# CONTRIBUTION TO THE PROBLEM OF THE HISTORY OF DEVELOPMENT OF THE CASPIAN AND BAIKAL SEALS

by

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It is hardly necessary to list the hypotheses that have been offered to explain the modes of penetration of seals into the Caspian Sea and Lake Baikal. These have been repeatedly cited in the works of L. S. Berg (1910), V. V. Bogachov (1927a, b), S. I. Ognev (1935), M. M. Kozhov (1947), and other authors, who give an account of the essence of the various standpoints contained therein. It should be mentioned that two fundamental points of view exist concerning this problem. According to one, Caspian (*Phoca caspica* Gmel.) and Baikal (*Phoca sibirica* Gmel.) seals are relatively recent emigrants from the North; according to the other—they have their origin in the Upper Tertiary seals of the interior Sarmatian-Pontian basin.

The absence of unity of opinion and the insufficient substantiation of both these hypotheses have induced the writer to express his own judgments based on the revision of

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the taxonomic features that are characteristic of the individual species of seals of the subgenus *Pusa* Scopoli. These judgments take into account paleontological and in part certain ecological data.

## Comparative morphological data

The solution of zoogeographical riddles, embodied in the contemporary distribution of Caspian and Baikal seals, is still made difficult by the scarcity of paleontological finds. The data of comparative morphological analysis acquire all the more importance in this connection, in spite of a certain subjectivity of the evaluation of the morphological distinctions especially, or those pertaining to older features.

The last circumstance, in turn, cannot fail to find its reflection in conclusions pertaining to the greater or lesser affinity of the individual species of the discussed subgenus.

A. Features of craniological similarity between the Baikal seal and the ringed seal:

1) "Brachycephaly": considerable shortening of the cerebral cranium, especially noticeable in comparison with its width (Fig. l);

2) Approximately equal dimensions (smaller than those of the Caspian seal) of the section of the rostral length confined between the middle part of the nasal aperture

[apertura nasalis][†] and eye socket [orbita] at the level or the upper margin of the zygomatic process of the upper jaw bones [maxillae] (Fig. 2).

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3) The size of the occipital opening [foramen occipitale magnum] (which is on the average considerably larger than that of the Caspian seal);

4) The shape and the size of the bone blade of the auditory duct [external auditory meatus] and the direction of its outer-posterior margin;

5) The shape of the nasal aperture: its maximum width in the upper posterior half (Fig. 2);

6) The steeper drop (when viewed in profile) of the intermaxillary bones limiting the nasal opening accompanied[†] by a certain break (in the majority of individuals) near its base;

7) Equal length of the cheek bone (without the branches of the processes) and the identical structure of its posterior processes, of which the upper one is shortened and the lower one is relatively sturdy;

8) Angular shape of the posterior margin of the palate [ossum palatum durum];

9) The structure of the lower jaw (except for teeth);

10) The presence of unfused roots of the first premolar of the upper jaw in a considerable number of individuals;

11) Non-coalescent tubercles [tuberculi] on the shoulder bone.

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[†] *N.b.* Here and throughout the following text Latin terms are appended [in brackets] to the colloquial anatomical terms whenever the translator has had any doubts about the appropriateness of the former terms [translator's remark].

[†] [translator's remark].

B. Features of craniological similarity of the Baikal seal with the Caspian seal:

1) Relatively small size of the braincase [cranium].

2) Small size of osseous cells ]bulla osseae] (Fig. 4).

3) Comparatively small depth of indentation of nasal bones into frontal bones;

4) Considerable extent of contact area of the nasal processes of intermaxillary bones with nasal bones;

5) A moderate divergence of the maxillary rows of teeth in the anterior-posterior direction;

6) Greater width of the anterior rim of cheek bones (of their articular surface) in comparison with the width between the most protruding points of the posterior processes of these bones.

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Therefore, the Baikal seal shows almost twice as many osteological features allying it to the ringed seal as compared with features relating it to the Caspian seal.

Finally the following series of craniological features must be noted, according to which the Baikal seal occupies, so to speak, an intermediate position between the ringed seal and the Caspian seal:

1) Width of the cranial case;

2) Length and width of the rostral part of the skull;

3) Width of the anterior rim of cheek bone (in young individuals – equal to the width between the extreme points of the posterior processes or less than this width, in the adult individuals – usually somewhat exceeding the width between the posterior (Fig. 5);

4) Relationship between the length of the osseous cells [bulla osseae] and the interval between them;

5) Position of the osseous cells [bulla osseae] in relation to the posterior process of the glenoid fossa;

6) The shape of the hook-like branches [processus coracoideus] of the pterygoid bone [os pterigoideum];

7) The presence of a noticeable diastema between the fourth premolar and first molar teeth.

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The craniological similarity between the Caspian seal and the ringed seal is relatively insignificant. It consists essentially of two features: first, in the structure of the teeth of the lover jaw (size, distribution on the jaw bone with intervals, and the sharp decrease in size of the crown of the first premolar); second, in the width of the nasal bones.

At the same time, the skull structure of the Caspian seal also shows features that are transitional between those of the ringed seal and the Baikal seal, such as the width of the skull at its cheek bones and the shape of the anterior rim of the nasal bones.

A rather complex interweaving of the features of similarity and dissimilarity thus arises between the compared species.

A simple computation of the number of similar morphological features would be insufficient to give a clearer idea as to which of the three compared species is more closely allied to one of the other two. Such morphological features can be the result of

parallel development under the influence of more or less similar ecological factors acting upon a different morphological starting base[†].

Such parallel features, which ally the Baikal seal partly with the ringed seal and partly with the Caspian seal, can be considered to include the outline of the posterior rim of the palatal bone [os palatum durum], the relationship between the width of the posterior and anterior rims of the cheek bones, the features of the structure of the lower law, and some other features.

The analyses of relatively ancient (primitive) features, which have simultaneously the greatest taxonomical value, is a firmer foundation for the construction of phylogenetic lines.

Such features, which arose in more ancient times and reflect taxonomic features of a more general character, also usually display a greater stability.

From among the features of the skull allying the ringed seal with the Baikal seal, the shape of bony blades of the auditory canal, the steep drop of the profile of the rostral part of the skull in the area of the nasal opening, the unfused roots of the first premolar, and other features may be considered as relatively primary and more primitive features. Among the features allying the Baikal seal with the Caspian seal, the lesser size of osseous cells [bulla osseae], the somewhat lesser indentation of nasal bones into the frontal bones, and the greater extension of the nasal processes of the intermaxillary bones along the nasal bones can be considered as such.

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[†] Morphologically different organisms are meant [translator's remark].

With regard to features in the structure of teeth, which have the greatest diagnostic value, a great similarity can be demonstrated between ringed seal and the Caspian seal.

All this appears to attest sufficiently to the ancient and intimate connections between all three forms.

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The separation of leading features, which are essential for phylogeny, – is a difficulty yet soluble problem. Without taking into account paleontological data, it is much easier to make an error in this instance than to do so while establishing the taxonomic importance of a feature[†]. Just the same, a thorough comparison of the craniological features of the discussed species does not give any reason for such categorical conclusions about the closer systematic affinity of the Baikal seal to the Caspian seal than to the ringed seal, as were reached by Nordquist (1890) and S. I. Ognev (1935). The data analyzed here lead sooner to the opposite conclusion. Such features as the dimensions of the braincase and osseous cells [bulla osseae], which create the greatest external craniological similarity between the Baikal and Caspian seals, are characterized by a considerable variability; they vary not only within the subtribe (subgenus) but also within a species. The size of the bulla osseae shows also individual variability.

From Nordquist's data it follows that the average length of osseous cells in the Ladoga seal (*Phoca hispida ladogensis* Nordq.) amounts to 33.1 mm[1)]. Their length in

[†] Poor wording in original [translator's remark].

[1)] The collections of the Ladoga seal in the ZIN [probably stands for the Zoological Institute of the Academy of Sciences of the U.S.S.R.; translator's remark] (unfortunately rather poor) completely bear out O. Nordquist's data about small size of osseous cells in this subspecies.

this species occupies consequently an intermediate position between the length of osseous cells in the northern seals (36.0 mm) and in the Baikal seal (30.5 mm).

At the same time the average length of osseous cells in the Saima seal (*Phoca hispida saimensis* Nordq.) amounts, according to the data of the same author, to 36.5 mm; thus it even exceeds slightly the average length of the same in the Pomorie seal (*Phoca hispida pomororum* Smirn.).

The larger dimensions of osseous cells of the northern seals, as well as of the Greenland seal, should apparently be evaluated as a more modern feature. It is also characteristic that in the ringed seal, specimens with comparatively small osseous cells sometimes occur.

The results of the previously discussed analysis of morphological similarity between the three species[†] do not allow us to consider any of them as a descendant of any contemporary form, as each of the three species has evolved in its own direction in a greater or lesser degree, after it was isolated in the specifically conditioned environment.

The separated ancestors of the Caspian seal have developed toward further simplification and reduction of size of the first premolar; toward the reduction of the collateral crests of all other teeth of the upper jaw row; toward the alteration of the facial part[†], and changed also with respect to some other craniological features. Among other osteological peculiarities the most noticeable is the increase of shoulder tubercles [tuberculi humeri] to their ring-like fusion. The pattern of the pelt has also developed in a peculiar direction.

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[†] The Baikal, Caspian, and ringed seals are meant [translator's remark].
[†] Of the skull [translator's remark].

The evolution of the Baikal branch of the subgenus *Pusa* in the closed basin underwent a type of adaptation tending toward feeding in the great depths that are characteristic of Lake Baikal. The transition toward almost exclusive fish feeding has, naturally, favored the development of such peculiarities of structure as facilitate the pursuit and capture of a more or less large and mobile prey, such as enlargement of the eyeballs (intensification of sight in conditions of insufficient illumination), lengthening of the muzzle, and enlargement of teeth. The first feature was apparently the principal cause of the widening of the zygomatic arches and has caused the contraction of the infraorbital space. The enlargement of the ossified nasal opening leads to the backward movement and [p. 205] reduction of the middle protuberance of the anterior rim of the nasal bones. The anterior area of the intermaxillary bones has moved somewhat forward and increased in length, apparently in connection with the strengthening of the sphincters of the nostrils. The enlargement of teeth, especially in the lower jaw, has led to the disappearance of diastemata between them; it has also resulted in the convergence of the ipsolateral crests and partly in some tilting of these latter toward the principal crown.

Together with a series of progressive features, the structure of the first premolars of the upper jaw of the Baikal seal (the number of the collateral crowns and a high percentage of not completely fused double roots) reflects the rather ancient features of ancestral forms to a greater extent than those of other contemporary or fossil species of the given subgenus.

In this connection it is interesting to note also that the Pontic seal (*Phoca pontica* Eichw.), in spite of its primitive state, had already at that time outstripped other representatives of subgenus *Pusa*, as can be judged from the fragment of its skull (A. K.

Alekseev, 1924a) in the secondary simplification of the first premolar of the upper jaw; indeed, this latter tooth has completely lost any traces of the double root characteristic of $pm^1$ of the Baikal seal and of the majority of individuals of the ringed seal.

Already this small but rather demonstrative detail makes it extremely difficult to postulate a direct phylogenetic connection of the Baikal seal with either *Phoca pontica* or another Sarmatian-Pontian species closely related to the latter; yet it testifies to the phylogenetic closeness of *Phoca sibirica* to the ringed seal.

The immediate ancestors of the contemporary ringed seal have in their turn progressed somewhat after the branching off of the predecessors of the Baikal seal from them. The craniological evolution of this species went in the direction of: (1) noticeable enlargement of osseous cells, (2) greater depth of indentation of the tip of the nasal bones into the frontal bones, (3) specific development on the hook-like branches [processus coracoideus] of the pterygoid bone, and (4) reduction of the collateral crowns of the upper premolar and molar teeth.

Consequently, all three contemporary species of the subgenus *Pusa* have, all things considered, arisen from a fairly ancient common ancestor; this ancestor had probably combined many of those primary features that determine to a greater or lesser extent the similarity of its contemporary descendants.

In the opinion of the writer, the hypothetical ancestor might have possessed the following craniological features.

The braincase was not characterized by its great bulging; accordingly, the osseous cells were apparently not of large dimensions; they possessed an undeveloped bony blade of the external auditory duct with a broad base. The broad, wedge-like nasal bones with

three anterior projections were apparently only relatively insignificantly indented with the frontal bones. The nasal processes of the intermaxillary bones came in contact with the nasal bones over a considerable stretch. The cheek bones approached those of the contemporary ringed seal in their form (short posterodorsal and moderately long anterior processes). The posterior margin of the hard palate [os palatum durum] was apparently cut out in the form of an angle. The lateral rims of the nasal opening possibly rose fairly steeply toward the anterior end of the nasal bones. It is difficult to say what kind of teeth this ancestor could have possessed. It is very probable that they were situated rather independently and that the well-developed collateral crowns of the teeth of the lower jaw were somewhat deflected sideways (fan-shaped) from the principal crown, etc.

The dim contours of the primary seal, which formed the initial step in the evolution of the three presently existing species, take on approximately the shape described above.

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According to some comparable features, the Upper Miocene seal *Phoca pontica* Eichw. (see fragment of the facial part of the skull figured in the article by A. K. Alekseev [1924a]) corresponds fairly well morphologically to this roughly sketched appearance of the cranium of the hypothetical common ancestor of the seals discussed here, as it appears to the writer on the basis of the study of the craniology of the new existing species of subgenus *Pusa*.

In some of its features, specifically in the structure of the rostral part of the skull and in the shape of the nasal and cheek bones, this hypothetical ancestral form of seals of the subgenus discussed here appears to be closer to the contemporary ringed seal; at the

same time, however, a whole series of other primitive features allies it with the contemporary Baikal, as well as with the Caspian seals.

It is, of course, difficult to establish within which geographical boundaries and during which segments of geological time this hypothetical ancestral form could have existed. Because of the presence of some indicators of the more advanced evolutionary level of *Ph. pontica*[1)] in comparison with the hypothetical ancestral form reconstructed here, and considering that the forms discovered by Van Beneden (1877) in the Pliocene of Belgium are, according to this worker, already very close to the contemporary species of various genera of seals, it is possible to assume that the common ancestor of the three now separated representatives of the subgenus *Pusa* lived as far back as the Miocene period; they were evidently fairly widespread at that time.

## Some Ecological Data

Some comparative ecological data characterizing seals of the subgenus discussed here may play a partial role in the solution of the problem of the history of formation of the existing isolated species of this subgenus.

Specific conditions of its habitat have put their stamp upon the way of life and the character of the periodic actions on the Caspian seal. Perhaps because of the higher temperature of the winter months and, in comparison with the north, the less abundant snowfalls, the Caspian seal breeds in the open on the ice without resorting to the

[1)] Using the above name, the writer has to make a reservation that the genetic ties of this fossil seal, which is usually brought forward in connection with *Phoca vitulina* L., are established on the fragment of its skull reproduced by A. K. Alekseev (1924a) under the name *Phoca pontica* Eichw.; this latter shows obvious phylogenetic ties with seals of subgenus *Pusa*.

construction of the snow lairs and burrows characteristic of the ringed seal and the Baikal seal. In its turn, the presence of a tougher and longer hair cover (which in its pelt qualities does not rank below pelts of the "green pup" and the "white pup" of the Greenland seal) on "white pups" of the Caspian seal is perhaps connected with the circumstance pointed out above.

Apparently because of the limited character of the ice areas fit for breeding, the concentration of the Caspian seal toward breeding time proves to be higher than that of the northern seal†. It is therefore quite possible to speak about the accumulations of pups of the Caspian seal, even though these are comparably less dense than the accumulations of the Greenland seal.

Therefore, there are certain circumstances favoring the emergence of a gregarious way of life for the Caspian seal. Even though this habit is not developed to the same degree as that of the "bald seal" of the White Sea, at any rate it distinguishes [p. 207] the Caspian seal from the ringed seal, which as a rule is not characterized by gregarious habits during its breeding period. It is true, of course, that in some areas of its habitat (White Sea, Gulf of Finland, Ladoga Lake, etc.) the northern seal† congregates in herds for rest on some islands; however, this happens only in the summer and fall when there is no ice. During the remaining part of the year this seal leads a more or less separated type of life. The necessity to breed on ice, which as is known only forms in the northern part of the Caspian Sea, have caused the yearly northerly migrations of seals. At the same time the strong warming up of the shallow parts of the sea forces the migrations of seals into the deep-water regions of the southern Caspian Sea with the beginning of summer.

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† *Ph. hispida* is meant [translator's remark].
† Ringed seal is actually meant [translator's remark].

The migratory habits of this species have apparently come into being in the manner postulated above. In this respect it is again rather similar to the Greenland seal, while at the same time differing from the ringed seal and Baikal seal, the migrations of which are not of such a marked character.

The ability to make holes through the ice is the common feature of all species of the subgenus *Pusa*, although it is characteristic of other species as well. The principal craniological feature of similarity of the Caspian seal and ringed seal, namely the form of the premolar and molar teeth, can possibly be explained by the somewhat similar nature of their food. In the food of both these species, a distinct role is played by closely allied fishes, as for example those of the herring family (for seals of the White Sea and Gulf of Finland, and probably those of the Soviet Far East and Caspian Sea), carp family (especially for seals of Ladoga Lake, Baltic Sea, and Caspian Sea), and also possibly in part those of the salmon family.

The ringed seal is at any rate closer to the Caspian seal than to the Baikal seal in its food habits, as the latter species feeds mainly on Gobiidae and *golomianka*[†].

In its life habit the Caspian seal differs substantially from both the northern seal (ringed seal) and the Baikal seal, these species exhibiting actually only one essential ecological distinction—that of the objects of their feeding.

Thus the ecological data agree completely with the conclusions resulting from the morphological analysis, that is, that the ringed seal is more similar to the Baikal seal than to the Caspian seal.

## Considerations concerning the time of separation

[†] A local fish species characteristic of deep waters in Lake Baikal [translator's remark].

of the Caspian branch of the subgenus *Pusa*.

As can be assumed from the comparison of morphological and ecological features, the separation of that branch of the subgenus from which, in the course of time, the Caspian seal has developed in its contemporary appearance, has apparently greatly preceded the separation of the Baikal seal.

A series of considerations indicates that the origin of the Caspian form should be referred to an older period of geological time than the Ice Age.

Judging by occurrences of pinniped bones, hitherto known from the post-Pliocene deposits of the New Siberian (Novosibirskich) Islands (Cherskil, 1891) from Chaplino Kamas (Gromov, 1939a), morphological distinctions between contemporary seals and their ancestors of the time of Ice Age are either quite nonexistent or so unimportant that there are no objections to using the same names for contemporary and Quaternary forms. V. I. Gromov (1939a), when discussing the Chaplino seal occurrence, names this latter form *Phoca hispida* in spite of the fact that he writes that this form "cannot be brought in connection with the contemporary small form of seal or with the Ladoga seal" (? – K. Ch.).

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Especially interesting is the occurrence of the shank of a seal in the alluvial deposits of the lower Ural, approximately 500 km north of the existing shore of the Caspian Sea (Verestchagin and Gromov, 1952). The complete identity of this fossil bone with the shank of the contemporary Caspian seal indicates clearly that the Ice Age seal

which inhabited the closed southern basin (perhaps it was the Chvalynsk Sea) already possessed morphological features of the contemporary Caspian seal.

The remains of bones of the Neolithic *Phoca hispida* from various localities in Scandinavia, Jutland, and the southern shores of the Baltic basin[1)], naturally, does not show at that point any taxonomical distinctions in comparison with the skeleton of the contemporary ringed seal.

On this background, morphological distinctions between extant ringed and Baikal seals are so great that the possibility or their emergence since the Quaternary period only appears to be unlikely.

Taking into account the peculiarities of ecology of the seals discussed here, it is difficult to agree with the opinion concerning the ability of seals to penetrate into the Caspian Sea under the influence of glaciation or because of any other reason in post-Pliocene time. It is hardly possible to admit the ability of seals to penetrate into the Caspian Sea in the same manner (through bifurcation of rivers) as the representatives of such amphipod genera as *Gammaracanthus*, *Pontoporeia*, and others have penetrated there from the Arctic basin. Let us remember that in order to explain the occurrence of the representative of the genus *Pseudalibrotus* in the Caspian Sea, E. F. Gurianova (1939) was forced to resort to the hypothesis of a brackish water inlet supposedly in existence during post-Pliocene time somewhere to the east of the Urals.

It is therefore very tempting to connect the Caspian branch[†] with the Sarmatian-Pontian seals, and in particular with *Phoca pontica* Eichw., whose craniological features on the one hand (judging by the fragment of its skull) closely agree with the features of

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[1)] Collett, 1911-1912; Ekman, 1922; Libicz, Niezabitowski, 1934 and others.

[†] Of seals [translator's remark].

the hypothetical common ancestor, roughly sketched here; and on the other show a certain similarity with the contemporary *Ph. caspica* Gmel. This idea is not new. Andrussov (1888) was the first to imply it, having pointed out the remains of seals from the Bakinsky stage. Hoernes (1897) has already definitely expressed himself in the sense that the Caspian and Baikal seals should be considered as relicts of the Tertiary fauna of the Sarmatian-Pontian basin. Neither author has, however, supported their assumptions by any particularly convincing reasoning.

The first attempt to prove this assumption was undertaken by V. V. Bogachov (1927a) who compared, sketchily, some features of the Pontian seal based on the skull fragment reproduced by A. K. Alekseev (1924a) with the corresponding features of the Caspian seal. After having noted some structural features common to both these forms, and having made some remarks about the primitive appearance of *Ph. caspica*, Bogachov nevertheless did not come to any clear conclusions about the affinity of the fossil form with the contemporary form. Some material of other parts of the skeleton used additionally by him (apparently belonging to another form) showed such strong differences that it seemed impossible to Bogachov to compare *Ph. caspica* with *Ph. pontica*.

Here obviously visible is the influence of the widespread conviction that *Ph. pontica* allegedly represents a form closely related to the contemporary seal *Ph. viltulina*. And yet the fragment mentioned above of the facial part of the skull referred to *Ph. pontica* Eichw. actually belongs to an old individual (Chapski, 1952, p. 88), which is nevertheless closer to the seals of the subgenus *Pusa* than to the seals of subgenus *Phoca*.

At the same time Bogachov has noted an "amazing similarity" (as he wrote in the English abstract) in the size, shape, and proportions of some bones of the Caspian seal with the corresponding bones of *Phoca vindobonensis* Toula.

Apparently under the influence of this similarity discovered in the structure of the shoulder and thigh bones, Bogachov (while postponing the final decision about the relationship of the Caspian seal to *Ph. vindobonensis* and other forms until more extensive collections were made) found it possible to write in conclusion that the Miocene seal "could quite possibly be preserved in the form of the convergent and representative relict of *Ph. foetida* in the Caspian Sea" (p. 147).

L. S. Berg has shown a great interest in this problem over a considerable period of time. On the basis of the verbal communications of N. A. Smirnov about the sharp distinction of the Caspian seal from the northern circumpolar (ringed) seal, and also taking into account the notes of V. V. Bogachov (1927a, b), Berg (1928) wrote that the Caspian seal "is, possibly, the old endemic form, a descendant of those seals which lived here in the Middle Miocene time and, perhaps, even later" (p. 109).

The collections in the ZIN of the Academy of Sciences of the U.S.S.R. of Tertiary seals from the south of the U.S.S.R. are too limited to permit any conclusions to be made concerning the evolutionary ties of the Sarmatian-Pontian forms to the existing Caspian seal. However, the fragments, specifically those of the shoulder boner of a series of fossil species, show a sufficient morphological similarity with the corresponding parts of the skeleton of the Caspian seal.

Nordman's materials, forming the major portion of the ZIN collection, belong for the greater part to the remains of *Phoca maeotica* Nordm.; a form that in the structure of

the shoulder bone is an unquestionable predecessor of the contemporary monk-seal (*Monachus monachus* Hermann). The most important feature—the delta-like ridge considerably more extended toward its distal end and wide in its proximal part—imparts a very characteristic shape to the bone as a whole. This shape sharply distinguishes *Monachus monachus* (and its immediate Tertiary predecessors) from all seals of the subfamily Phocinae.

The considerable richness and diversity of the fauna of aqueous mammals of the Sarmatian, Meotean, and probably Pontian sea basins is now sufficiently well known. There are about ten species[1)] of seals of the one genus *Phoca* in this fauna. Their list increases all the time thanks to new finds (Simionescu, 1931; Kretzci, 1941) and also with the revision of previously made collections (Friant, 1944).

It is possible that a more thorough study of paleontological collections will somewhat diminish the number of these forms, which were described on the basis of individual fragments of skeletons and without adequate consideration of individual and age variability, at the expense of their transfer into synonymies. Macarovici (1942) notes, for example, that the fossil forms found in the Miocene deposits of Kishinev, and described by A. K. Alekseev as the independent species *Ph. sarmatica* and *Ph. novorossica*, are actually identical with the species described by other authors; the first mentioned form is a variety of *Ph. pontica*, and the second is the synonym of *Ph. bessarabica* Simion.

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[1)] *Ph. viennensis* Blainville (1839), *Ph. pontica* Eichwald (1850), *Ph. maeotica* Nordman (1860) (this form is considered to be allied to the contemporary *Monachus monachus*), *Ph. vindobonensis* Toula (1897), *Ph. bessarabica* Simionescu (1925), *Ph. sarmatica* Alekseev (1924), *Ph. novoroissica* Alexeev (1924), and others. It is difficult to say how many of these forms lived contemporaneously and whether all of them are really independent species.

Principal among all the obstacles that can be put forward against the admission of evolutionary affinity between Tertiary seals and their hypothetical ancestor, which "became transformed" directly into the contemporary Caspian seal, is the biological tie of this latter seal with the ice and, as the consequence of this tie, the presence of white and fluffy fur on the newly born pup of the Caspian seal; this fact does not agree at all with inhabitants of the relatively warmer Sarmatian basin. It is because of this that N. A. Smirnov (1912) assumed that "the Caspian seal has entered southern seas with the already formed pagophilous† inclinations, that it did so not before Ice Age" (p. 14).

These arguments can be met, however, with serious objections and cannot be of a decisive importance.

Actually there is nothing improbable in the assumption that the Sarmatian seals already possessed pagetodous† properties. As far as we know, the climatic conditions of the territories which then corresponded to the southern regions of the U.S.S.R. underwent considerable changes during Tertiary time from the Oligocene to the Pliocene. Even during relatively warm epochs, as for example in the Miocene, winters remained frosty just the same (Berg, 1947). The alternation of seasons already existed in the Oligocene. At that, the presence in the composition of the indigenous arboreal vegetation of that time, of trees with deciduous leaves, can, it would seem, testify to the fact that winters already occurred at that time.

Thus, the premises for the emergence of the "white pup" hair cover in seals could possibly have been present even since the Oligocene. In the Miocene the impulses for the appearance of pagetodous inclinations in seals are even more convincing. An ice cover,

† Or "ice-loving" [translator's remark].
† This appears to be another form of "ice-loving" [translator's remark].

slightly resembling that occurring now in the northern Caspian Sea, could have formed for a short period along the northern borders of the Sarmatian sea (this could have already indisputably happened in the Meotean Sea).

According to the opinion of N. A. Sokolov, the ice that floated in the Pontian sea was thick enough to carry on its surface boulders up to half a meter in diameter (Berg, 1947).

During these remote epochs of geological history, climatic conditions were evidently emerging that were close to the contemporary conditions of the northern Caspian Sea. At that, the Sarmatian Sea extended northward beyond the limits of the existing Caspian Sea. In this connection it is worthwhile to remember the words of N. Andrussov (1891) on the subject, that "the northern shore of this sea is difficult to restore with precision" (p. 4), as erosion has destroyed the Sarmatian deposits there.

The so-called "embryonic" or "white pup" fur covering newly-born seals as a dense and heavy cover is a special adaptation; it has undoubtedly arisen under the influence of changed environmental conditions, which have induced seals to use ice as a hard substratum.

That this is so is proven by embryological data. The fur cover of a seal pup cannot be completely likened to the fluffy cover of newly born terrestrial carnivorous animals.

In the course of embryonic development, the appearance of "white pup" fur is preceded by the appearance of typical fur seals' short, smooth hairs, which cover the fetus (for example, that of the ringed seal) for several months prior to birth. At that, this embryonic hair cover already shows the pattern characteristic for the species (in *Ph.*

*hispida* Schr. – ring-like; in *Pagophoca groenlandica* (Fabric.) – spotted, of the *seroch'ego*† type).

The "white pup" fur appears in the last stages of uterine development; it quickly outstrips in growth and conceals beneath itself the "definitive" hair, which has appeared earlier.

[p. 211]

Therefore, on the basis of the sequence of appearance of various kinds of hair discussed above, and proceeding from the continuity of phylogenesis with ontogenesis, it is possible to reach the following conclusion.

The "white pup" cover is chronologically a later formation; it arose in pups as an adaptation to the prevention of an excessive loss of heat† in connection with changed environmental conditions. Consequently, the primary ecological form of seal was really, as it was actually assumed by N. A. Smirnov (1912), a "dry land-liking" (geophyloid or egialoid) form, which gave raise to the "ice-loving" (pagetodous) form.

However, this phenomenon ill agrees with the principle of recapitulation in its original sense as it was formulated by Haeckel and Müller.

Following the letter of this biogenetic law, and proceeding from the sequence discussed above of the appearance of both types of hair cover in ontogeny, it would be necessary to admit that the "white pup" cover was formed in the process of evolution after the contemporary species were already formed. In other words, it is necessary to admit that it developed in a parallel and independent way in each of the contemporary forms, and it is difficult to agree with this admission.

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† Do not know this word and could not find it in dictionaries available to me [translator's remark].

† Or heat emission [translator's remark].

N. A. Smirnov (1912) has given an excellent sketch of the hypothesis of the transition of seals to life on ice. The picture sketched by him could be almost equally successfully referred in its entirety to the Tertiary periods when, as we have already seen, the premises for the emergence of an ecological connection with the ice were already present in the predecessors of the contemporary seals of the subfamily Phocinae.

The emergence of such "ice-loving" habits (and consequently the emergence of the "white pup" cover in seals of this particular phylogenetic branch) should be referred to an earlier period than the Quaternary because it is otherwise difficult to understand the emergence of this adaptation in the striped seal (*Histriophoca fasciata* Zimmerm.), which, as a species of an independent genus, undoubtedly arose in pre-Quaternary time, without the postulation of convergent development. Therefore, the concept which holds that seals did not enter the Caspian Sea before the Ice Age does not find sufficient support.

It is perhaps impossible to insist on the immediate descent of *Ph. caspica* from *Ph. pontica* (or from some other Upper Tertiary ancestor closely allied to this latter species); yet the participation of the endemic Neogene seals in the ancestry of the contemporary Caspian seal appears to be unquestionable to the writer.

It is not out of place to note that N. Andrussov (1888), who has analyzed the history of development of the Caspian fauna, maintained that "the Pontian epoch should be considered to be the principal and most important moment in its development" (p. 113). In this sense he also suggests (without, however, directly saying so) the possibility of the descent of the Caspian seal from its late Tertiary ancestors found in the Sarmatian basin.

It is rather probable that the reason for the absence of ectoparasites of the genus *Echinophthirius* (Stchupakov, 1936), which are characteristic not only of the northern seals but of the Baikal seal as well, lies just in the very early disrupted ties of *Ph. caspica* with the remaining seals of the family Phocinae.[1)]

[p. 212]

Here it is out of place, of course, to give a review of the fauna of aquatic mammals of the Sarmatian basin and the modes of its formation; nevertheless, it is impossible to pass by the undoubted fact that prior to the moment of isolation of this basin, it must have possessed wide and numerous connections with the world ocean.

Simionescu (1931) goes even further. The abundance of Pinnipedia, cetaceans, and sirenians in the Sarmatian† contradicts, in his opinion, the concept of the Sarmatian fauna as a relict fauna (according to the calculations of this author, there were 22 species of aquatic mammals in the Sarmatian basin).

One way or the other, the Tertiary fauna of aquatic mammals of the southern areas of the U.S.S.R. was not only rich and diversified, but also included forms with very different requirements as to environmental conditions. Side by side with those species, which at that time were undoubtedly already adapted to life under fairly low temperature conditions (some pagetodous seals, cetaceans, including even *Delphinapterus*), there undoubtedly occurred more or less warmth-loving forms. Sirenians (particularly *Dinatherium*), some porpoises, and seals representing the ancestors of the contemporary *Monachus monachus* can be referred to the latter group.

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[1)] Supposedly explaining the reason of absence of tapeworms in the Caspian seal by the disappearance of some crustaceans (most likely – Copepoda), which serve as the first intermediate host of Cestodes, from the Caspian fauna, I. Stchupakov writes further: "The absence of *Anoplura* depends on some other, at the present time inexplicable, causes" (p. 141).

† Rocks [translator's remark].

## The origin of the Baikal Seal.

The origin of the Baikal seal presents a riddle that is more difficult to solve. The absence of any paleontological data at all that could indicate the mode of penetration of this form into Lake Baikal has forced workers to search for the solution by means of comparison of morphological features.

On the basis of some common features observed in the skull structure of the Baikal and Caspian seals (shape of nasal bones, extension of the contact between intermaxillary and nasal bones, extraordinary size of the orbits[1)], Nordquist (1899) expressed the opinion that both of these forms have a common origin and had become separated from the root form[2)] earlier than the remaining forms of the same species. Nevertheless, Nordquist did not consider it possible to accept the point of view of B. Dybowsky (1873) that the Baikal seal is an independent species. He wrote that even the Caspian seal, "which is even more distinct from the usual type" (spacing is mine; – K. Ch.), should be better considered as a subspecies.

N. A. Smirnov (1908), disputing the above opinion, separated the Caspian seal into a separate species, while at the same time leaving the Baikal seal in its former rank of subspecies. The difference in the degree of divergence of both forms from the ringed seal was thus expressed.

Later, however, the same author (1929) found it possible to consider the Baikal seal as an independent species as well. Discussing the genetic relationships of this seal

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[1)] These features are not characteristic in light of new investigations.
[2)] Nordquist recognized the ringed seal (*Phoca hispida* Schreb.) as the root form.

with the remaining members of the subgenus *Pusa* in another paper (1912), N. A. Smirnov wrote that the Baikal seal apparently became separated at a later period than the Caspian seal but, as one would expect, earlier than such forms as the Ladoga and Saima seals.

S. I. Ognev (1935) has come to the conclusion that the Baikal seal has a closer affinity to the Caspian seal than the ringed seal.

[p. 213]

Because of this, he considered it possible to accept the origin of the former from the Upper Tertiary ancestors of the inner (Sarmatian-Pontian) basin.

The hypothesis of Hoernes (1897) about the relict character of the now-isolated forms has been extended to cover the Baikal seal; according to Hoernes, this species could not have penetrated into Lake Baikal along rivers because during the comparatively short time†, the species would not become so changed as to lose its similarity to its ancestors.[1)]

L. S. Berg (1940) did not subscribe to any of the existing points of view. He wrote: "it is possible that the Baikal seal is a derivative of the Arctic Ocean seal. Yet the possibility is not excluded that it is allied to the Upper Tertiary seals. This problem should be solved with the aid of paleontology" (p. 50).

The results of the morphological-systematic comparison undertaken in this paper of the three species of the subgenus *Pusa* show the relatively minor similarity of the

† It would take to travel along the rivers [translator's remark].

1) The northern seal is meant, from which, according to the view of I. D. Cherskii (1886), P. Kredner (1887), and M. M. Korzhov (1947), arose the Baikal seal by way of migration from the Arctic Ocean along a system of rivers and lakes.

Baikal seal to the Caspian seal. There are considerably more reasons to connect the Baikal seal with the ringed seal.

That the common ancestors of the contemporary ringed and Baikal seals have given rise to the latter branch is proven not only by craniological similarity but by other arguments as well. The greater genetic connection between both above-mentioned species, as contrasted with their lesser affinity to the Caspian seal, can also be seen in some ecological features they posses in common (e.g. in their capacity to make a snow den for their pups, etc.) and in the presence of the common ectoparasite *Echinophthirius* on both of them.

There is also some reason to speak about the possibility of the atavistic appearance of the skin pattern in the Baikal seal.

N. A. Smirnov (1908, p. 60) for example, writes in a footnote: "In the Zoological Museum under No. 1861 from Radde, there is one skin of the Baikal seal with small light and dark specks and with light-colored ring-like spots" (spacing is mine; K. Ch.).

Yet, as far as is known to the writer, there is no more evidence of the appearance or the ringed coloring of skin of the Baikal seal. Therefore, natural doubts arise about the correctness of the determination of the locality from which this skin in the collection of ZIN of the Academy of Sciences of the U.S.S.R. was obtained.

Generally speaking, it would be more logical to consider the single-colored skin as the primary pattern for all seals of this particular subgenus. Such an interpretation would provide an easily understandable phylogenetic explanation (as a reminiscence of a long-passed stage) of the transitional single-colored appearance of the young of the

Caspian seals; these young are accordingly called "sivar"† after they shed their "embryonic", "white pup" cover. Such marking of the Baikal seal could be interpreted as having been preserved without change from very ancient time. At the same time the pattern of the ringed seal could be so interpreted, assuming that it evolved even further in this respect and has completely lost the single-colored appearance of is skin.

The skin collection mentioned here, of doubtful origin, could force us to give up this natural explanation of the evolution of color† in seals and to admit that the single-colored appearance of the Baikal seal represents, so to speak, a secondary return to the original type.

Return to previous lost properties is, however, rarely encountered in the realm of the Pinnipedia.

[p. 214]

The incompletely known function of the embryonic hair cover in the so-called common seal – *Ph. vitulina vitulina* L. could be cited as an example.

After having broken its ties with the ice in the process of evolution since Miocene time, and returned to the littoral (egialoidal) mode of life, this Atlantic species has also lost its "white pup" hair cover, a change that occurs in the fetus during the embryonic period just before birth.

Such a return to the morphological features of the remote past experienced under the influence of the corresponding changes of environmental conditions approaching the original ones (of the remote ancestor; translator's remark) is, however, a rather lengthy process; it is indeed, connected with the overcoming of a conservative heredity. Grey seal

† A local name that means "the grey one" [translator's remark.]
† Or skin [translator's remark].

(*Halichoerus grypus* Fabr.) can serve as an example of the stability of the earlier acquired features and properties. In Atlantic population of this species, pups are born in the same light “white pup" hair cover which is characteristic of the pups or the pagetodous (Baltic) populations which gives birth to pups on ice; this happens in spite of the fact that the Atlantic population has lost its ties with the ice and has changed its breeding time (it sometimes falls within the summer months).

It is difficult to assert just how the ancestors of contemporary seals did get into Lake Baikal. At any rate, entrance into the lake could hardly lead from the Caspian branch[†], which was already completely isolated at that time. There are other reasons to assume that the Baikal seal arose out of a later root form, which was a common ancestor to both the Baikal and ringed seals. It is very difficult now to restore the region of distribution of this common ancestral form. It can be assumed that it spread to the more northerly provinces and was partly preserved in some lagoons and vast freshwater basins, which apparently existed at that time and probably had sufficiently wide and short connections among themselves and with the sea. In the process of further paleogeographic changes the part of the seal population that was most remote from this sea could at some stage of the Neogene have been cut off and so became the ancestor of the Baikal seal.

This assumption finds some support in the hypothesis of M. M. Kozhov (1947), according to which “a system of large and mutually connected inner basins, of which one of the last members and the last developmental link is Lake Baikal, existed in ancient times in the province surrounding Lake Baikal” (p. 118).

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[†] Of seals [translator’s remark].

In the opinion of the vast majority of workers who have touched upon the history of the Baikal fauna (Michaelsen, 1902; Andrussov, 1902a; Berg, 1910, 1940, and others), the contemporary faunistic appearance of Baikal is based on the oldest freshwater fauna. M. M. Kozhov (1947) asserts with sufficient reason that "the Baikal fauna was not only fundamentally formed, but was already isolated as well, toward the middle of the Tertiary period" (p. 102).

Because of reasons discussed above, it can be assumed that seals penetrated into Lake Baikal approximately at that time. The assumption of their penetration from the Arctic basin along the Yenisei-Angara river system as late as the Quaternary causes great doubts. These doubts are caused by the rather substantial morphological distinctions between the Baikal seal and the ringed seal, as well as by the inability of seals to overcome a riverway extending for thousands of kilometers.

Indirect support for the idea of pre-Quaternary separation or the Baikal seal is derived from the circumstance that recently isolated forms of the ringed seal in the Baltic Sea, its gulfs, and in the Ladoga and Saimen Lakes do not exhibit even a semblance of those morphological [p. 215] distinctions of the Arctic and Far-Eastern forms of *Ph. hispida* that are present in the Baikal seal.

It is to be expected that new palaeontological discoveries will bring about the final solution of this problem concerning the time of the entrance of seals into Lake Baikal.

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FIGURE CAPTIONS

Fig. 1. Outlines of the cerebral cranium (view from above) of the Baikal (a), ringed (b), and Caspian (c) seals.

Fig. 2. Rostral part of skull (side view) of seals of the subgenus *Pusa*: ringed seal (a), Baikal seal (b), Caspian seal (c).

Fig. 3. Structure of the nasal bones and the outline of the nasal opening in seals: (a) ringed seal, (b) Baikal seal, (c) Caspian seal.

Fig. 4. Structure of the osseous air cells [bulla osseae] and of the bony blade of the auditory duct [external auditory meatus] in seals of the subgenus *Pusa*: Baikal seal (a); Ladoga seal (b); Arctic ringed seal ($b^1$); Caspian seal (c).

Fig. 5. Schematic drawings of structure of the left cheek bone of the Caspian (a), Baikal (b), and ringed (c) seals.