of Eichwald (1853).

The fossils which were described in the original publication without designation of a holotype were all from the Kerch peninsula. Among them were a part of the cranium, a few teeth, some vertebrae, part of the sternum, a fragment of the scapula, the pelvic girdle, humerus, femur, radius, tibia, patella, some of the bones of the carpus and tarsus, and some phalanges. Eichwald mentioned the larger Bessarabian fossils, which later became *Monotherium maeoticum* (Nordmann, 1860), but these did not acutally enter into his description of *Phoca pontica*. Indeed, Eichwald thought that his fossil seal must have resembled closely the modern harbor seal, *Phoca vitulina*, and apparently used the skull of this living species as a model from which to outline the missing portions of his fossil skull. Thus we may take Eichwald's *Phoca pontica* as based on specimens from the small species of *Phoca* which were actually included in the collection which he described. Of those who have sought to define or rename *Phoca pontica*, Alekseev (1924a) was the first, and he alone has described further material (the anterior fragment of a skull) which has given us a more precise conception of this small species of seal and which agrees with at least part of Eichwald's type material. It is felt that the posterior part of the skull, well matched by the anterior part discovered by Alekseev (as shown here in fig. 2), should serve as the restricted type material, and it is therefore designated as the lectotype of *Phoca pontica* Eichwald. Other parts of the skeleton included in the original description are problematical. They were collected over a period of time from beds in two localities and we are given no information on which bones were found grouped together. For reasons which will be given later (p. 59) the first metatarsus illustrated by Eichwald can safely be placed in the same species as the skull. Although the femur appears perfectly suitable as part of a small species of *Phoca*, it has been the subject of so much controversy that it had best be excluded from

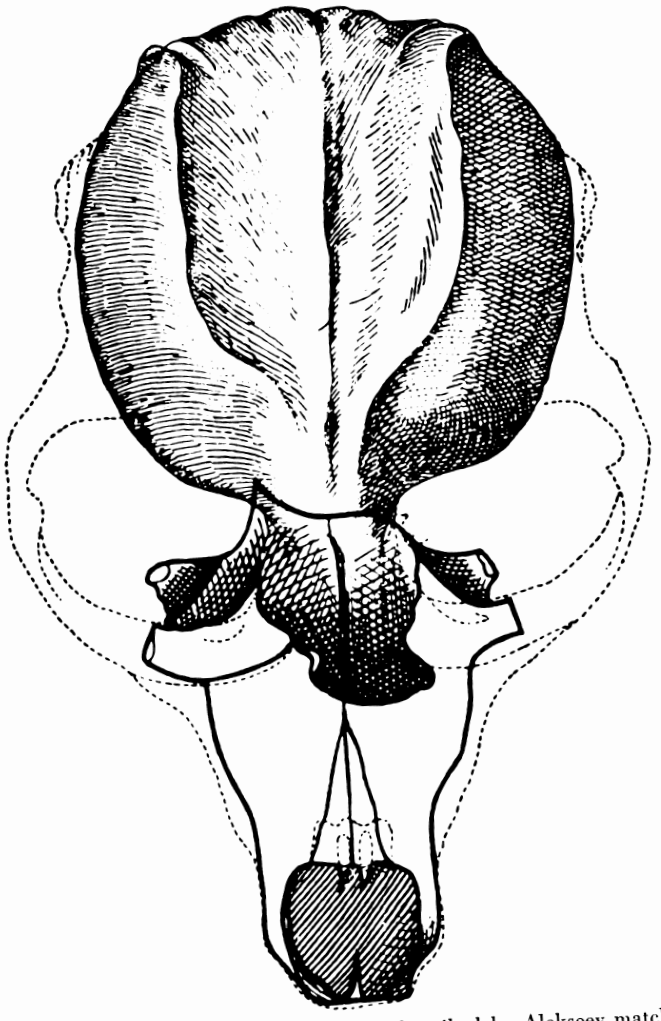

Fig. 2. The anterior fragment of the skull described by Alekseev matched with the posterior fragment illustrated by Eichwald (1853) as the type of *Phoca pontica* (×1). The dotted outline represents Eichwald's attempt to reconstruct the skull, using *Phoca vitulina* as a model. From Alekseev (1924a).

Phoca pontica for the present; the same is true of the humerus. Other bones should be referred to *Phoca pontica* only if they can be shown in future studies to belong to the same species of seal represented by the skull and first metatarsus.

Eichwald had supposed that the fragment of the cranium of *Phoca pontica* indicated close affinities with *Phoca vitulina*. In fact, the small size of the cranium which he has reconstructed, which is evidently from an adult, makes a relationship with the subgenus *Pusa*, or ringed seal group, far more likely.

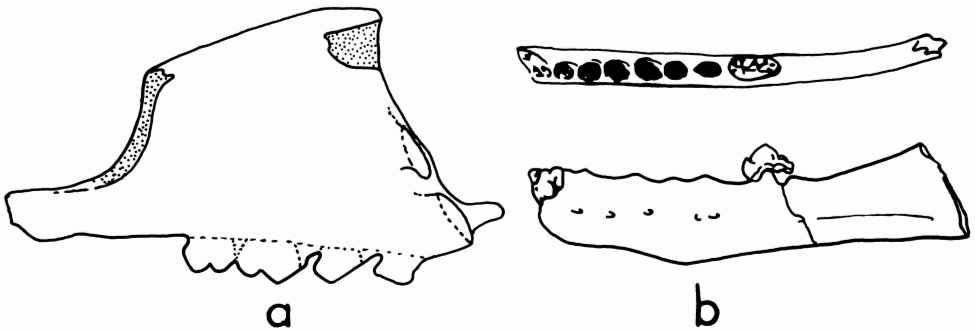

Fig. 3. Significant fossils from the upper Miocene (×1). At left (a) outline sketch from a photograph of the anterior fragment of the skull attributed to *Phoca pontica* by Alekseev (1924a). The teeth appear to be obscured by matrix in his photograph. At right (b) the lower jaw described by Kretzoi (1941) as *Praepusa pannonica*, as redrawn from his sketch.

The facial portion of the skull (outlined here in fig. 3a) which Alekseev (1924a) referred to *Phoca pontica* is most important. Alekseev compared it with skulls of *Phoca hispida*, *P. vitulina*, and *Pagophilus groenlandicus*, but did not ascribe it to any of these species. Although he found most points in

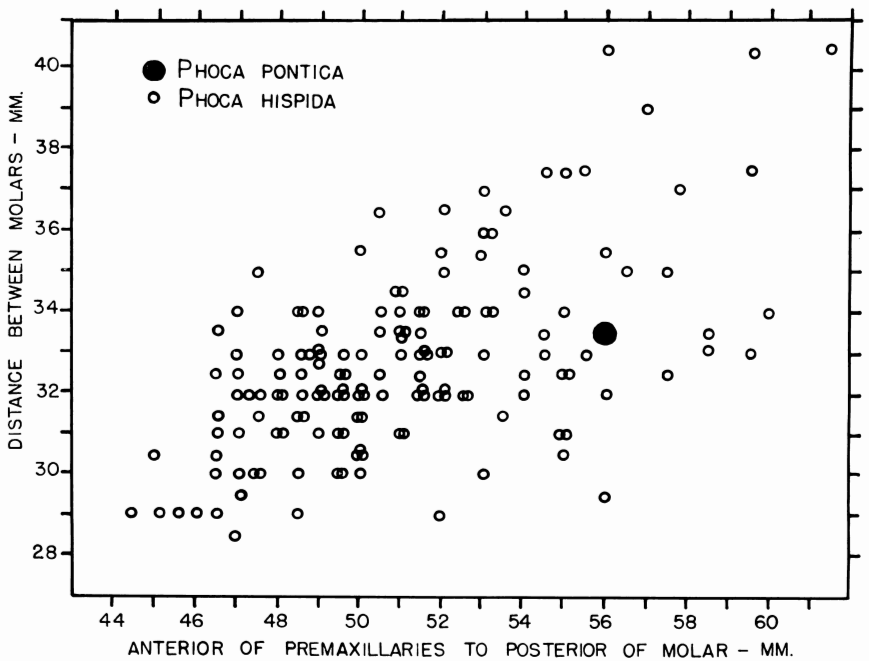

Fig. 4. Comparison of general form and size of the snout of *Phoca pontica* with the range shown by adult *Phoca hispida* (all aged at more than 7 years) from various localities in the Canadian Arctic. The distance between the molars (M_1) of *Phoca pontica* is listed by Alekseev (1924a): the distance from the anterior tip of the premaxillaries to the posterior margin of the molar was measured from his photograph.

common with *Phoca hispida*, he supposed that the muzzle was in general too elongate to resemble that of the living form. In fact, such elongation is typical of adult *Phoca hispida*. It is plain from figure 4 that Alekseev's specimen, here referred to *Phoca pontica*, does not differ from *Phoca hispida* in size or relative length of snout. A few years after Alekseev's study, Bogachov (1927) compared Alekseev's specimen with the equivalent part of the present Caspian seal and found many points in common. However, perhaps because he was misled by the skeletal material discussed above, it seemed impossible to Bogachov that *Phoca pontica* could be ancestral to the living form. Chapsky (1955b) has left no doubt that Alekseev's find belongs to the subgenus *Pusa* and the present author agrees completely with this conclusion.

The northern seals (Phocinae) can most readily be separated on the structure of the jaws and teeth, and Chapsky seemed unaware that Kretzoi (1941) had made a very significant find. Kretzoi described from middle Sarmatian deposits near Budapest a fragment of a mandible (fig. 3b) which is unquestionably of the subgenus *Pusa*, in view of its light structure and small last molar (the only tooth remaining). He was fully aware of its relationships and named it *Praepusa pannonica*. Since *Praepusa* has no characters separating it from *Phoca* (*Pusa*), Kretzoi's generic name must be changed to *Phoca*.

Bogachov (1927) believed that a humerus and a femur from Sarmatian deposits of the Caspian basin were referable to *Phoca vindobonensis* Toula (1898). These fossils were also noted as being very similar to the equivalent bones of the present Caspian seal, and Bogachov offered this as evidence of the late Miocene origin of the modern species. Chapsky (1955b) also stressed the resemblances between parts of *Phoca vindobonensis* and *P. caspica*.

Undoubtedly more of the bones of Phocinae described from Sarmatian deposits will prove to belong to the subgenus *Pusa*. In the author's opinion these fossils are best considered as marking a southward extension in the range of ancestors of *Phoca hispida*, which have since been isolated to give rise to the present Caspian seal. It seems unlikely that more than one species of this subgenus existed in Sarmatian waters, and while a conservative attitude must be taken at present, it is probable that fossils from this subgenus will be shown in future to be referable to *Phoca pontica*, as here restricted. Information is badly needed on the extent of variation of the limb bones of the living species in order that species may be more sensibly defined among the fossil seals.

The formal synonymy of the relevant species is summarized here. Lectotypes are chosen for all species in which a holotype was not designated and comments are offered on some of the referred material. Kellogg (1922) is the most useful source of further references, not involving the status of *Phoca pontica*, but concerning some of the listed species.

Subfamily Monachinae

Monotherium maeoticum (Nordmann)

Phoca pontica (p.p.) Eichwald, 1853.
Ph(*oca*) *maeotica* Nordmann, 1860.
Phoca maeotica Alekseev, 1924b; Simionescu, 1926; Macarovici and Oescu, 1941; Macarovici, 1942.

(*Monatherium*) *maeoticum* Trouessart, 1897.
Monotherium maeoticum Kellogg, 1922.
Monatherium maeoticum Friant, 1947.

Lectotype: The femur described and illustrated by Nordmann (1860, text p. 321, atlas pl. 23, figs. 8 and 9) as part of the type material.

Comments on referred material: According to Alekseev (1924b) the femur, humerus, radius, and pelvis in Nordmann's figures are attributable to this species, while the cubitus and the tibia belong to *Pontophoca sarmatica*.

Range: Lectotype from Sarmatian limestone in vicinity of Kishinev. Apparently confined to Bessarabian deposits.

Subfamily Monachinae?

Pontophoca sarmatica (Alekseev), n. comb.

Phoca sarmatica Alekseev, 1924b.
Phoca pontica Simionescu, 1926; Macarovici and Oescu, 1941; Macarovici, 1942.
Phoca pontica var. *sarmatica* Macarovici, 1942.
Pontophoca simionescui Kretzoi, 1941.
Monachus ponticus Friant, 1947.

Lectotype: The femur described and figured by Alekseev (1924b, p. 203, fig. 6) as part of the type material.

Comments on referred material: The humerus described and figured in the type material may belong with *Phoca bessarabica* according to Macarovici (1942). Other material acceptable as this species includes the femurs described as *Phoca pontica* by Simionescu (1926) and Macarovici and Oescu (1941).

Range: Precise locality of lectotype not given. Found in middle Sarmatian beds near Kishinev and also near Tsmiliansk on the Don River.

Subfamily Phocinae

Phoca (Pusa) pontica Eichwald

Phoca pontica (p.p.) Eichwald, 1853.
Phoca pontica Alekseev, 1924a: Kirpichnikov, 1953.
Phoca pontica (?) Bogachov, 1927. (See below).
Monachopsis pontica (?) Kretzoi, 1941. (See below).
Phoca novorossica (p.p) (?) Macarovici, 1942. (See below).
Not: *Phoca pontica* Peters, 1867.
Phoca pontica Simionescu, 1926; Macarovici and Oescu, 1941; Macarovici, 1942.
Phoca pontica var. *sarmatica* Macarovici, 1942.

Lectotype: The fragment of the cranium described and figured by Eichwald (1853, text p. 391; atlas pl. 13, fig. 1).

Comments on referred material: The metatarsus I of Eichwald's type material and the anterior fragment of the skull described by Alekseev (1924a) are safely referable to this species. Possibly also the femur illustrated by Eichwald, renamed *Monachopsis pontica* by Kretzoi (1941), and attributed to *Phoca novorossica* by Macarovici (1942). The humerus (also renamed as part

of *Monachopsis pontica* by Kretzoi and found in Caspian basin deposits by Bogachov, 1927) is problematical.

Range: Lectotype from upper (?) Sarmatian of Kerch Peninsula (Crimea), but precise locality not given. Other specimens were collected later from Sarmatian limestone near Kishinev and (possibly) from the Sarmatian of the Caspian basin near Baku.

The following are maintained as separate species, with the understanding that parts of any of them may in future be referable to *Phoca pontica* Eichwald or that synonymies may exist between them.

Phoca vindobonensis Toula

Phoca pontica Peters, 1867.
Phoca vindobonensis Toula, 1898, and all subsequent authors.
Phoca vindobonensis Bogachov, 1927.

Lectotype: The femur described and illustrated by Toula (1898, p. 62-63, pl. 2, fig. 2a, b, c) as part of the type material.

Comments on referred material: No problems of the affinities of the type material have been raised.

Range: Lectotype from Sarmatian near Vienna (Kreindl's brickyard on the Nussdorf road near Heiligenstadt). Since from Vienna basin and Sarmatian deposits near Baku, on the Caspian Sea.

Phoca novorossica Alekseev

Phoca novorossica Alekseev, 1924b; Friant, 1947.
Phoca novorossica (exclusive of parts belonging to *P. bessarabica*) Macarovici, 1942.
Not: Femur illustrated by Eichwald as *Phoca pontica* and referred to *Phoca novorossica* by Macarovici, 1942.

Lectotype: The femur described and illustrated by Alekseev (1924b, p. 203, fig. 10) as part of the type material.

Comments on referred material: Some parts of the type material may belong with other species according to Macarovici (1942). Although Macarovici thought the femur resembled that of *P. bessarabica*, this is not so (see fig. 1c and f here), and the femur is safely chosen as the lectotype. The small pelvis seems validly included with the femur of this species.

Range: Locality of lectotype not given. Found in Sarmatian of Bessarabia, Odessa, on the lower Dnieper River, and near Stavropol.

Phoca bessarabica Simionescu

Phoca bessarabica Simionescu, 1926; Macarovici and Oescu, 1941.
Phoca novorossica (p.p.) Macarovici, 1942.

Lectotype: The pelvis described and figured by Simionescu (1926, p. 187, pl. 2, fig. 1) as part of the type material.

Comments on referred material: Unfortunately, the femur had not been discovered when this species was described and the pelvis must serve as the lectotype. The femur was described and figured by Macarovici and Oescu (1941). Macarovici (1942) then reduced this species to synonymy with *P.*

bessarabica, but this is rejected here for reasons given above.

Range: Lectotype from middle Sarmatian limestone near Kishinev, and since only from that locality.

Phoca (Pusa) pannonica (Kretzoi)

Praepusa pannonica Kretzoi, 1941.

Holotype: As defined by Kretzoi (1941, p. 275, fig. 1), the fragment of a left lower jaw.

Comments on referred material: Kretzoi defined as paratypes the proximal and distal ends of the left tibia and the distal end of the left fibula.

Range: Type and paratypes from the lower middle Sarmatian (Ukrainium) of Erd, near Budapest (6 m. deep in Cerithian chalk on the property of Franz Bitter).

Pleistocene fossils.—Another form of paleontological evidence is the demonstration that seals very like the modern Caspian species were present during early Quaternary times. A fossil tibia, indistinguishable from the comparable bone of the present Caspian seal, has been described by Vershchagin and Gromov (1952) from a site on the Ural River, over 500 km. north of the shore of the present Caspian Sea. They could not give the precise stratigraphic position, but attempted to correlate it by indirect means with the Kvalinsk transgression of the Caspian Sea (last or Würm glaciation). This find cannot be adduced as evidence for a pre-Pleistocene arrival, for the proponents of Pleistocene origin suggest that the previous glaciation (third, or Riss) was responsible for the arrival of seals. It should be noted, however, that the Pleistocene fossils of ringed seals are in their turn indistinguishable from the modern species, *Phoca hispida* (see Kellogg, 1922).

A more significant fossil was described by Kirpichnikov (1953) from the south coast of the Sea of Azov, from deposits which are correlated with the Bakinsk transgression of the Caspian Sea of the early Pleistocene (second or Mindel glaciation). At this time the Black (Azov) and Caspian Sea basins were connected. The bone, a first metatarsal, was found in fluvial deposits, along with the remains of early Pleistocene terrestrial mammals (*Elephas meridionalis, Equus sussenbornensis*, etc.). Since the deposit contained redistributed fragments of the middle Sarmatian marine mollusc, *Cryptomactra pesanseris*, it had been considered possible that the seal bone was of Sarmatian age as well. However, Kirpichnikov rejects this conclusion by comparing the metatarsal with equivalent bones from one contemporary *Phoca caspica* and three upper Sarmatian seals referred to *Phoca pontica* (and wholly comparable with the first metatarsal illustrated by Eichwald, 1853). Indeed his measurements and figures do suggest that the fossil from the Sea of Azov matches best with *Phoca caspica*, but they also stress that there is very little difference between the metatarsal of the modern seal and those of the Sarmatian species. Kirpichnikov cites records of the entry of the present Caspian seal far into rivers as pointing to the way in which the fossil bone came to be found in fluvial deposits, along with remains of terrestrial mammals.

The evidence suggests, then, that a seal very like the modern Caspian seal was present in the Black Sea basin during early Quaternary times, before the

putative Riss glacial entry of seals into the Caspian Sea. Kirpichnikov does not concern himself with the possibility of genetic ties between the late Miocene seals and the modern form, but if his argument on the age of his fossil is disputed, the only alternative is that a seal very like the modern Caspian seal was present in the Black Sea basin during Sarmatian times, which has already been shown on other evidence.

Apparently other remains of seals (cited by Bogachov, 1927, Kirpichnikov, 1953, and Chapsky, 1955b) were found in the Bakinsk (lower Pleistocene) deposits of the Caspian Sea itself, but unfortunately these do not appear to have been compared with material from the Recent species.

If seals of the subgenus *Pusa* were thus present in Sarmatian waters, and if seals very like the present *Phoca* (*Pusa*) *caspica* were found there during early Quaternary times, then we must accept these as substantial refutations of the theory of later Pleistocene origin of the Caspian seal.

While there is no fossil evidence for the Baikal seal, it would be an economy of theory to explain their presence in the same way. We must finally fall back on the fact that the Baikal seal is more than slightly differentiated from the ringed seal.

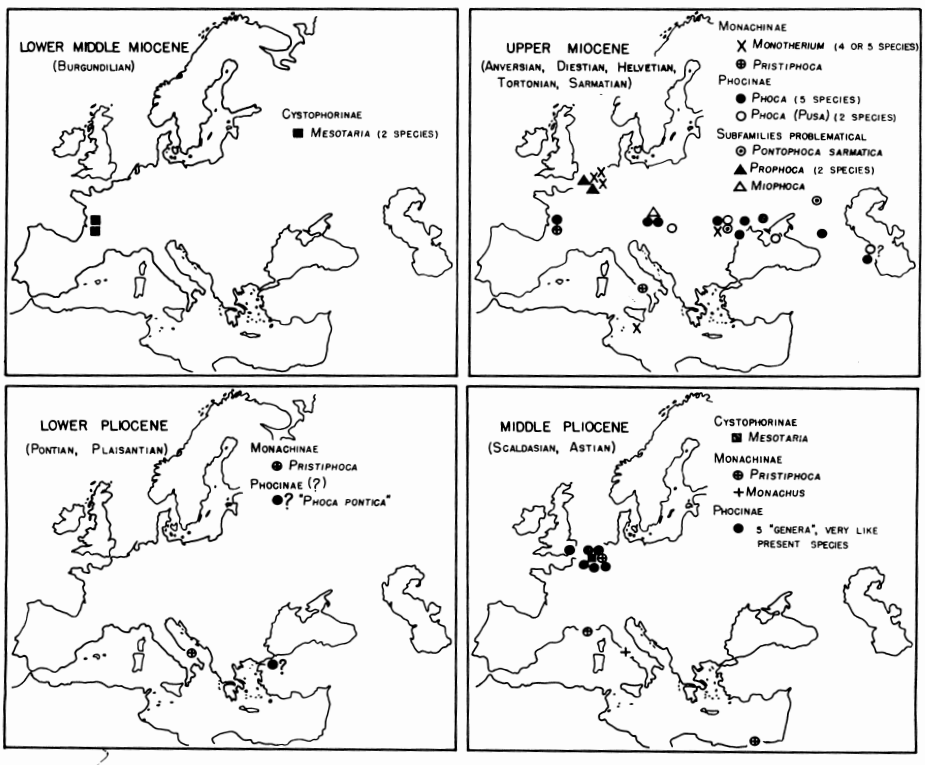

Fig. 5. Geographic and stratigraphic distribution of fossil seals in Europe. Each symbol represents a described species in each locality.

THE ROUTES OF ENTRY OF THE SEALS

It will be profitable to refer briefly to the overall fossil record (fig. 5). Although Cetacea are known earlier, the first fossils of seals in Europe are teeth found in the middle Miocene of southwest France. These are problematical, but are referred to the subfamily Cystophorinae (elephant and hooded seals).

Numbers of seals are described from the marine deposits of the upper Miocene, including those dealt with above. It can be noticed on figure 5 that, while the Sarmatian basin had several species of *Phoca* as well as seals of the tropical-Antarctic group, the Mediterranean and western European fossils are mostly of the Monachinae, except for a single femur from southwest France described as *Phoca couffoni* by Friant (1947) and two large hair seals (*Prophoca*), certainly not closely related to the modern northern seal group, from Anversian deposits.

The lower Pliocene has not produced much fossil material, but fragmentary remains from Turkey were referred to "*Phoca pontica* (see p. 53) and a seal (*Pristiphoca*) from Italy is close to the modern tropical seal (Friant, 1947, has in fact referred *Pristiphoca* to the genus *Monachus*).

In the middle Pliocene a whole host of species appears in the deposits of Belgium and Holland. One is of the Cystophorinae and one of the tropical-Antarctic group, while the others are "genera" (Friant, 1947, has reduced all but one to *Phoca*) quite close to the modern Phocinae. In the Mediterranean, the modern tropical seal was present.

Davies (1958b) has argued cogently for the origin of the Pinnipedia in the Arctic basin, and for the continuous restriction of the Phocinae to the northern hemisphere, by stressing the relative stenothermy of all except the Monachinae (all others live only in waters of less than 20°C maximum). There is little doubt that for the northern seal group during the late Miocene, the route around western Europe, through the Mediterranean, and into the Sarmatian Sea would have been too warm. The discovery of only one species of *Phoca* in deposits of that time in western Europe also suggests this (and *P. couffoni*, based on only one specimen, might bear re-examination). We must then consider a route of entry from the north.

Kretzoi (1941) saw no difficulty in connecting his *Praepusa pannonica* of Hungary with living seals of the same group, and with a zoogeographical flourish he created a "paratethys" in which the ancestral seals were developed. Along with two openings to the Arctic, one to the Mediterranean, and one to the Pacific, this Paratethys Sea was extended to cover Lake Oron, the Aral Sea, and Lake Kuku-nor, where no seals exist (p. 48). Kretzoi's Paratethys is purely imaginary, although his fossil find cannot be denied.

The northern shore of the Sarmatian Sea is difficult to restore with precision, since erosion has destroyed the deposits (Chapsky, 1955b). Although a connection between the Tethys Sea and the Arctic Ocean was present during early Tertiary, its existence during Miocene times seems problematical (Ekman, 1953). Nevertheless, it is felt that some connection must be invoked to get northern seals into southeastern Europe in the late Miocene. Seals are quite capable of moving into fresh water, and the connection need not have

been strictly marine. However, as well as the ringed seal group, other types of northern seals appear to have been present, including forms which may have resembled more the modern *Phoca vitulina* and *Halichoerus* (the jaw of *Miophoca vestuta* Zapfe is supposed by Chapsky, 1955a, to resemble that of *Halichoerus*). All in all, a fully marine connection seems more likely, although not absolutely necessary to the argument.

Probably the late Miocene marine transgressions, well known in Europe, extended either from the Arctic or from the Sarmatian Sea and brought the seals close to Lake Baikal. Certainly the fauna of this ancient lake, except for the seal and possibly an amphipod, has otherwise been isolated from marine invaders from a time earlier than late Miocene (Brooks, 1950). The Arctic ringed seal probably swims in and out of Nettilling Lake, Baffin Island, (see Manning, 1943) and the same capacity might have enabled the late Miocene seal to enter Lake Baikal, even if that lake were above sea level. Davies (1958) cites evidence for epeirogenetic uplift during Pleistocene, arguing that the entrance of the lake by the seal occurred during Pleistocene before that uplift; the same evidence might indicate that the lake was even more accessible in late Miocene.

In summary, the progenitors of the Caspian seal and probably of the Baikal seal can be considered to have arrived from the northern seas by connections, which were essentially marine, in late Miocene times.

THE IMPLICATIONS FOR PLEISTOCENE ZOOGEOGRAPHY

It can be seen that the demonstration of the probable Tertiary origin of the Caspian seal casts at least some doubt on the significance of the great Siberian ice-dammed lake as an agency in zoogeography. Certain Russian and western European authors have made wide use of this lake in their theories. Segerstråle (1957) used it to get an amphipod (*Pallasea*) into Europe during the third glaciation. All the northern elements in the Caspian Sea are explained by it (Pirozhnikov, 1937). Gur'ianova (1939) demanded that it be brackish for some zoogeographical purposes, and suggested that it has been concerned in establishing certain brackish water animals in North America as well. Perhaps a note of caution should be offered. Many of the relict species in lakes which have been analysed in the light of Pleistocene events are widespread (some Holarctic) and very successful. They are also geographically little differentiated, but this may reflect stability rather than recent isolation. It would be profitable to reexamine some of these species to determine whether they were established as fresh-water relicts before Pleistocene times in parts of their present range. This applies particularly to the presumed Pleistocene relicts of the Caspian Sea.

THE IMPLICATIONS FOR PALEOCLIMATOLOGY

As Chapsky (1955b) has pointed out, the presence of the progenitors of the Caspian seal in Sarmatian Seas implies that ice must have formed at that time. Actually, accepting the fossil evidence and its correlations does not absolutely necessitate that we believe ice formed in the Sarmatian Sea, but makes it almost certain that ice formed somewhere during that time, as the following arguments will show.

It might be argued, against all probability (see p. 48), that the white-coat pup arose independently in the several groups of the subfamily Phocinae. But the argument that it arose independently in the three closely related species of a subgenus within that subfamily is even more untenable. If one of this primitively ice-breeding group has lived continuously in the Caspian basin since late Miocene, then ice was almost certainly present somewhere at that time.

Although it seems more simple to suppose that the seals retained the ice-breeding habit in the Sarmatian Sea, it could be argued that they lost this habit when they spread into southern regions, where ice was not available. This has happened to different degrees in two modern species (see p. 48). The Caspian seal has lost the specialized relationship to fast ice shown by the ringed and Baikal species (see p. 49) and this might be taken as an indication of adaptation to periods when there was much less ice and snow than found today. It is also possible that the fossils of *Phoca pontica* from southern Russia are from seals which died far to the south of their breeding range. The modern Caspian species finds ice only in the north, although it migrates annually to the southern end of the sea.

In considering the climatological significance of the Monachinae, related to the modern tropical seals, it should be remembered that there were several types of Monachinae present, and that the modern group also includes four Antarctic species. The subfamily was quite likely Tethyan in origin, and their eurythermy may have permitted them to transgress the tropics during Miocene times, thence to colonize Antarctica (Davies, 1958b). Thus the admixture of fossils from the tropical-Antarctic and northern seals is not as paradoxical as it seems at first. Perhaps significant also are the facts that only near Kishinev is *Phoca pontica* found in the same locality with other seals, and *Phoca pannonica* is found alone. Unfortunately, the precise stratigraphic positions of many of the fossils are not given, but it is quite possible that seals of the subgenus *Pusa* were not strictly contemporaneous with seals belonging to the Monachinae.

There is also the problem of why only the Caspian seal of the several Phocinae present and none of the Monachinae should have survived to the present day. This can be attributed to post-Miocene climatic vicissitudes, and it is noteworthy that only the members of the ringed seal group normally keep open holes in the ice during an entire winter season, although other northern species may maintain holes briefly.

Other evidence can be brought forward to suggest that the climate of the late Miocene was sufficiently cool to form ice.

In the seas, there is evidence (in displacement of large boulders; Chapsky, 1955b) that ice was present in the Pontian Sea, at least. Ekman (1953) discussed the climatic deterioration in the Caribbean and elsewhere during Miocene. Today's marine temperatures were essentially reached in the Pliocene (the late Miocene was only a little warmer) on the west coast of North America (Durham, 1950).

MacGinitie (1958) has recently reviewed our knowledge of climate since the late Cretaceous, with special reference to the history of the floras of west-

ern North America. The late Miocene was certainly warmer than at present, although most of the southward migration of the forests was completed by that time. Climatic zonation certainly existed in late Miocene, and while the western United States seemed little influenced by polar air masses, MacGinitie suggests that winter conditions occurred and snow probably fell in the northwestern United States. The European floras seem to have been affected more by Pliocene cooling.

In conclusion, ice undobutedly formed in the northern seas and probably in at least the innermost reaches of the Sarmatian Sea during late Miocene. This emphasizes the statement of Barghoorn (1953) that

> the great trend of Cenozoic climate which culminated in Pleistocene glaciation began in the mid-Tertiary, probably more than 20 million years ago. Pleistocene glaciation itself . . . may then be regarded as a geologic and climatologic event the antecedents of which extend over a fair segment of recent geologic time and is not to be viewed as a sudden change in the history of the earth's climate.

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