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SOLAR VARIATIONS, CLIMATIC CHANGE, AND RELATED
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Part VI. Paleotemperatures and Cycle Effects

FAUNAL EVIDENCE FOR PLEISTOCENE CLIMATES

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Although the paleoclimatic sequence of the Pleistocene will always be dependent chiefly on the investigation of processes of sedimentation, erosion, and denudation, fauna often provides valuable information and, in some cases, this is far superior to information obtained from geological evidence alone. Much of our knowledge of the average temperatures prevailing during the subdivisions of the Tertiary, as well as of the Pleistocene, is based on association of species in fossil faunas. It is usually assumed that these species, when identifiable with recent forms, had the same climatic requirements in the past as they have today. This is true in a large number of cases, but not in all. Elementary mistakes were made in the past as, for instance, in the middle of the last century, when elephants and lions found in the Pleistocene of Europe were both regarded as representatives of a warm climate. It required abundant evidence of the association of these species with other members of the fauna (in the case of the mammoth with reindeer and of the lion with horses, red deer, and other temperate species) to make clear that generalizations of this type are sometimes erroneous. This is especially true of groups in which evolutionary processes took place at a fast rate, such as the mammals. The opposite is likely to be the case in groups that evolve slowly at the present time, for instance, marine mollusca. Climatic deductions based on these are likely to be more reliable from the point of view of their climatic stability. On the other hand, they suffer a good deal (and even more than mammalian remains) from redeposition. One of the best examples known to me is the cliffs of early Pleistocene marine Craggs which, on the coast of East Anglia, often collapse in such a way that their contained fossils are embedded in the present beach together with Recent species. That this must have happened repeatedly in the past is evident, and it is likely that all the Crag deposits contain a certain number of shells derived from older stages. In such faunas the newcomers are more significant than the survivors (Zeuner, 1937*b*). Apart from the difficulties thus caused by sedimentary processes, the correct identification of the species and subspecies is a matter of extreme importance. It is conceivable, for instance, that *Cyprina islandica*, so frequently quoted as evidence of cold conditions in the Sicilian stage of the Mediterranean, is not the same form as that which occurs now in the north Atlantic. Whilst this summary estimate of the character of faunas will always remain a useful approach to the problem of past climates, it can by no means be regarded as infallible.

For this reason, it is desirable that more research be carried out on the morphological, anatomical, and physiological functional characters of species that make it possible for them to live under certain definable climatic conditions and, indeed, often compels them to do so exclusively (Zeuner, 1936). Most groups are not sufficiently sensitive to be significant, and it is therefore necessary

to look for special cases. Two will be quoted here: one from the mammals and one from the insects.

The Relation Between Form of Skull and Manner of Life of the Rhinoceroses

The Pleistocene and Recent rhinoceroses afford a good example for the close connection between the shape of organs and mode of life (Zeuner, 1934a). It can be shown that the Recent species of rhinoceroses are accustomed to carry their heads in different ways in accordance with their usual manner of feeding. The average carriage of the head is exhibited by individuals when they are walking or standing at ease, although this is not the position in which the head is carried most frequently in the course of life. The skull is constructed to conform to this average carriage, as may be seen in TABLE 1.

TABLE 1

	Species			
	<i>sondaicus</i>	<i>unicornis</i>	<i>bicornis</i>	<i>simum</i>
Biotope	Virgin forest	Virgin forest and jungle	Forest steppe	Steppe
Food	Foliage	Foliage and grasses of the jungle	Foliage and grass	Grass
Average carriage of the head	Horizontal	Horizontal	Somewhat inclined	Strongly inclined
Angle of occipital crest (<i>O</i>)	94°	82°	70°	64°
Angle between occiput and palate (<i>PO</i>)	45°	48.5°	67°	88°
Angle between vertical axis of Foramen magnum and palate (<i>Y</i>)	74.5°	71°	90°	110.5°

The angles employed to describe the shape of the skull are: the angle over the occipital crest (*O*), which is smaller the more the crest is extended backwards; the angle between palate and occiput (*PO*); and that between foramen magnum and palate (*Y*), both of which vary in the same direction but opposite to *O*. They indicate the extent to which the face is inserted below the cranial part of the skull.

The Recent species show clearly that forest forms have small occipital crests and jaws inserted more or less in front of the brain case (*R. sondaicus* and *R. unicornis*, the Indian rhinoceros), while in the open country forms (*R. simum*), the skull is of the "hanging type," with facial portion attached distinctly below the cranium. These differences are evident from TABLE 1, and they imply that forest rhinoceroses carry their heads more or less horizontally forward; those of forest-steppe (*R. bicornis*), somewhat inclined; and those of grasse-steppe, strongly inclined. The skull is constructed accordingly. There is sufficient evidence for this law to be regarded as generally applicable, and it enables one to argue from Recent to fossil forms. In this way it is possible to obtain information about the biotope and climate in which the extinct species was

living. Of the Pleistocene rhinoceroses of Europe, the best known is the woolly species (*Coelodonta antiquitatis*), and the average figures for skull measurements have been found to be $O = 54^\circ$, $PO = 98^\circ$, and $Y = 95^\circ$. A special feature of this species is a combination of a very large PO and a much less wide Y . It finds its explanation in the fact that in this species both neck and head were strongly stretched when feeding, indicating that the food must have been very low-growing. The body of a female, complete with skin, preserved in a Pleistocene oil swamp in the Carpathians at Starunia, near Lvov, Union of Soviet Socialist Republics, bears this out as, of course, does other fauna and the flora found in association.

While *Coelodonta antiquitatis* thus indicates the steppe of the cool, periglacial belt of climate, two other Pleistocene species are typical of a more favorable climate. These are *Dicerorhinus etruscus* (chiefly Lower Pleistocene) and *Dicerorhinus kirchbergensis* (Merck's rhinoceros, chiefly Middle and Upper Pleistocene). Both these species are closely allied to each other and have indices very near to those of *Dicerorhinus bicornis*, as shown in TABLE 2.

According to these results, *etruscus* and *kirchbergensis* were inhabitants of a semiopen country bearing some bushes and trees. That these were able to

TABLE 2

	O	PO	Y
<i>Dicerorhinus etruscus</i>	73°	71°	98.5°
<i>Dicerorhinus kirchbergensis</i>	77.5°	67°	95.5°
<i>Dicerorhinus bicornis</i>	70°	67°	90°

grow indicates that the climate must have been warmer than in the glacial phases, and there is every reason to suppose that these two species lived in the more temperate interglacial phases.

This evidence is based on purely biological and anatomical arguments but, again, independent geological evidence confirms our conclusions about the climatic conditions under which these species lived, for they are found exclusively in interglacial deposits.

It appears to be possible, therefore, to use the skull structure of the rhinoceroses as a guide to the environmental conditions in the Pleistocene.

An Insect Fauna as Evidence of Glacial Climate

Starunia became well known in 1907, when the forehalf of a woolly rhinoceros was discovered. In 1929, the Polish Academy of Sciences and Letters, Cracow, Poland, carried out new excavations (Nowak *et al.*, 1930) at the same place and discovered not only the complete female, mentioned above, but also a rich glacial flora and insect fauna. Of the insects, the grasshoppers are particularly interesting, as they have made possible a determination of the average temperatures of the summer months during a glacial phase.

The fossil orthopterous fauna of Starunia contains 14 species, all of which either belong to Recent species or have very close Recent relatives. Of these,

8 are climatically highly specialized. They all prefer grass lands and, except for one species, occur at the present day on alpine meadows above the limits of the forests. Some of them are found on meadows with high grass, whilst others are found where there are small bushes. As a whole, the fauna is surprisingly uniform, and from it we may conclude that when the woolly rhinoceros was present the countryside around Starunia consisted of meadows dotted with bushes. According to the orthopterous evidence, these bushes may have been *Pinus montana*, *Rhododendron*, *Juniperus*, and *Vaccinium*.

The fossil flora agrees very well with this inference, the following forms having been found: *Betula nana* L., *B. humilis* Schrk., *Salix reticulata* L. and other willows, *Dryas octopetala* L., *Polygonum viviparum* L., *P. lapatifolium* L., *Calluna vulgaris* var. *hirsuta* Presl., *Vaccinium uliginosum* L., *Thalictrum alpinum* L., *Thymus sudeticus* Borb., *Armeria* sp., *Phaca* cf. *alpina* Wulf., *Taraxacum* sp., several species of *Carex*, needles of a spruce, and numerous other forms. The following mosses have been found (Szafran, 1934; Gams, 1934): *Distichium capillaceum* (Sw.), *Tortula ruralis* (L) Ehrh., *Tortula norvegica* (Web.) Lindb., *Climacium dendroides* Web. et Mohr, *Thuidium abietinum* Br. Eur., *Polytrichum juniperinum* Willd. There is thus no doubt about the biotope of the Starunia grasshoppers.

At present all the grasshopper species occur in climatic zones not favorable to the growth of forests. Nevertheless the number of species is comparatively high, being about the same as that of favorable localities in the temperate zone of Central Europe. The ecological conditions of Starunia, therefore, must have been rather propitious for Orthoptera, a group that generally requires heat for its development. As purely arctic species are not represented in the fauna but are replaced by forms needing a rather high amount of heat, the summer temperature must have reached a minimum that satisfied the latter. Thus the climatic specialization of Orthoptera enables us to obtain figures for the temperature of those months of the year during which Orthoptera were living.

For this purpose it is necessary to know the minimum temperature requirements of the species most sensitive to cold, that is, *Isophya* sp. This gives us the limit below which the mean summer temperature cannot have fallen. Equally, we need to know the highest temperature that can be borne by *Podisma frigida* Bohem., the species present most sensitive to heat. This gives us the upper limit of the mean summer temperature.

Naturally, the other species lying between these two extremes could exist under the conditions determined in this way.

During the months of the year with an average temperature below 0° C., Orthoptera cannot develop; they do not hatch from their eggs unless the thermometer rises a few degrees above zero. The hatching time of most of the German species, for example, is May or late April, when the average is about 8° to 11° C. Forms more adapted to a cold climate may start their development earlier, and in accepting an average of 3° C. for them we have certainly put the limit very low, the danger of frost being considerable for the newly hatched larvae.

In TABLES 3, 4, and 5 intervals of 3° C. are chosen to avoid a too special form and to express, at the same time, the seasonal fluctuations of temperature. A

typical locality where *Isophya* lives under cold conditions, shows the kind of climate shown in TABLE 3.

Isophya being the form most sensitive to cold, these figures indicate the minimum average temperatures that must have prevailed at Starunia. On the other hand, one of the warmest places where *Podisma frigida* is found shows the climate described in TABLE 4.

The climate of Starunia cannot have been much warmer than indicated in this table. Comparing Pontresina, Switzerland, with the Riesengebirge, we find

TABLE 3
RIESENGEBIRGE, EAST GERMANY, IN THE SUDETEN MOUNTAINS,
1415 METERS ABOVE SEA LEVEL

Above 0° C.:	May–October:	6 months
Above 3° C.:	May–September:	5 months
Above 6° C.:	June–September:	4 months
Above 9° C.:	July–August:	2 months
Highest average: July 9.9° C.		

TABLE 4
PONTRESINA, SWITZERLAND, 1805 METERS ABOVE SEA LEVEL

Above 0° C.:	April–October:	7 months
Above 3° C.:	May–September:	5 months
Above 6° C.:	June–September:	4 months
Above 9° C.:	June–August:	3 months
Highest average: July 11.8° C.		

TABLE 5

Above 0° C.:	April or May–October:	6–7 months
Above 3° C.:	May–September:	5 months
Above 6° C.:	June–September:	4 months
Above 9° C.:	June or July–August:	2–3 months
Highest average: July 9.9–11.8° C.		

a surprisingly small overlap in the climatic ranges of the two species within which the climate of Starunia must have lain (TABLE 5).

This result is in good agreement with those of numerous independent investigations bearing on the glacial climate.

On the basis of our knowledge of the Recent relatives of the fossil species, and of the ecology of the Orthoptera in general, we have come to the conclusions briefly outlined above. The probability that the results are correct is very high in a case such as this, as the results obtained with the aid of single species check each other, and there is no species whose requirements are in contradiction to the general result. Moreover, the space of time that has elapsed since the deposits of Starunia were formed is comparatively short (roughly 100,000 years), and nearly all the fossils belong to Recent species and to genera the representatives of which are highly specialized in their mode of life. The

whole fauna exhibits a uniform character, and the conclusions based on the Orthoptera of Starunia all point in the same direction. This would be quite extraordinary if some of the species had altered their climatic requirements in the meantime without differentiating their morphological characters.

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