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The Pliocene and Pleistocene *Sciuridae (Mammalia, Rodentia)* from Poland

[Pp. 461—486, pls. XII—XVII]

Plioceńskie i plejstoceńskie *Sciuridae* (*Mammalia, Rodentia*) z Polski

Плиоценовые и плейстоценовые беличьи Польши
(*Mammalia, Rodentia, Sciuridae*)

Abstract. Fossil remains of *Sciuridae* from Polish localities ranging in age from Middle Pliocene to Late Pleistocene are described. 15 forms belonging to the genera *Sciurus, Tamias,* cf. *Sciurotamias, Pliopetaurista, Blackia, Pliopetes, Cryptopterus, Petauria* and *Citellus* are recognized with two of them, *Pliopetaurista meini* n. sp. and *Blackia polonica* n. sp. new for science. In the faunal assemblages from the Pliocene tree-squirrels are numerous. In the Late Villafranchian the first representatives of ground-squirrels appear and the arboreal forms successively vanish.

INTRODUCTION

Squirrels of the rodent family *Sciuridae* are widely distributed, occurring today on all continents except Australia. The family first appears in the early Oligocene of North America and shortly thereafter in the European record (BLACK, 1972). Members of the family occupy a diversity of habitats from Arctic tundra to tropical jungles, and from tree tops to underground burrows. Sciurids are commonly divided into two subfamily groups, flying squirrels (*Petauristinae*) and all other squirrels (*Sciurinae*) including true squirrels, chipmunks, ground squirrels or susliks, marmots and prairie dogs.

Ground squirrel types are most common in Tertiary deposits in North America while tree squirrels and flying squirrels are common elements of many European Miocene, Pliocene and Pleistocene faunas. Species of squirrels are quite useful in ascertaining certain aspects of the plant community and climatic regime around the site of the deposition. Spermophiles are abundantly represented in faunas found in fluviatile sediments representing stream and flood plain deposits. Tree squirrels and flying squirrels are common elements of cave and fissure deposits. The latter sorts of depositional environments are most often, though not always, found on hilly, wooded slopes, occurring today in hardwood deciduous-coniferous forest zones in Europe and North America. Stream and flood plain environments, on the other hand, are commonly associated with more open habitats including parkland-savannahs, grasslands, and riparian woodlands of limited extent. These woodlands are most often of insufficient development to support tree squirrel and flying squirrel populations.

In Poland, only a few localities with remains of fossil sciurids were previously known. From the Miocene fauna of Opole *Miopetaurista albanensis* (MAJOR), *Cryptopterus gaillardi* MEIN and *Spermophilinus bredai* (v. MEYER) have been reported by WAGNER (1913), KOWALSKI (1967) and MEIN (1970). From the late Pliocene faunal assemblages of Węże I and Węże II SULIMSKI (1964) described *Sciurus warthae* (SULIMSKI), *Pliopetaurista dehneli* (SULIMSKI), *P. schaubi* (SULIMSKI) and *Pliopetes* cf. *hungaricus* (KRETZOI). From the early Pleistocene faunas of Kadzielnia and Kamyk (KOWALSKI 1958, 1960b) *Sciurus* sp. and *Citellus* cf. *nogaici* have been recorded. Better material from these two localities made it possible for GROMOV (1965) to determine that the material belonged to a new species, *Citellus polonicus* I. GROMOV. Finally, in the late Pleistocene sediments of the caves Nietoperzowa and Raj, KOWALSKI (1961, 1964, 1972) recognized two species of squirrels, *Citellus citelloides* KORMOS and *C. superciliosus* KAUP.

The faunas considered here display contrasting sciurid components. Four of these faunas, Podlesice, Węże, Rębielice and Zamkowa Dolna, are dominated by woodland species, in the younger faunas of Zalesiaki and Kozi Grzbiet there are woodland and open country species side by side while at Kadzielnia and Kamyk there are no forest species but only a single ground squirrel, *Citellus* (*Urocitellus*) *polonicus*. In the late Pleistocene sediments of the Polish caves two species of ground squirrels form the sciurid fauna. The environmental differences reflected in these faunas which are recognized on the basis of other faunal elements are strongly confirmed by the sciurids.

The material described was collected at the following localities:

Podlesice: It is a deep cave with deposits containing for the most part remains of bats. In addition, scanty fossils of reptiles, insectivorous and carnivorous mammals, and rodents were occasionally found. Originally, KOWALSKI (1956) determined the age of this locality as Early Pleistocene. Further study of the very rich new material made it possible to point out that the locality

is older than the other fissure deposits in Poland and probably dates from the Middle Pliocene. The fauna suggests the presence of both forest environment and open areas as well as a fairly mild climate, perhaps of the Mideterranean type.

Węże I: Abundant Pliocene (Early Villafranchian) fauna with large numbers of reptiles, amphibians, and mammals, both small and large. The literature referring to this locality has been given in the latest studies of KOWALSKI (1962a, 1962b), MŁYNARSKI (1962) and SULIMSKI (1962a). The cave, with a vertical opening in the vault, was probably a trap in which remains of animals accumulated. The fauna points to a climate of the Mediterranean type and the presence of open areas and forests in the vicinity.

Rębielice Królewskie I: A rich Villafranchian fauna very similar to the fauna from Arondelli in Italy (CHALINE & MICHAUX, 1972). It contains a large number of small and middle-sized vertebrates which lived under climatic and vegetational conditions similar to those prevailing at Węże. There are, however, in the fauna some signals of the deterioration of climate (e. g. the presence of *Lemmus*). The mammals collected during early excavations has been discussed by KOWALSKI (1960a). The exploration carried out at this locality in 1962 provided new, rich material. About 0·5 km from this locality a fissure-filling named Rębielice Królewskie II produced a rich fauna probably of the same age as the main locality. Material from these two sites is here described jointly.

Zamkowa Dolna Cave in Olsztyn near Częstochowa: In this cave, under the sediments accumulated during the last glaciation, a karst pocket filled with reddish sediments (layer C) was discovered during archaeological investigations. It contained a rich fauna of mammals, not yet published. The fauna is slightly younger than the fauna from Rębielice, with more elements characteristic of boreal and continental environment (*Lemmus*, Ochotonids).

Kadzielnia in Kielce: Remains of small vertebrates were found here in the filling of a karst pit. These date from the Early Pleistocene, probably from the Tegelen interglacial (Upper Villafranchian). The climate at the time of formation of the cave was fairly mild, as is seen from the make-up of the fauna and the type of deposits. However, such animals as tortoises, common in Węże and Rębielice, are lacking here. The fauna includes mostly species inhabiting open areas (KOWALSKI, 1958, 1962b).

Kamyk: This locality presents another filing of a karst pit, probably from the time of the Günz glaciation. The fauna of reptiles and small mammals (*Allophaiomys*, *Lemmus*) found here suggests a rather cool climate and steppe vegetation. The earlier finds have been described by KOWALSKI (1960b). A considerably richer material was found during the excavation carried out in 1961.

Zalesiaki: Sediments of a cave were discovered during the work in a quarry, and soon thereafter destroyed. The fauna of small mammals, not yet studied in detail, contains mostly species characteristic of the Cromerian Interglacial (Günz-Mindel), but an admixture of older (Pliocene) elements is present.

Kozi Grzbiet: These are also cave sediments, dating probably from the Cromerian (*Mimomys*, *Pitymys*, *Microtus*). The excavations are not yet finished.

Cave Raj near Kielce: The sediments were accumulated in the Early Würm (from the end of Broerup interstadial and the beginnings of Würm II) and contain, besides a rich fauna (KOWALSKI, 1972), two layers with Mousterien artifacts.

Nietoperzowa Cave in Jerzmanowice: A thick series of sediments accumulated between Late Riss and Late Würm. During archaeological investigations ground-squirrel remains were found only in layer 8 (Moereshoofd interstadial).

Mamutowa Cave in Wierzchowie: Archaeological excavations of this cave are not yet finished. Remains of *Citellus* were discovered in the upper layers which accumulated during the late Würm.

Rock-shelter Żytnia Skała near Ojców: Ground-squirrel remains were found during archaeological excavations (KOWALSKI et al., 1965) in layers from the Middle Pleniglacial of the Last Glaciation.

As synonyms, only names used for Polish specimens of respective species are given. All the specimens described in this paper are preserved in the collections of the Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, Cracow, Poland. All measurements are in millimeters. The first measurement is the anteroposterior length of the tooth, the second is the maximum width for an upper tooth or for lower teeth, the maximum anterior width followed by the maximum posterior width.

SYSTEMATIC SECTION

Family *Sciuridae* GRAY

Subfamily *Sciurinae*

Genus *Sciurus* LINNAEUS, 1758

Sciurus warthae SULIMSKI, 1964

Sciurus warthae n. sp.; SULIMSKI 1964.

Material. Węże I (MF/1097): RM_{1-2} (2·28, 2·28—2·48), RM_{1-2} (2·27, 2·31—2·55), RM_3 (2·71, 2·56—2·41).

Description: M_{1-2} are nearly square in occlusal outline with prominent entoconids and an almost squared off postero-internal corner. The posterolophid is low and there is no distinct ectolophid but there is a strong mesoconid in the buccal valley. The anterior cingulum is strong and the trigonid basin large.

There is no distinct metastylid but there is a thickened posterior crest from the metaconid. M_3 is quite similar to M_{1-2} except that the hypoconid and posterolophid are greatly swollen posteriorly and a prominent metastylid is present.

Discussion: These teeth are somewhat smaller than those measured by SULIMSKI (1964, p. 164), which can, however, result from different techniques of taking measurements. They would seem, nevertheless, to pertain to that species.

Sciurus cf. *S. warthae* SULIMSKI, 1964
[Pl. XII, Figs. 1—2]

Material. Podlesice (MF/1096): 1096—1 LdP^4 (2·18, 2·07), 1096-2 RM^{1-2} (2·39, 2·80), 1096-3 LM^{1-2} (2·23, 2·40), 1096-4, LM_{1-2} (2·17, 2·26—2·36), 1096-5 LM_3 (2·48, 2·20—2·03).

Rębielice Królewskie (MF/1098): 1098-1 RP^4 (2·37, 2·41), 1098-2 RM^{1-2} (2·45, 2·85), 1098-3 RM^{1-2} (2·16, 2·70), 1098-4 RM_3 (2·71, 2·39—2·15).

Zamkowa Dolna (MF/1117): RdP^4 (2·38, 2·30), LP^4 (2·52, 2·75), RM^{1-2} (2·75, 3·20), RM^{1-2} (2·45, 2·90), LM^{1-2} (2·45, 2·95), RM^{1-2} (2·37, 2·90), RM^3 (2·80, 2·95), RdP_4 (2·00, 1·25—1·60), LP_4 (2·20, 1·90—2·20), RP_4 (2·15, 1·75—2·10), LM_{1-2} (2·65, 2·50—2·90), LM_{1-2} (2·70, 2·80—3·00), RM_{1-2} (2·70, 2·70—2·80), RM_3 (3·05, 2·85—2·65).

Description: The deciduous upper premolar is triangular with a large parastyle and narrow protocone. The protoloph and metaloph are low and broad with no indication of conules. The mesostyle is quite large. P^4 is less triangular in occlusal outline than dP^4 with the parastyle a less pronounced antero-external bulge. On M^{1-2} the protocone is elongated anteroposteriorly, giving the tooth a rectangular occlusal outline. The protoloph and metaloph are very low, narrow ridges which drop abruptly from the paracone and metacone and pass into the base of the internal face of the protocone. A distinct but small mesostyle is present. M^3 is triangular in occlusal outline with no lingual notch between the protocone and the posteroexternal lobe of the tooth. On P_4 the protoconid and metaconid are separate with a narrow trigonid basin present. There is a small mesoconid on the ectolophid. M_1—M_2 are somewhat rhomboidal in outline. The metaconid is somewhat higher than the protoconid. The trigonid basin is small but completely closed by the anterior cingulum and metalophid. Well-developed mesoconids and metastylids are present. There is a narrow notch between the entoconid and metastylid. The posterolophid is narrow and elevated slightly above the floor of the talonid basin. The buccal valley is quite narrow. M_3 is a simple tooth with the broad talonid basin ringed by a thick, moderately elevated posterolophid from the hypoconid around the metaconid. There is no trigonid basin, only a slight ectolophid and no mesoconid.

The few teeth from Rębielice Królewskie, from Podlesice and from Zamkowa Dolna morphologically cannot be distinguished from the Węże sample of *Sciurus warthae*.

Discussion: The material from Podlesice, which in size and general pattern is similar to these of *Sciurus warthae* from Węże, is the earliest record for this species. The species persisted probably to the time of accumulation of the fauna from Zamkowa Dolna. *Sciurus warthae* has not been discovered outside Poland, but specifically undetermined material belonging to *Sciurus* has been found in Csarnota in Hungary (Kretzoi, 1962) and Shernfeld in Germany (Dehm, 1962).

Genus *Tamias* Illiger, 1811

Tamias orlovi (Sulimski, 1964)
[Pl. XII, Fig. 3]

Eutamias orlovi n. sp.; Sulimski, 1964.
Material. Węże I (MF/1103): twenty-three cheek teeth and one jaw fragment with P_4.
Rębielice Królewskie (MF/1105): 1105-1 RM_{1-2} (1·57, 1·64—1·53), RM_{1-2} (1·47, 1·61—1·56), RM_{1-2} (1·53, 1·68—1·54), LM_{1-2} (1·48, 1·75—1·67), LM_{1-2} (1·58, 1·62—1·55), RM_3 (1·81, 1·67—1·52), RM_3 (1·69, 1·55—1·53).
Description: Sulimski (1964) has already given a complete description of the dentition of this form from Węże I and the new material adds nothing to it.

There are no reasons for separating the population from Rębielice Królewskie from that of Węże.

Tamias cf. *T. orlovi* (Sulimski, 1964)

Material: Podlesice (MF/1099): a single LM_{1-2} (1·63, 1·60—1·67).
Description: The single lower molar is somewhat rhomboidal in occlusal outline with the metaconid and entoconid set anterior to the protoconid and hypoconid. As a result the anterior and posterior borders of the tooth are skewed relative to the long axis. There is a distinct notch between the protoconid and the free buccal end of the anterior cingulum. There is no indication of a trigonid basin due possibly to advanced wear on the anterior cingulum. The buccal valley is partially filled by a large mesoconid pillar. A mesostylid is present on the posterior slope of the metaconid and there is a deep notch between the mesostylid and entoconid.
Discussion: In all details of crown pattern this tooth resembles teeth of *Tamias orlovi* from Węże described first by Sulimski (1964). The occlusal outline of the molar, the free buccal termination of the anterior cingulum and the large mesoconid are all characters found in *T. orlovi* but not seen in any other of the Polish sciurid species. This is the earliest record of *Tamias* in Poland (Black, 1972) and perhaps in Eurasia although Gromov, et al. (1965, p. 54, 125) report *Tamias* (?) from the Upper Miocene of Siberia. „*Eutamias* (?*Eutamias orlovi*)" was also reported from Frontignan in France (Chaline & Michaux, 1973).

?Tamias sp.
[Pl. XII, Figs. 5—6]

Material. Kamyk (MF/1109): 1109-1 RM^{1-2} (1·32, 1·61), 1109-2 LM_3 (1·70, 1·76—1·54).
Discussion: These two teeth are smaller than those of *Tamias orlovi* known from various Pliocene faunas in Poland. However, morphologically they resemble *Tamias* more than any other sciurid type and are provisionally considered to represent a small species of *Tamias*.

Sciurine indet.
[Pl. XII, Fig. 7 and Pl. XIII, Figs. 1—5]

Material: Podlesice (MF/1095): RP^4 (1·61, 1·64), $LM^{1 or 2}$ (1·71, 1·99), LM^{1-2} (1·63, 1·93), LM^{1-2} (1·63, 1·89), LM^3 (2·21, 2·15), LM^3 (2·10, 2·00), LP_4 (1·55, 1·22—1·42), LM_{1-2} (1·84, 2·01—2·06), RM_{1-2} (1·80, 1·72—1·90), RM_{1-2} (1·85, 1·75—1·95), RM_3 (1·94, 1·79—1·71).
Description: All teeth are low crowned. The upper premolar is triangular in occlusal outline with a prominent parastyle but no anterior cingulum shelf. The protoloph is short passing to the anterior margin of the tooth not to the protocone. The metaloph is long and passes into the posterior slope of the protocone. The posterior cingulum is narrow and does not reach the external margin of P^4. The mesostyle is distinct and fills the gap between paracone and metacone. The upper M^{1-2} are rectangular in outline with their long axis set transversely. The protocone is quite broad but low. The protoloph and metaloph drop quickly from the paracone and metacone and merge into the internal face of the protocone. There are no distinct conules on these low lophs. The anterior cingulum reaches the external border of M^{1-2} but there is no parastyle. The posterior cingulum is narrow and does not pass to the external margin of the teeth. The crown pattern of M^3 is simple with a narrow anterior cingulum and low protoloph. The posterointernal corner of the tooth is expanded.

P_4 is longer than wide with no trigonid basin, separate protoconid and metaconid and low entoconid and hypoconid. The lower M_{1-2} are rhomboidal in occlusal outline with a high metaconid and lower and nearly equal protoconid, hypoconid and entoconid. The anterior cingulum and metalophid are low, short crests which on some teeth completely enclose a very small, shallow trigonid basin while on other molars no trigonid basin is present. The ectolophid is nearly marginal and is also low with no mesoconid. There is no hypoconulid and the posterolophid is low. Between the entoconid and mesostylid a narrow notch opens from the broad talonid basin to the outside. The mesostylid itself lies well down on the posterior slope of the metaconid. M_3 is a robust tooth with a very simple occlusal pattern. There is no trigonid basin, rather the anterior cingulum and metalophid are merged into a single crest. The hypoconid, hypoconulid and entoconid are all fused into a heavy, curving posterior

lophid. The large talonid basin is closed internally by a thick wall which passes from the entoconid through the mesostylid to the metaconid. Externally, the talonid is closed by a low, indistinct entolophid.

Discussion: KRETZOI (1951) named a new genus of sciurid, *Csakvaromys sciurinus*, from the Hipparion fauna of Csakvar. The genus was based on a single mandible with worn cheek teeth. GROMOV (1965, p. 137) placed *Csakvaromys* as a subgenus of *Sciurotamias*. TOPACHEVSKY (1971) described an additional species *Sciurotamias* (*Csakvaromys*) *gromovi* from late Miocene deposits in the Ukraine.

In all instances diagnostic characters for the assignment of these specimens to *Sciurotomias* (*Csakvaromys*) reside in the mandible itself. Characters of the cheek teeth are all quite conservative. On the basis of dention alone all that can be said is that these animals are more tree squirrel-like than ground squirrel-like. The pattern is simple with low lophs, broad basins and no accessory cusps or crests. The enamel is smooth.

The collection from Podlesice may represent a species which belongs in the *Sciurotomias* (*Csakvaromys*) group but this cannot be definitely ascertained on the basis of the material available.

Subfamily *Petauristinae*

Genus *Pliopetaurista* KRETZOI, 1962

Pliopetaurista dehneli (SULIMSKI, 1964)
[Pl. XIV, Figs. 1—4]

Pliosciuropterus dehneli n. sp.; SULIMSKI, 1964.
Pliopetaurista dehneli (SULIMSKI); MEIN, 1970.

Material. Rębielice Królewskie (MF/1107): Fifteen isolated upper and lower cheek teeth. 1107-1 RP^4 (2·84, 2·61), 1107-2 RP^4 (3·05, 2·85), 1107-3 LP^3—M^1 (2·78, 2·53 : 2·41, 2·68), 1107-4 RM^{1-2} (2·47, 2·61), 1107-5 RM^1 (2·41, 2·62), 1107-6 LM^{1-2} (2·41, 2·61), 1107-7 LM^{1-2} (2·36, 2·47), 1107-8 RM^2—M^3 (2·37), 2·46 : 2·63, 2·19), 1107-9 RM^3 (2·67, 2·34), 1107-10 LP_4 (2·63, 2·01—2·37), 1107-11 LM_{1-2} (2·41, 2·62—2·57), 1107-12 RM_{1-2} (2·66, 2·79—2·65), 1107-13 LM_2 (2·64, 2·73—2·60), 1107-14 LM_3 (3·43, 2·33—2·14), 1107-15 RM_3 (3·39, 2·43—2·21).

Description: The dentition of this species has already been adequately described by SULIMSKI (1964), who reports this form from the locality Węże II. Measurements of this sample fall within those given by SULIMSKI for the Węże II population. There is no basis for separating the two populations. Besides Poland, *P. dehneli* is known from France, where it was discovered in two Pliocene localities: Hautimagne (MEIN, 1970; MEIN & MICHAUX, 1970) and Chabeuil Serre-Peloux (MEIN, 1970).

Pliopetaurista cf. *P. dehneli* (SULIMSKI, 1964)
[Pl. XIV, Figs. 5—7]

Material. Podlesice (MF/1100): 1100-1 RM^{1-2} (2·29, 2·41), 1100-2 RP_4 (2·24, 2·10—2·33), 1100-3 RM_{1-2} (2·80, 2·80—2·75), 1100-4 RM_3 (3·09, 2·60—2·36), 1100-5 LdP_4 (2·33, 1·32—1·52).

Description: The upper molar is nearly square in occlusal outline, with two prominent cusps, the paracone and the protocone. The lingual face of the protocone is broadly concave posteriorly. There is a long crest passing from the apex of the protocone to the anterior border of the tooth. Between the anterior border and the protoloph there is a broad valley or anterior cingulum. The protoloph is a very low, narrow crest passing directly across the tooth crown from the paracone to the anterior protocone crest. The metacone is much smaller than the paracone and is set at the postero-external corner of the crown. The metaloph is stronger than the protoloph and passes through a large metaconule into the protocone. There is a small lophule from the posterointernal corner of the metacone to the posterior margin of the molar and a second lophule from the metaconule to the posterior margin. The posterior cingulum is thus broken into three re-intrants as described by SULIMSKI (1964, p. 174).

The lower premolar is unworn and shows that the protoconid and metaconid are distinctly separated by a narrow but quite deep trigonid basin which is closed anteriorly by a short but thick anterior cingulum and posteriorly by a short, thin metalophid. There is a prominent metastylid on the posterior slope of the metaconid and a deep cleft between metastylid and entoconid. The posterolophid from hypoconid to entoconid is high and only slightly curved. The ectolophid is high, narrow and carries a well-developed mesoconid. The buccal valley between protoconid and hypoconid is broad. M_{1-2} is rectangular in occlusal outline with the anterior half of the tooth considerably narrower than the posterior. The protoconid, paraconid and hypoconid are high, sharp cusps while the entoconid is much lower. The mesoconid is large and connected through a thin low ectolophid to the protoconid and hypoconid. The trigonid basin is only partially closed by the low crest from the protoconid. The talonid is open lingually by a broad notch between the entoconid and metastylid. Internal to the entoconid there is a short swollen entoconid crest which terminates well internal to the hypoconid. M_3 is elongate with the posterior third of the tooth constricted. The crown surface is divided into four subequal basins. The trigonid basin is large due to the posterior position of the metalophid. A second basin lies between the metalophid and a low, narrow hypolophid which connects the entoconid and ectolophid. A third basin lies between the hypolophid and posterolophid. And, finally, the buccal re-intrant between protoconid and hypoconid is deep and broad.

Discussion: These teeth are only slightly smaller than those of *Pliopetaurista dehneli* known from Węże II. They exhibit all the morphological features seen in that species and appear to be directly ancestral to the Węże II population.

Pliopetaurista meini n. sp.
[Pl. XV, Figs. 1—5)

Holotype: LP^4—M^3 from Zalesiaki (MF/1118).
Material: Zalesiaki, Holotype: P^4 (1·57, 1·82), M^1 (1·62, 1·92), M^2 (1·71, 2·00), M^3 (1·65, 1·87), 1118-2 LP^4 (1·47, 1·72), 1118-3 RM^{1-2} (1·70, 1·95), 1118-4 RM^{1-2} (1·65, 1·91), 1118-5 LP_4—M_1: P_4 (1·45, 1·15—1·45), M_1 (1·60, 1·50), M_2 (1·72, - -), 1118-6 RM_{1-2} (1·72, 1·76—1·86), 1118-7 RM_{1-2} (1·83, 1·80—1·85), 1118-8 RM_3 (2·10, 1·72—1·57).
Diagnosis: Small flying squirrel with smooth enamel on cheek teeth, almost no accessory lophs (ids); metaloph of M^1—M^2 discontinuous; metaconule large connected to metacone by thin loph; protocone with anterior and posterior indentations on lingual border of P^4—M^2; M^3 reduced, no larger posteroexternal expansion; P_4 with anteroconid; P_4—M_2 with distinct mesoconid.
Description: The P^4 is triangular with a small parastyle and narrow anterior cingulum. The protoloph is narrow, moderately high, and complete as it is also on M^1—M^3. On P^4—M^2 the metaloph is incomplete with a deep notch between the metaconule and the protocone. The metaloph and metaconule are also developed on M^3. The anterior cingulum of M^1—M^3 is wide and there is no distinct parastyle as the anterior border of the cingulum is raised throughout its course. There is no mesostyle. A short crest passes from the metacone posterointernally to the posterior cingulum on P^4—M^3. The protocone is compressed anteroposteriorly with anterior and posterior indentations on the lingual border of P^4—M^3.

The mandible is quite deep for its size with a short diastema. There is a single mental foramen just anterior to the termination of the masseteric fossa. The masseteric fossa ends in a rather accute angle beneath the anterior end of P_4. The dorsal and ventral margins of the fossa are well defined and there is a raised base at the anterior termination of the fossa.

P_4 is quite similar to M_1 and M_2 in most regards, but is smaller. There is a distinct anteroconid on P_4 which is absent on M_1 and M_2. The small trigonid basin or pit is completely enclosed on P_4 and M_1 but opens posteriorly on M_2 and M_3 where the metalophid is incomplete. On P_4—M_3 there is a distinct mesoconid. The ectolophid is present but weak. The hypoconulid is strong on P_4 but not distinct on M_1—M_3. On M_1—M_3 there is a short buccal extension of the anterior cingulum which remains free of the protoconid leaving a narrow notch between the anterior cingulum and protoconid. M_3 is somewhat expanded anteroposteriorly with an elevated posterior margin which curves from the entoconid to the hypoconid.
Discussion: *Pliopetaurista meini* is similar to *P. bressana* (Mein, 1970, p. 37) although it is considerably younger. It differs from *P. bressana* in being slightly smaller and in having upper and lower molars without indication of accessory lophs. The two species share such characters as a distinct anteroconid on P_4, absence of a mesostyle and mesostylar crest, large metaconule and distinct

metaloph, and the free buccal end of the anterior cingulum. *Pliopetaurista meini* is considerably smaller and less complex than *P. pliocaenica*, *P. dehneli* and *P. schaubi*. They are also less complex than the two lower molars from Podlesice here referred to *Pliopetaurista* sp. It would seem that there were at least two late Miocene to Pleistocene lineages of *Pliopetaurista*, one the *P. bressana* - - *P. dehneli* - - *P. pliocaenica* line and the other considerably smaller also possibly derived from *P. bressana* and giving rise to *P. meini* of the Pleistocene.

Pliopetaurista cf. *P. pliocaenica*

Material: Zamkowa Dolna (MF/1116): 1116-1 LP^4 (3·35, 3·50), 1116-2 RM^{1-2} (3·15, 3·45), 1116-3 LM^{1-2} (3·18, 3·45), 1116-4 RM^{1-2} (3·00, 3·46), 1116-5 RM^{1-2} (2·90, 3·33), 1116-6 RM^3 (3·10, 3·00), 1116-7 RM^3 (3·05, 3·00).
Discussion: This small sample of upper cheek teeth compares well in most respects to the few teeth known of *Pliopetaurista pliocaenica* from Perpignan (MEIN, 1970). However, these teeth are generally larger in overall dimensions. Also, there is no distinct hypocone as described by MEIN (1970, p. 42). The protocone and protoloph are displaced posteriorly as he describes. MEIN indicates that *P. pliocaenica* evolved from *P. dehneli*. We would agree and believe that the Zamkowa population represents an even later stage in this sequence.

Pliopetaurista sp.
[Pl. XV, Fig. 6 and Pl. XVI, Fig. I]

Material: Podlesice (MF/1101): 1101-1 RM_{1-2} (1·75, 1·70—1·75), 1101-2 LM_{1-2} (1·59, 1·50—1·64).
Description: Both molars are essentially square in occlusal outline with prominent cusps and minor cuspules. The anterior cingulum is free buccally on one tooth while joined to the protoconid on the other. The trigonid basin is completely open in one case and partially blocked by a low metalophid on the other. Doubled metastylids and large mesoconids are present in both cases as is a swollen hypoconid. The talonid basin is open internally via a narrow but deep notch between the entoconid and metastylid.
Discussion: There specimens are close morphologically to lower molars of *Pliopetaurista bressana* MEIN, 1960. They are, however, smaller than the three lower first and second molars referred to that species by MEIN (1970, p. 37). Teeth of *Pliopetaurista* differ from those of *Forsythia* MEIN, 1970 primarily in proportions of the lower molars with those of *Forsythia* being generally wider than long (approximately 1·8 mm. to 2·0 mm.) while those of *Pliopetaurista* have nearly equal length and width measurements. The two Polish specimens are more similar to *Pliopetaurista* in this character and appear to represent a small species of that genus co-existent with the larger *Pliopetaurista dehneli*.

Sulimski (1964) described *Pliopetaurista schaubi* from Węże I, a species which is slightly larger than *P. dehneli* from Węże II. The former was not represented in the material studied by us from this locality.

Genus *Blackia* Mein, 1970

Blackia polonica n. sp.
[Pl. XVI, Figs. 2—8]

Holotype: RM^{1-2} from Podlesice (MF/1102/1).
Material: Podlesice (MF/1102): besides holotype (1·00, 1·27), 1102-2, LM^{1-2} (1·15, 1·45), 1102-3 RM_{1-2} (1·11, 0·85—0·99), 1102-4 LM_{1-2} (1·18, 1·00—1·12). Węże I (MF/1104): 1104-1 LM^{1-2} (1·12, 1·41), 1104-2 RM^{1-2} (1·04, 1·37), 1104-3 RM_{1-2} (1·02, 1·07—1·17), partial LP_4.
Rębielice Królewskie (MF/1108): 1108-1 LP_4 (0·98, 0·69—0·92), 1108-2 LP_4 (1·03, 0·89—0·97), 1108-3 LM_1 (1·02, 1·06—1·21), 1108-4 LM_2 (1·23, 1·33—1·52), 1108-5 LM_2 (1·24, 1·30—1·42).
Diagnosis: Enamel of molars finely wrinkled: smaller than *Blackia miocaenica* Mein or *B. wolfersheimensis*; lophs on M^{1-2} very low; posterior cingulum narrow on M^{1-2}; small external cingulum on M_{1-2}; anterior cingulum on M_{1-2} free and joins external cingulum around base of protoconid.
Description: Material from Podlesice. The molar pattern is quite simple with low lophs and no accessory crests or conules. The anterior cingulum on M^{1-2} is narrow and terminates low on the anterior face of the protocone. The protoloph passes directly across the crown from paracone to protocone while the metaloph passes diagonally from the metacone to the protocone. The posterior cingulum is greatly reduced buccally and remains primarily as a small shelf just behind and internal to the metacone. There is no distinct metastyle but there is a small external cingulum just behind the paracone. The lower molar is rectangular with a deep talonid basin. The trigonid basin is small and closed anteriorly by the anterior cingulum which drops sharply around the anterobuccal face of the protoconid to merge with the external cingulum shelf. There is no metastylid, ectolophid, or mesoconid.
Material from Węże I. The protocone and paracone are extremely high, sharp cusps while the metacone is considerably smaller. The anterior cingulum on M^{1-2} is raised into a thin ridge and there is a broad valley between it and the protoloph. The posterior cingulum is low and there is almost no valley between it and the metaloph and both are quite narrow. There is no indication of either a protoconule or metaconule. The lower M_{1-2} is compressed anteroposteriorly and is rhomboidal in occlusal outline. The trigonid basin is minute with almost no trace of a distinct anterior cingulum. The metaconid is very high with the protoconid, hypoconid and entoconid much lower. The buccal valley is narrow, and there is no ectolophid or mesoconid. There is no metastylid.

Material from Rębielice Królewskie. P_4 is longer and narrower than M_1—M_2. The metaconid of P_4 is much higher than the other principal cusps. There is only a small, open trigonid slope rather than basin between the protoconid and metaconid. On M_1 there is a small, enclosed trigonid basin while on M_2 there is no basin whatsoever. The anterior area of the hypoconid is low and narrow on P_4, M_1 and M_2 and does not show any true ectolophid development. The enamel on all teeth is very finely wrinkled.

Discussion: It is unfortunate that more material of this tiny flying squirrel is not available. However, these few teeth are clearly referable to MEIN's Genus *Blackia* (MEIN, 1970, p. 44) and just as clearly represent a distinct species. *Blackia polonica* is by far the smallest Tertiary flying squirrel yet known. With the slight wrinkling of the molar enamel and overall simple occlusal pattern this species is close to *B. miocaenica*. *Blackia* is also somewhat similar to *Pliopetes hungaricus* (KRETZOI, 1959) from Csarnota and also known from Węże I (SULIMSKI, 1964). These two genera while distinct are closely related as suggested by MEIN (1970, p. 52). *Blackia* and *Pliopetes* are both small flying squirrels with finely wrinkled enamel and little or no accessory lophs. *Blackia* differs from *Pliopetes* in its smaller size and more sharp and angular major cusps.

The *Blackia* lineage persists through the Polish Pliocene until the Middle Villafranchian as is evidenced by populations found at Węże I and Rębielice Królewskie I. There may be some slight increase in size between the time of deposition of the fauna from Podlesice and that from Węże, but this is difficult to be certain of. There is little or no difference between the populations from Węże and Rębielice Królewskie I.

Genus *Pliopetes* KRETZOI, 1959

Pliopetes hungaricus KRETZOI, 1959
[Pl. XVI, Fig. 9]

Pliopetes cf. *hungaricus* SULIMSKI, 1964, p. 181.

Material: Podlesice (MF/1111): 1111-1 LP^4 (1·32, 1·43), 1111-2 RM^{1-2} (1·48, 1·73), 1111-3 LM^{1-2} (1·38, 1·64), 1111-4 RM^{1-2} (1·48, 1·65), 1111-5 LM^3 (1·46, 1·57), 1111-6 RM_{1-2} (1·61, 1·73—1·65).

Węże I (MF/1110): A number of jaw fragments and isolated teeth (see SULIMSKI, 1964, p. 181 and figure 10) together with 1110-1 LM^{1-2} (1·43, 1·70), 1110-2 RM^3 (1·55, 1·65), 1110-3 RM_3 (1·97, 1·75—1·35).

Description: SULIMSKI (1964) has already supplied a general description of the dentition. Additionally characters to those he noted are short accessory ridge from the protocone of M^1—M^3, one anterior to the protoloph and the other between the protoloph and metaloph: quite low lophs with no distinct conules; an anteroposteriorly elongate protocone; and a large entoconid and metastylid on M_1—M_2. The enamel on all the cheek teeth is finely wrinkled.

There is essentially no difference between the teeth in the Podlesice and Węże sample.

Discussion: The upper and lower molars of *Pliopetes hungaricus* average about one third larger (.5 mm) than those of *Blackia polonica* also from Podlesice Węże I. They are about one fifth larger than those of *B. miocaenica* (.20—.25 mm) and *B. wolfersheimensis*. Both genera have finely wrinkled enamel and lack accessory lophs and lophules seen in some other flying squirrels. The cheek teeth of *Pliopetes* have more rounded major cusps, more prominent protoloph and metaloph, a distinct mesoconid, and a less angular occlusal outline to the molars than do the teeth of *Blackia*.

MEIN (1970, fig. p. 52) has suggested that *Pliopetes* and *Blackia* may have shared a common ancestor sometime in the mid to late Miocene. This seems quite reasonable. The dentition of *Pliopetes* is not as highly specialized as that of *Blackia* but they share many common features.

Genus *Cryptopterus* MEIN, 1970

Cryptopterus cf. *C. thaleri* MEIN, 1970
[Pl. XVI, Fig. 10]

Material: Rębielice Królewskie (MF/1106): 1106-1 a left $M^{1 \text{ or } 2}$ with the internal border missing (4·32, —), 1106-2 LM_3 (5·30, 5·00—4·30), 1106-3 right lower incisor (3·6, 1·61).

Description: On M^{1-2} the enamel is smooth and there are no accessary cusps or lophs. The protoloph and metaloph are complete, thin ridges without conules. There is a low, very short mesoloph from the buccal mesostyle passing only a short way internally. The anterior cingulum is broad and terminates buccally in a low parastyle. The posterior cingulum does not reach the buccal margin of the crown but ends internal to the metacone. The third lower molar is low crowned with smooth enamel and low accessory ridges. The trigonid basin is essentially confluent with the talonid as the posterior protoconid arm is quite low and short. There are two low ridges from the ectolophid which pass lingually into the talonid basin with the posterior ridge passing across to the entoconid which is distinct. The posterolophid is thick but low and forms a broad arc from the entoconid around to the hypoconid. The metaconid is the only high cusp on the crown. A small mesoconid is present on the ectolophid.

The lower incisor is extremely compressed laterally and has a long wear facet on its internal face. The enamel is finely striated and confined to the anterior face and about one quarter of the medial face.

Discussion: These three teeth record the presence of a large flying squirrel in the Rębielice fauna. This species is close in size of the upper molar to *Cryptopterus thaleri* (MEIN, 1970) while the lower M_3 is close to *C. tobieni*. Morphologically the two teeth could belong to either species of the genus.

Petauria DEHM, 1962

Petauria sp.
[Pl. XVII, Fig. 1]

Material: Kozi Grzbiet (MF/1112-1): $LM_{1 or 2}$ (4·20, 3·80—3·80).
Description: This lower molar is quite similar to the M_2 of *Petauria helleri* (DEHM, 1962, p. 5, fig. 2a). It differs from *Petauria* in that the crown pattern is not as complex with no accessory lophid passing from the ectolophid into the talonid basin. The ectolophid, metalophid, and hypolophid are high, rather narrow ridges. The protoconid and hypoconid are compressed anteroposteriorly into high, thin cusps. There is a deep, wide notch between the protoconid and anterior cingulum. The buccal valley between the protoconid and hypoconid is also wide and deep. On the internal slope of the metaconid there is a high, curving ridge which is completely separate from the metalophid.
Discussion: DEHM (1962) considered the fauna from Schernfeld bei Eichstätt to be of Cromerian age. There are no ground squirrels present in that fauna. The fauna from Kozi Grzbiet may be somewhat younger, although this is difficult to ascertain. The Eichstätt fauna is clearly that of a woodland assemblage while the fauna from Kozi Grzbiet is a woodland and more open country mixture. The single tooth of *Petauria* from Kozi Grzbiet would appear to be somewhat less advanced than the dention of *P. helleri* from Eichstätt particularly in having a less complex crown pattern.

Genus *Citellus* OKEN, 1816

Subgenus *Urocitellus* BRANDT, 1827

Citellus polonicus GROMOV, 1965
[Pl. XVII, Figs. 2—9]

Sciurus sp.; KOWALSKI, 1958.
Citellus cf. *nogaici*; KOWALSKI, 1960.
Citellus polonicus sp. nov.; GROMOV, 1965.
Material. Zamkowa Dolna (MF/1115): 1115-1 LM_{1-2} (2·50, 2·55—2·60).
Kadzielnia (MF/38): LP^4 (2·49, 2·63), LM^{1-2} (2·48, 3·15), LM^3 (2·74, 3·00), RdP_4 (2·12, 1·57—1·95), LP_4 (2·21, 1·85—2·34), RP_4 (2·37, 1·90—2·40), RM_{1-2} (2·70, 2·79—2·94), RM_{1-2} (2·59, 2·95—3·12), RM_{1-2} (2·54, 2·68—2·78), LM_{1-2} (2·55, 2·82—2·90), LM_{1-2} (2·40, 2·73—2·85).
Kamyk (MF/83): 83-1 LP^4, 83-2 LM^{1-2}, 83-3 RM^{1-2}, 83-4 RM^3, 83-5 $RM_{1 or 2}$, 83-6 $LM_{1 or 2}$, 83-7 $LM_{1 or 2}$, 83-8 LM_3 plus many more isolated upper and lower cheek teeth including the holotype (RP^3, MF/83-9).
Zalesiaki (MF/1114): Many isolated upper and lower cheek teeth.

Kozi Grzbiet (MF/1113): RM^{1or2} (2·80, 3·38), RM^{1or2} (2·70, 3·25), LP_4 (2·60, 2·25—2·40), LM_{1or2} (2·90, 2·35—2·55), LM_3 (3·70, 3·30—3·05).

Description. P^4—M^2 are triangular in occlusal outline with narrow, high protocones and large, buccal parastyles. The lophs are high and narrow. The metaloph is complete and generally shows a distinct metaconule. The anterior margin of the anterior cingulum is also elevated into a thin cutting edge. Mesostyles are present but small. The posterior cingulum is reduced on all teeth. On M^3 the protoloph is a sharp, high crest. There is an expansion of the posterior lope of the protocone on M^3 but no indication of the metaloph or metaconule. Buccally a low but enlarged mesostyle is present.

P^4 is longer than wide whereas M_1—M_2 are compressed anteroposteriorly. The metalophid and posterior cingulum of P_4—M_3 form high, narrow cutting ridges. The ectolophids are low and there is no mesoconid on any of the teeth. On M_1—M_3 the trigonid basins are reduced to narrow valleys open posteriorly into the talonids. On P_4 the trigonid basin is slit-like and open on the anterior face of the tooth. The hypoconid, posterior cingulum, entoconid are enlarged on M_3 to form a high enclosing wall around the posterior margin of the tooth.

Discussion. The sample from Kamyk formed the basis for Gromov's naming of a new species of ground squirrel. At that time Gromov (1965, p. 182—184) suggested that the Kadzielnia ground squirrel might represent a species distinct from *C. polonicus* of Kamyk. This separation was based on larger size and somewhat greater hypsodonty of the cheek teeth in the Kadzielnia population. These teeth, however, are not separable from those at Kamyk and are referable to *Citellus polonicus*.

The samples from Zalesiaki and Kozi Grzbiet suggest that this lineage of ground squirrels increased in size from the time of accumulation of the Kadzielnia sample to that of the sample Kozi Grzbiet. Other than larger size for the later populations there is no basis for separating these various temporal populations and all specimens are here referred to *Citellus polonicus*. The one specimen from Zamkowa Dolna is somewhat of an anomally. The lower molar is indistinguishable from those found in younger faunas such as Kamyk and Kadzielnia. Perhaps this tooth is a contaminant from the younger levels at Zamkowa Dolna.

C. polonicus is advanced over the North American ground squirrels of the subgenus *Otospermophilus* as it displays cheek teeth with high, narrow transverse lophs (ids) and some anteroposterior compression of the molars. No members of the more generalized *Otospermophilus* stock are known from Eurasia and it seems likely that only one of the more advanced ground squirrels from the *Citellus* (*Citellus*) *mckayensis* line invaded Eurasia during the mid Pliocene. Several species of *Citellus* are known from the Pleistocene of eastern Europe. These included *Citellus primigenius* (distributed also in western Europe, including the British Isles), *C. nogaici* and *C. polonicus*. The interrelationships of these species are not clear at present but they all are of the more ad vanced ground squirrel morphology.

Subgenus *Colobotis* BRANDT, 1843

Citellus (*Colobotis*) *superciliosus* KAUP, 1839

Citellus ex. gr. *major* (PALLAS)-*birulai* I. GROMOV; KOWALSKI, 1961.

Citellus superciliosus KAUP; KOWALSKI, 1972.

Material: Cave Raj near Kielce (MF/1087). Layer 6: LM^{1-2} (2·60, 3·44), LM^3 (3·42, 3·52); layer 9: LP^4, partial; layer 10: RP^4 (2·60, 3·10), RP_4 (2·56, 2·68—2·77) RM_1, partial; layer 11/I: RdP_3 (2·22, 2·33), RM^{1-2} (2·48, 3·00), RM_2 (2·68, 3·12—3·67); layer 11/II: RM_2 (2·60, 3·18—3·46).

Cave Mamutowa in Wierzchowie (MF/1088). Layer 2: RM_1 (2·40, 2·94—3·10); layer 3: RM^{1-2} (2·73, 3·27); layer VIII: LP_4 (2·73, 2·52—2·75); layer IX: LM^{1-2} (2·75, 3·27), LM_2 (2·37, 2·88—2·90).

Rock-shelter Żytnia Skała near Ojców (MF/918): LP^3 (1·50, 1·53).

Cave Nietoperzowa in Jerzmanowice, layer 8 (MF/858): LM_3 (3·12, 3·35—3·12).

Description: Cheek teeth large, hypsodont. Unique P^3 (from rock-shelter in Żytnia Skała) has a conspicuous furrow along the inner side of the root. Two specimens of P_4: from cave Raj and cave Mamutowa are rather different. In the first the anterior part of the crown is markedly broader. P_4 has four roots, the posteroexternal root is minuscule but fully independent. M_1 is shorter than M_2, more quadrangular.

Discussion: The make-up of the cheek-teeth points to their membership in the subgenus *Colobotis*. The specimen from Nietoperzowa cave was studied also by I. M. GROMOV who verified its specific determination. According to GROMOV (1965) representatives of the subgenus *Colobotis* from the upper Pleistocene of western and middle Europe belong to the species *Citellus* (*Colobotis*) *superciliosus*, which developed into the recent *C. major* PALLAS. In Poland *C. superciliosus* was unearthed in the cave sediments dating from the pleniglacial of the last glaciation (Würm II). The material from cave Raj is from the lower part of the pleniglacial, that from Nietoperzowa from the interstadial Moereshoofd, and the specimens from Mamutowa cave were discovered in the sediments from the upper pleniglacial. It is interesting, that in the cave Raj the appearance of *C. superciliosus* is connected with the vanishing of *C. citelloides* and with the change of climate, which becomes colder and drier.

C. superciliosus was distributed during the last glaciation all over Europe. It was reported under the names of *C. superciliosus*, *C. major* or *C. rufescens*. In Hungary it was also found in the layers from the beforelast glaciation (Riss): Uppony I, layer 6 (JANOSSY, 1969). In north Germany it persisted until early holocene (Pisede; HEINRICH, 1969). In eastern Europe it is represented by somewhat different subspecies, *C. superciliosus birulai* GROMOV 1961. It was connected with a habitat of arid arctic semidesert.

Subgenus *Citellus* OKEN, 1916

Citellus (*Citellus*) *citelloides* KORMOS, 1916

Citellus citelloides; KOWALSKI, 1961, 1972.

Material. Cave Raj near Kielce (MF/1089). Layer 2: RM^{1-2} (1·90, 2·62), LM_{1-2} (2·00, 2·43—2·50), LM_{1-2} (1·90, 2·39—2·53), RM_{1-2} (1·90, 2·50—2·53); layer 3:

LP^3 (1·43, 1·41), RM_{1-2} (1·90, 2·51—2·63); layer 4: fragment of right maxilla with M^1 (1·97, 2·78) and M^2 (2·15, 2·88), LP^3 (1·52, 1·46), RP^3 (1·48, 1·49), LP^4 (1·96, 2·31), RM^{1-2} (1·91, 2·37), LM^{1-2} (2·01, 2·72), LM^{1-2} (1·77, 2·69), LM^{1-2} (1·85, 2·55), RM^3 (2·69, 2·63), RM^3 (2·66, 2·61), LM^3 (2·63, 2·63), LM^3 (2·62, 2·53), LP_4 (1·90, 1·91—2·03), LP_4 (1·94, 2·05—2·17), LP_4 (1·83, 1·77—2·00), RM_{1-2} (1·96, 2·46—2·58), RM_{1-2} (1·96, 2·53—2·62), RM_{1-2} (2·02, 2·36—2·54), LM_{1-2} (1·89, 2·57—2·44), LM_{1-2} (1·84, 2·49—2·41), partial M_{1-2}, LM_3, RM_3; layer 5: partial RM_{1-2} and LM_3, layer 6: RP^3 (1·46, 1·39), LP^4 (1·88, 2·24), LP^4 (1·91, 2·30), LM^{1-2} (1·81, 2·64), LM^{1-2} (2·13, 2·73), RM^3 (2·76, 2·70), RM^3 ($\pm$2·56, 2·60), 4 partial upper molars, LP_4 (1·52, 1·77—1·95), RP_4 (1·90, 1·81—2·03), LM_{1-2} (1·89, 2·30—2·47), LM_{1-2} (1·89, 2·30—2·47), LM_{1-2} (1·87, 2·45—2·48), LM_{1-2} (2·00, 2·42—2·50), RM_{1-2} (1·98, 2·40—2·64), RM_{1-2} (1·83, 2·38—2·40), RM_{1-2} (1·93, 2·38—2·50), 3 partial lower molars; layer 8: partial lower molar; layer 9: RP^4 and RM^3, both partial; layer 11/I: LM_{1-2} (2·29, 2·46—2·77); material without stratigraphic position: RM^3 (2·55, 2·78), LP_4 (1·90, 2·00—2·12). Cave Zamkowa Dolna in Olsztyn near Częstochowa, layer 6(MF/1092): RM^{1-2} (1·98, 2·64).

Cave Nietoperzowa in Jerzmanowice, layer 8 (MF/857): LM_3 (2·43, 2·70—2·48).

Description. Cheek teeth small, rather hypsodont. P^3 has a conspicuous furrow on the inner side of the root. P_4 with two large roots. Posterointernal root of this tooth is fused along its whole length with the external root and is marked on its internal border as a broadening reaching from 1/3 to 1/2 of its length.

Discussion. The morphology and dimensions of the teeth suggest that they belong to the subgenus *Citellus*. Late Pleistocene representants of this subgenus were described by KORMOS (1916) on the base of the material from Hungary as *C. citelloides*. To this form belong the remains described above. Probably *C. citelloides* is the ancestor of both recent European species of this group: *C. citellus* (LINNAEUS) and *C. suslicus* GÜLDENSTAEDT. I. M. GROMOV (1965) described *C. severkensis* from the late Pleistocene of European Russia but its differences from *C. citelloides* are very subtle and it seems more convenient to give this form a subspecific rank.

C. citelloides was present in Poland during the last glaciation (Würm). In the cave Raj its numerous remains are found in the layers deposited at the end of Broerup interstadial and at the beginning of the succeeding pleniglacial. When the climate became colder and drier this species vanished, and its niche was occupied by *C. superciliosus*. In layers 6—9 of this cave, however, both species coexisted. In the cave Nietoperzowa, *C. citelloides* was found in the layer from the Moereshoofd interstadial.

In Europe the representatives of the subgenus *Citellus* (reported under the names *C. citelloides*, *C. guttatus*, *C. suslicus* and *C. citellus*) appear during the Mindel glaciation (Hundsheim in Austria, THENIUS, 1947; Tarkö in Hungary, JANOSY, 1962). During the Riss glaciation they reached France (Mommenheim, CHALINE, 1973), in the Würm they are known from Germany, Czechoslovakia, Hungary, Poland and European Russia.

GENERAL REMARKS

The composition of the sciurid fauna of the Polish fossil localities is given on Table I. The remains of these rodents are relatively rare in fossil local faunas, thus the lack of particular species does not necessary prove that they were absent in the biocenoses at any particular time. The comparison of our faunas with those known from other countries is also difficult, because of the sporadic character of occurrence of sciurid remains.

Table I

Sciuridae in Pliocene and Pleistocene localities in Poland

Species \ Locality	Podlesice	Węże I	Rębielice Królewskie	Zamkowa Dolna	Kadzielnia	Kamyk	Zalesiaki	Kozi Grzbiet	Late Pleistocene
Sciurus warthae	?	+	?	?	—	—	—	—	—
Tamias orlovi	?	+	+	—	—	—	—	—	—
?*Tamias* sp.	—	—	—	—	—	+	—	—	—
Sciurine indet. (cf. *Sciurotamias*)	+	—	—	—	—	—	—	—	—
Pliopetaurista dehneli	?	+	+	—	—	—	—	—	—
Pliopetaurista meini	—	—	—	—	—	—	+	—	—
Pliopetaurista cf. *pliocaenica*	—	—	—	+	—	—	—	—	—
Pliopetaurista sp.	+	—	—	—	—	—	—	—	—
Blackia polonica	+	+	+	—	—	—	—	—	—
Pliopetes hungaricus	+	+	—	—	—	—	—	—	—
Cryptopterus cf. *thaleri*	—	—	+	—	—	—	—	—	—
Petauria sp.	—	—	—	—	—	—	—	+	—
Citellus polonicus	—	—	—	+	+	+	+	+	—
Citellus superciliosus	—	—	—	—	—	—	—	—	+
Citellus citelloides	—	—	—	—	—	—	—	—	+

The sciurid fauna from Podlesice is evidently different from all other localities described here in accordance with its much older age. It is exceptionally rich, seven forms of sciurids being present. From other Middle European localities containing small mammals, these from Kohfidisch (BACHMAYER & WILSON, 1970) and Eichkogel (DAXNER-HÖCK, 1970) in Austria seem to be slightly older. In the first one *Spermophilinus* cf. *bredai* and „*Pliosciuropterus* sp." (probably identical with *Pliopetaurista* sp. from Podlesice) are present; in the second, sciurids are relatively abundant and contain *Pliopetes* cf. *hungaricus*,

Pliosciuropterus sp. as well as *Spermophilinus* cf. *bredai-turoliensis*. The fossil fauna of Osztramos-1 in Hungary (JANOSSY, 1972) is, in contrast, rather younger then Podlesice and its sciurid fauna comprises *Sciurus* aff. *warthae* and *Pliopetes* sp.

The majority of forms known from Podlesice survived in the present territory of Poland until the Early Villafranchian (Węże I). The sciurid fauna is there still rich (5—6 forms). Similar mammalian assemblages are known from Wölfersheim in Germany (MEIN, 1970), where the genera *Cryptopterus* and *Blackia*, represented, it is true, by different species, are present, and from Csarnota in Hungary (KRETZOI, 1962) with the genera *Pliopetaurista*, *Tamias* and *Pliopetes*.

Rębielice Królewskie I and II are similar to Węże I in their sciurid fauna, but *Pliopetes hungaricus* is missing and *Cryptopterus* cf. *thaleri* appears as a new element. Mammals other then sciurids are also similar in Węże and in Rębielice, but some boreal elements (e. g. *Lemmus*) make their first appearance at Rębielice.

This boreal character is much stronger accentuated in the chronologically next fauna, i. e. this from Zamkowa Dolna. Notwithstanding the very numerous material of rodents, the squirrels are represented only by 3 forms: *Sciurus* cf. *warthae*, *Pliopetaurista* cf. *pliocaenica* and *Citellus polonicus*, the last appearing here for the first time in the fossil record of Poland. This is in accordance with other elements of the fauna, where besides some relicts of older groups (*Eomyidae*, *Baranomys*), boreal and eastern elements, like *Lemmus*, *Villanyia*, ochotonids and mole-rats are present. Zamkowa Dolna finds its close analogy in the faunas from Osztramos-3 in Hungary (JANOSSY, 1970) and Schernfeld in Germany (DEHM, 1962). In Osztramos-3 sciurids are represented only by „*Citellus* cf. *primigenius*", in Schernfeld by *Petauria helleri*. It is possible that *Petauria* is, like *Citellus*, an immigrant in the European fauna of that time. Its adaptation to colder environment is made probable by the fact, that it is a unique flying squirrel which survived in Central Europe into the Cromerian Interglacial (KOENIGSWALD, 1973; KRETZOI, 1965).

The Upper Villafranchian fauna of Kadzielnia and the still younger assemblage from Kamyk, both rich in rodents, contained only a few squirrel remains. *Citellus polonicus* is present in both of them, in Kamyk there is, in addition, ?*Tamias* sp.

The age of the fauna from Zalesiaki is doubtful and it is not certain whether *Citellus polonicus* and *Pliopetaurista meini* n. sp. were contemporary.

The typically Cromerian fauna of Kozi Grzbiet, not yet studied completely, has yielded only *Citellus polonicus* and *Petauria* sp.

There is a hiatus in the fossil record of small mammals in Poland between the Cromerian and Late Pleistocene. In the sediments accumulated during the last glaciation only modern forms of ground-squirrels, *Citellus superciliosus* and *C. citelloides* are present.

In general it can be stated, that the sciurid fauna in the Pliocene was rich

in arboreal species. This fauna seems to be rather uniform in all Europe, exception being made for Iberian Peninsula and Mediterranean Region, where quite different forms of this group existed. Most elements of this Pliocene fauna persist until the Middle Villafranchian. At the beginning of the Upper Villafranchian (Schernfeld, Osztramos-3, Zamkowa Dolna), probably in connection with climatic changes, a new wave of continental and boreal elements appear in Middle Europe. Among them are ground-squirrels of the genus *Citellus* and probably flying squirrels of the genus *Petauria*. This time sees the end of the old genera of tree squirrels, which existed in Europe in the Neogene. In the Cromerian only these new forms, together with *Sciurus*, exist in Middle Europe. The two last glaciations brought the immigration of new forms of ground-squirrels which reached the Atlantic coast and the British Isles.

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STRESZCZENIE

W faunach kopalnych z terenu Polski, obejmujących okres od środkowego pliocenu do młodszego plejstocenu stwierdzono 15 form z rodziny *Sciuridae*. Ich wykaz i występowanie w poszczególnych stanowiskach podaje tabela I na s. 479. Praca zawiera opis znalezionych szczątków *Sciuridae*, wśród których dwa gatunki, *Pliopetaurista meini* n. sp. i *Blackia polonica* n. sp., są nowe dla nauki.

Najstarsza z badanych faun, znaleziona w Podlesicach, datowana jest na środkowy pliocen. *Sciuridae* były tu liczne i obejmowały 7 form, głównie z podrodziny *Petauristinae*. Następna chronologicznie fauna z Węży I, datowana na górny pliocen (dolny wilafransz) zawierała jeszcze 5 gatunków nadrzewnych *Sciuridae*, zbliżonych do form z Podlesic. Nieco młodsza fauna z Rębielic Królewskich I i II ma w omawianej grupie gryzoni skład podobny do poprzedniej, jednakże brak tu *Pliopetes hungaricus*, pojawia się natomiast *Cryptopterus* cf. *thaleri*.

Fauna z jaskini Zamkowej Dolnej zbliżona jest w swym ogólnym składzie do fauny z Rębielic, jest jednak od niej młodsza i pojawiają się tu liczniej elementy borealne i kontynentalne, jak *Lemmus*, *Villanyia*, *Ochotonidae* i *Spalacidae*. W faunie *Sciuridae* zaznacza się wyraźne zubożenie składu gatunków nadrzewnych, z których obecne są tylko dwa: *Sciurus* aff. *warthae* i *Pliopetaurista* cf. *pliocaenica*. Po raz pierwszy pojawia się tu natomiast przedstawiciel susłów, *Citellus polonicus*. Fauna ta wykazuje podobieństwo z fauną Osztramos 3 na Węgrzech i Schernfeld w Niemieckiej Republice Federalnej i zawiera dowody pierwszego wyraźnego ochłodzenia i kontynentalizacji klimatu w Europie.

Fauna górnego wilafranszu Kadzielni dostarczyła tylko *Citellus polonicus* jako jedynego przedstawiciela *Sciuridae*. W młodszej od niej faunie z Kamyka towarzyszy mu ?*Tamias* sp. Fauna z Zalesiaków, w której wykazano *Pliopetaurista meini* n. sp. i *Citellus polonicus* jest prawdopodobnie mieszaniną elementów plioceńskich i pochodzących z interglacjału kromerskiego. Natomiast ssaki znalezione w Kozim Grzbiecie reprezentują niewątpliwie interglacjał

kromerski. Znaleziono wśród nich *Citellus polonicus* i *Petauria* sp. Ten ostatni rodzaj, znany także ze stanowisk tego samego wieku w Husarenhof 5 w Niemieckiej Republice Federalnej i Voigstedt w Niemieckiej Republice Demokratycznej, jest jedynym przedstawicielem polatuch (*Pelauristinae*) w faunach plejstoceńskich Europy i był zapewne przystosowany do chłodniejszego klimatu. Z następnych okresów ostatniego zlodowacenia brak w Polsce faun drobnych ssaków. Dopiero z czasu ostatniego zlodowacenia znane są dwa gatunki susłów, *Citellus citelloides* i *C. superciliosus*.

РЕЗЮМЕ

Из ископаемых фаун территории Польши, относящихся к отрезку времени от среднего плиоцена до раннего плейстоцена, известно 15 форм беличьих. Их перечень и данные о местах находок сведены в таблице I (стр. 479). Предлагаемая работа содержит описание всех найденных остатков *Sciuridae*; два вида из этого материала оказались новыми для науки: *Pliopetaurista meini* n. sp. и *Blackia polonica* n. sp.

Древнейшая из исследованных фаун — Подлесице — датируется средним плиоценом. Беличьи были здесь многочисленны и представлены 7 формами, главным образом из подсемейства *Petauristinae*. Следующая в хронологическом ряду фауна — Венже I — датируется верхним плиоценом (нижний виллафранк) и содержит еще 5 видов древесных беличьих, близких к формам из Подлесице. Более молодые фауны Рембелице Крулевске I и II по составу рассматриваемой группы грызунов близки к предыдущей, однако здесь отсутствует *Pliopetes hungaricus*, вместо которого появляется *Cryptopterus* cf. *thaleri*.

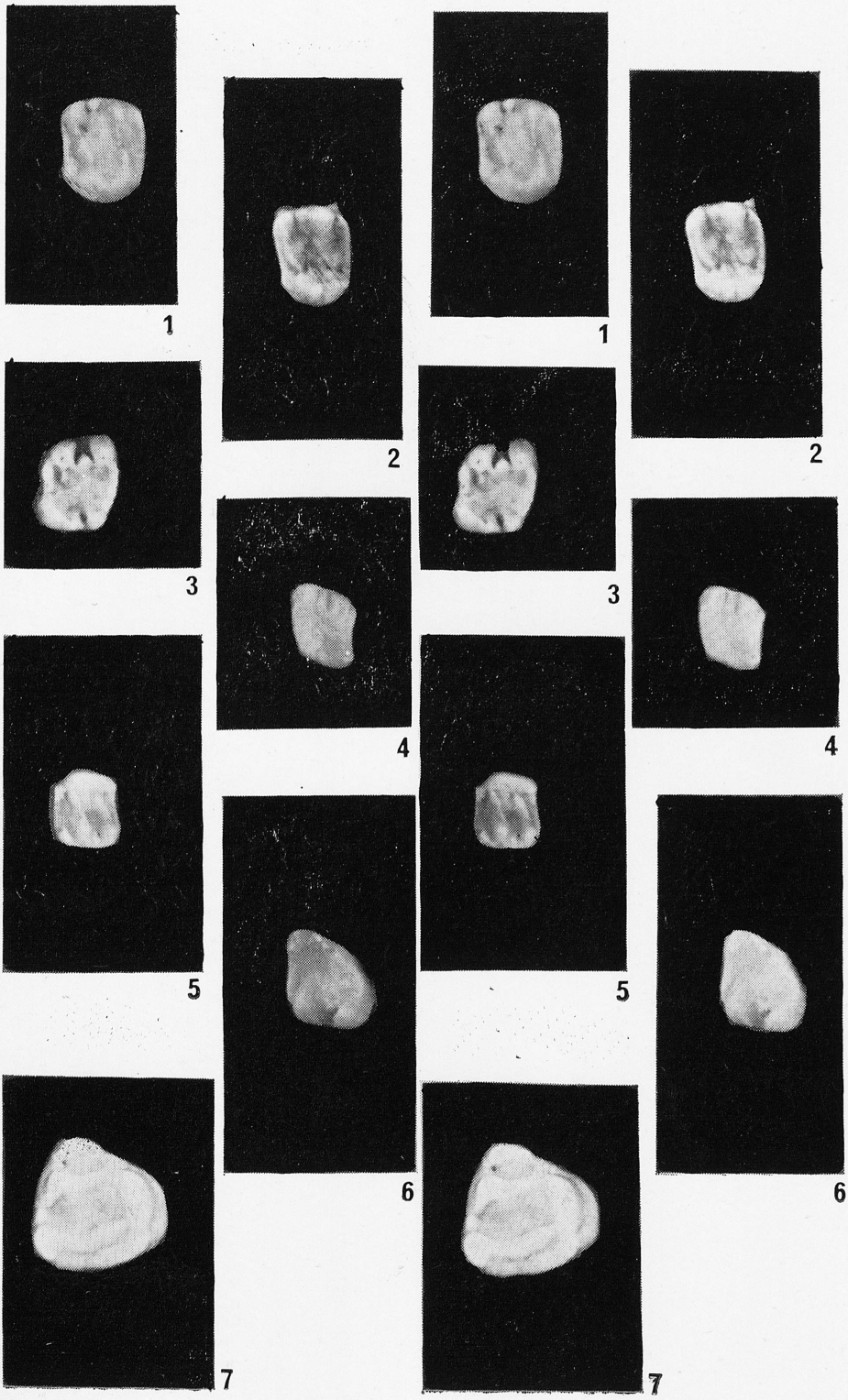
Фауна Замкова Дольна по своему общему составу близка к фауне Рембелице, однако на ее сравнительную молодость указывает появление бореальных и континентальных элементов, таких как *Lemmus*, *Villanyia*, *Ochotonidae* и *Spalacidae*. Что же касается беличьих, то здесь отмечается значительное обеднение состава древесных обитателей, представленных лишь двумя видами: *Sciurus* aff. *warthae* и *Pliopetaurista* cf. *pliocaenica*. Здесь впервые отмечается появление представителя сусликов — *Citellus polonicus*. Эта фауна проявляет известную близость с фаунами Острамош 3 в Венгрии и Схернфельд в Федеративной Республике Германии — как и эти две она несет на себе печать значительного охлаждения и континентализации климата Европы.

Единственным представителем беличьих из верхневиллафранкской фауны Кадзельня является *Citellus polonicus*. В более молодой фауне Камык этому виду сопутствует *Tamias* (?) sp. фауна Залесяки, в которой были обнаружены *Pliopetaurista meini* n.sp. и *Citellus polonicus*, вероятно, представляет собоюс месь разновозрастных остатков. В то же время, остатки млекопитающих, обнаруженные в местонахождении Кози Гжбет, представляют кромерский интергляциал — среди прочих здесь были обнаружены *Citellus polonicus* и *Petauria* sp. Последний род,

известный также из одновозрастных местонахождений Гусаренгоф 5 в ФРГ и Фойгштедт в ГДР, является единственным представителем летяг (*Petauristinae*) плейстоценовых фаун Европы, несомненно приспособленным к условиям более холодного климата. Из следующих отрезков плейстоцена остатки мелких млекопитающих на территории Польши неизвестны. Лишь время последнего оледенения сохранило остатки двух видов сусликов: *Citellus citelloides* и *C. superciliosus*.

Plate XII

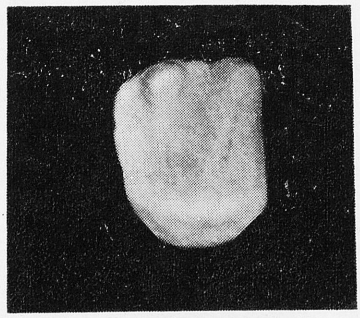
Fig. 1. *Sciurus* cf. *S. warthae* SULIMSKI. Podlesice. No. MF/1096/2. RM^{1-2}. × 5
Fig. 2. *Sciurus* cf. *S. warthae* SULIMSKI. Rębielice Królewskie I. No. MF/1098/3. RM^{1-2}. × 5
Fig. 3. *Tamias orlovi* SULIMSKI. Węże I. No. MF/1103/1. M_{1-2}. × 7
Fig. 4. *Tamias* cf. *T. orlovi* SULIMSKI. Podlesice. No. MF/1099. LM_{1-2}. × 5
Fig. 5. ?*Tamias* sp. Kamyk. No. MF/1109/1. RM^{1-2}. × 7
Fig. 6. ?*Tamias* sp. Kamyk. No. MF/1109/2. LM_3. × 7
Fig. 7. Sciurine indet. Podlesice. No. MF/1095/1. × 12



C. Black, K. Kowalski

Plate XIII

Fig. 1. Sciurine indet. Podlesice. No. MF/1095/2. LM^{1-2}. ×12
Fig. 2. Sciurine indet. Podlesice. No. MF/1095/8. RP_4. ×12
Fig. 3. Sciurine indet. Podlesice. No. MF/1095/9. LM_{1-2}. ×12
Fig. 4. Sciurine indet. Podlesice. No. MF/1095/10. RM_{1-2}. ×12
Fig. 5. Sciurine indet. Podlesice. No. MF/1095/12. RM_3. ×12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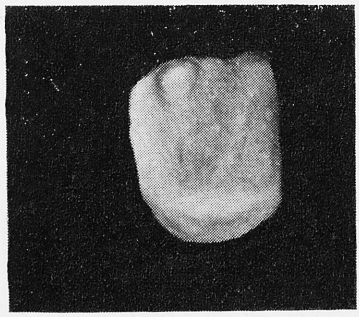
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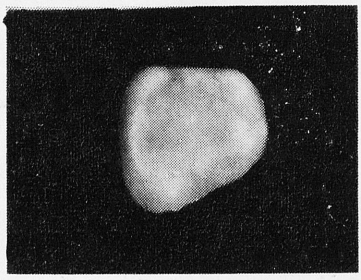
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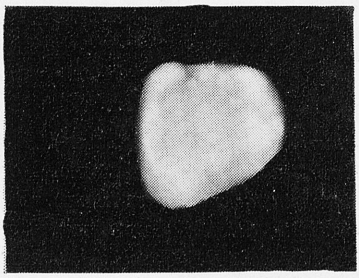
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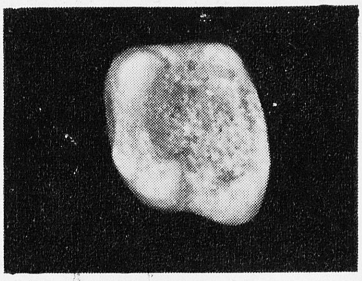
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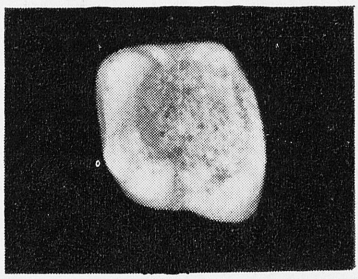
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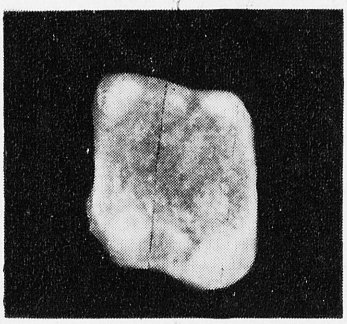
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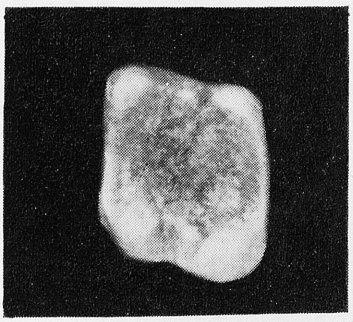
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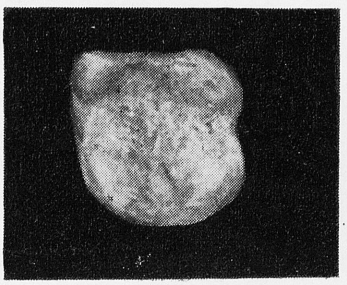
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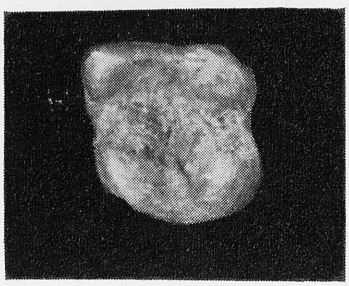

5

O. *Black, K. Kowalski*

Plate XIV

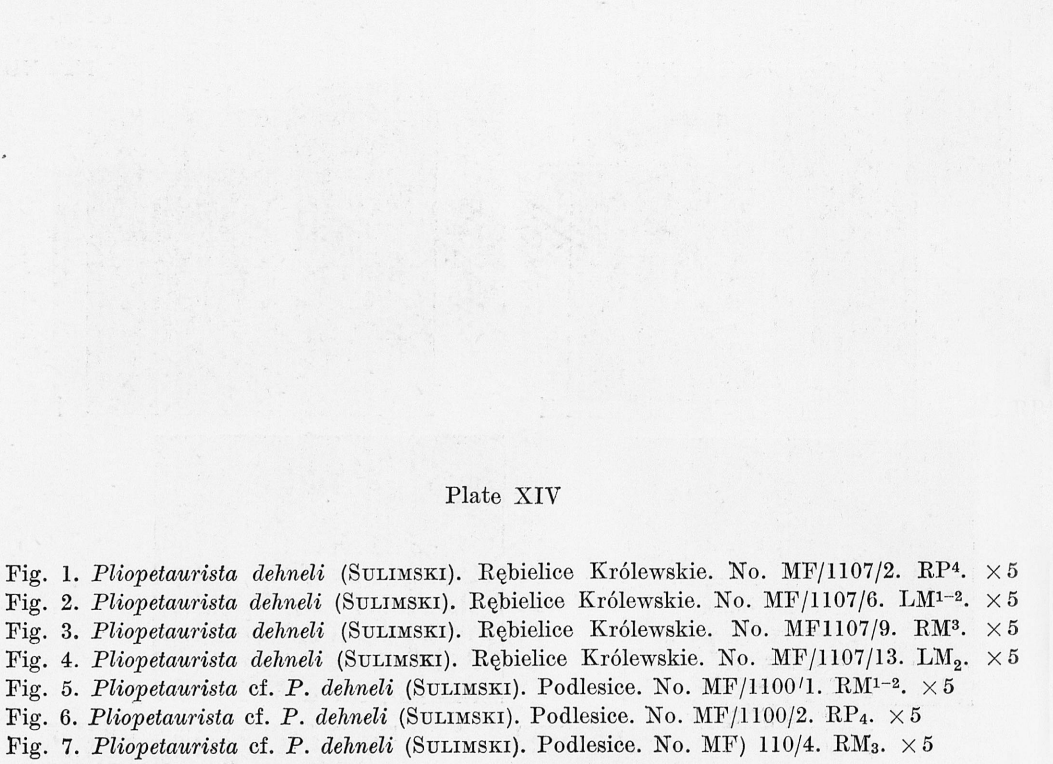
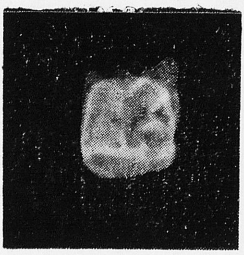


Fig. 1. *Pliopetaurista dehneli* (Sulimski). Rębielice Królewskie. No. MF/1107/2. RP^4. ×5
Fig. 2. *Pliopetaurista dehneli* (Sulimski). Rębielice Królewskie. No. MF/1107/6. LM^{1-2}. ×5
Fig. 3. *Pliopetaurista dehneli* (Sulimski). Rębielice Królewskie. No. MF1107/9. RM^3. ×5
Fig. 4. *Pliopetaurista dehneli* (Sulimski). Rębielice Królewskie. No. MF/1107/13. LM_2. ×5
Fig. 5. *Pliopetaurista* cf. *P. dehneli* (Sulimski). Podlesice. No. MF/1100/1. RM^{1-2}. ×5
Fig. 6. *Pliopetaurista* cf. *P. dehneli* (Sulimski). Podlesice. No. MF/1100/2. RP_4. ×5
Fig. 7. *Pliopetaurista* cf. *P. dehneli* (Sulimski). Podlesice. No. MF) 110/4. RM_3. ×5


1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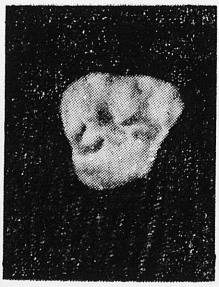
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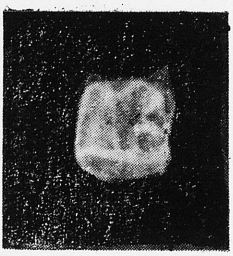
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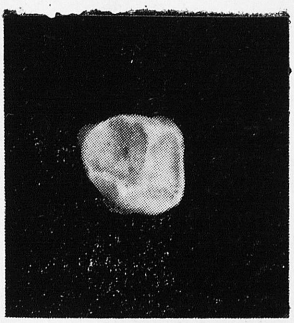
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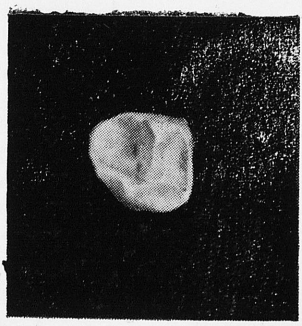
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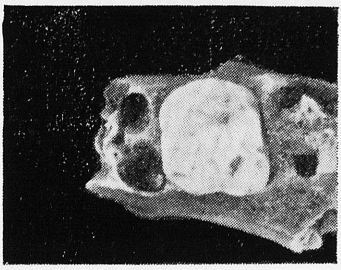
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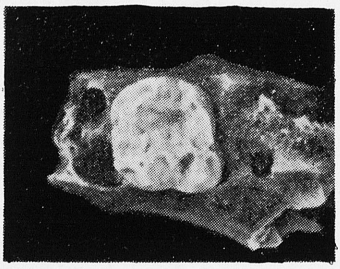
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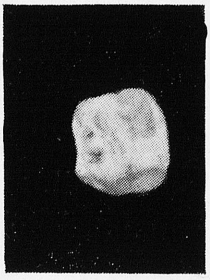
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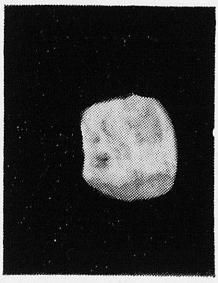
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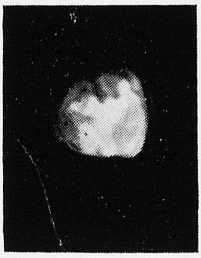
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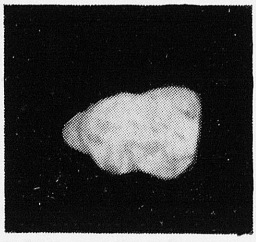
6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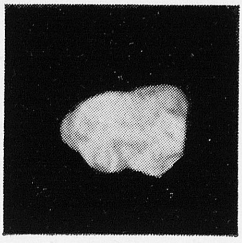
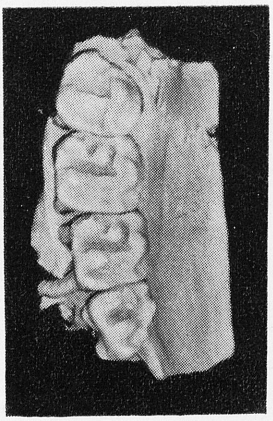

7

C. Black, K. Kowalski

Plate XV

Fig. 1. *Pliopetaurista meini* n. sp. Zalesiaki. No. MF/1118/1. LP^4—M^3 (holotype). ×6
Fig. 2. *Pliopetaurista meini* n. sp. Zalesiaki. No. MF/1118/3. LP_4—M_2. ×6
Fig. 3. *Pliopetaurista meini* n. sp. Zalesiaki. No. MF/1118/5, mandible. ×2·
Fig. 4. *Pliopetaurista meini* n. sp. Zalesiaki. No. MF/1118/6. RM_{1-2}. ×16
Fig. 5. *Pliopetaurista meini* n. sp. Zalesiaki. No. MF/1118/8. RM_2. ×16
Fig. 6. *Pliopetaurista* sp. Podlesice. No. MF/1101/1. RM_{1-2}. ×5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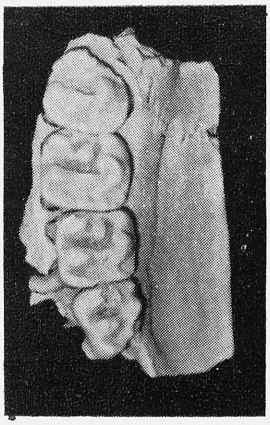
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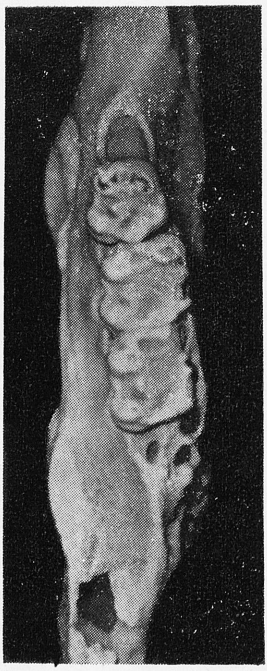
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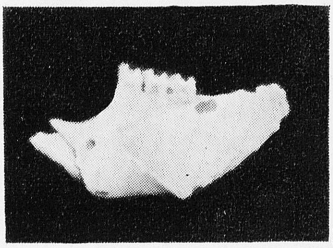
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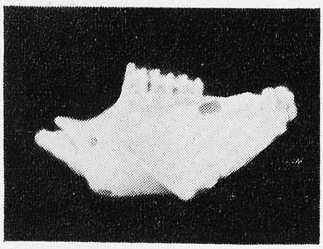
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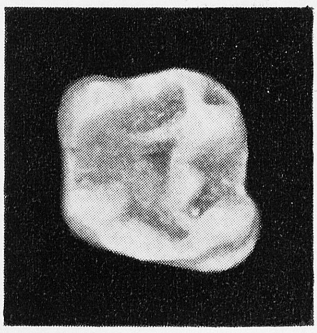
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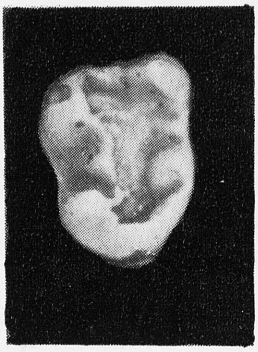
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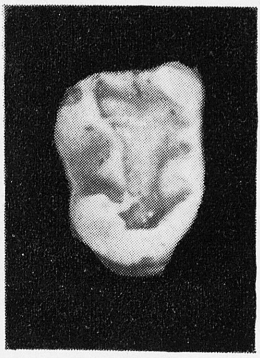
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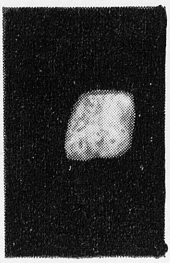
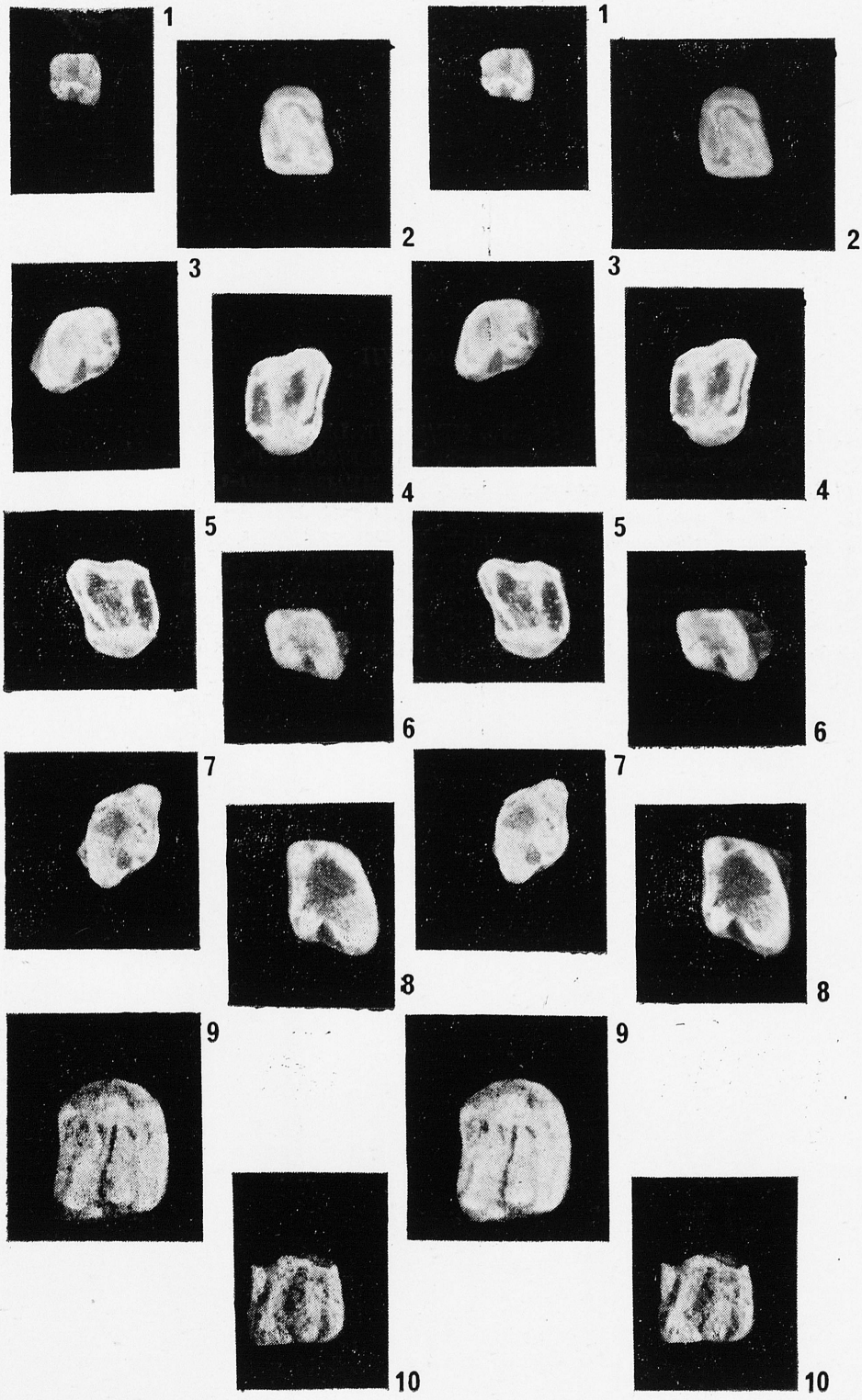

6


6

C. Black, K. Kowalski

Plate XVI

Fig. 1. *Pliopetaurista* sp. Podlesice. No. MF/1101/2. LM_{1-2}. × 5
Fig. 2. *Blackia polonica* n. sp. Podlesice. No. MF/1102/1. RM^{1-2} (holotype). × 10
Fig. 3. *Blackia polonica* n. sp. Podlesice. No. MF/1102/3. RM_{1-2}. × 10
Fig. 4. *Blackia polonica* n. sp. Węże I. No. MF/1104/1. LM^{1-2}. × 10
Fig. 5. *Blackia polonica* n. sp. Węże I. No. MF/1104/2. RM^{1-2}. × 10
Fig. 6. *Blackia polonica* n. sp. Rębielice Królewskie I. MNo. MF/1108/1. LP_4. × 10
Fig. 7. *Blackia polonica* n. sp. Rębielice Królewskie I. No. MF/1108/3. LM_1. × 10
Fig. 8. *Blackia polonica* n. sp. Rębielice Królewskie I. MF/1108/4. LM_2. × 10
Fig. 9. *Pliopetes hungaricus* Kretzoi. Węże I. No. MF/1110/1. LM^{1-2}. × 10
Fig. 10. *Cryptopterus* cf. *C. thaleri* Mein. Rębielice Królewskie. No. MF/1106/1. LM^{1-2}, damaged. ×



C. Black, K. Kowalski

Plate XVII

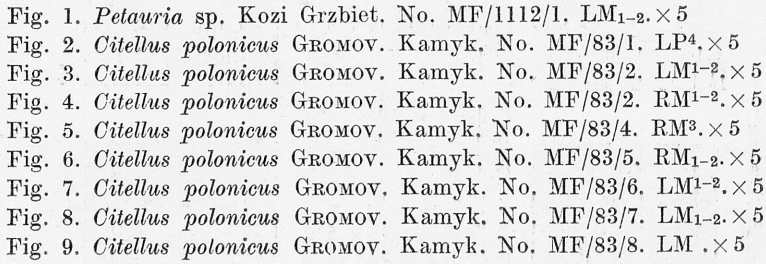
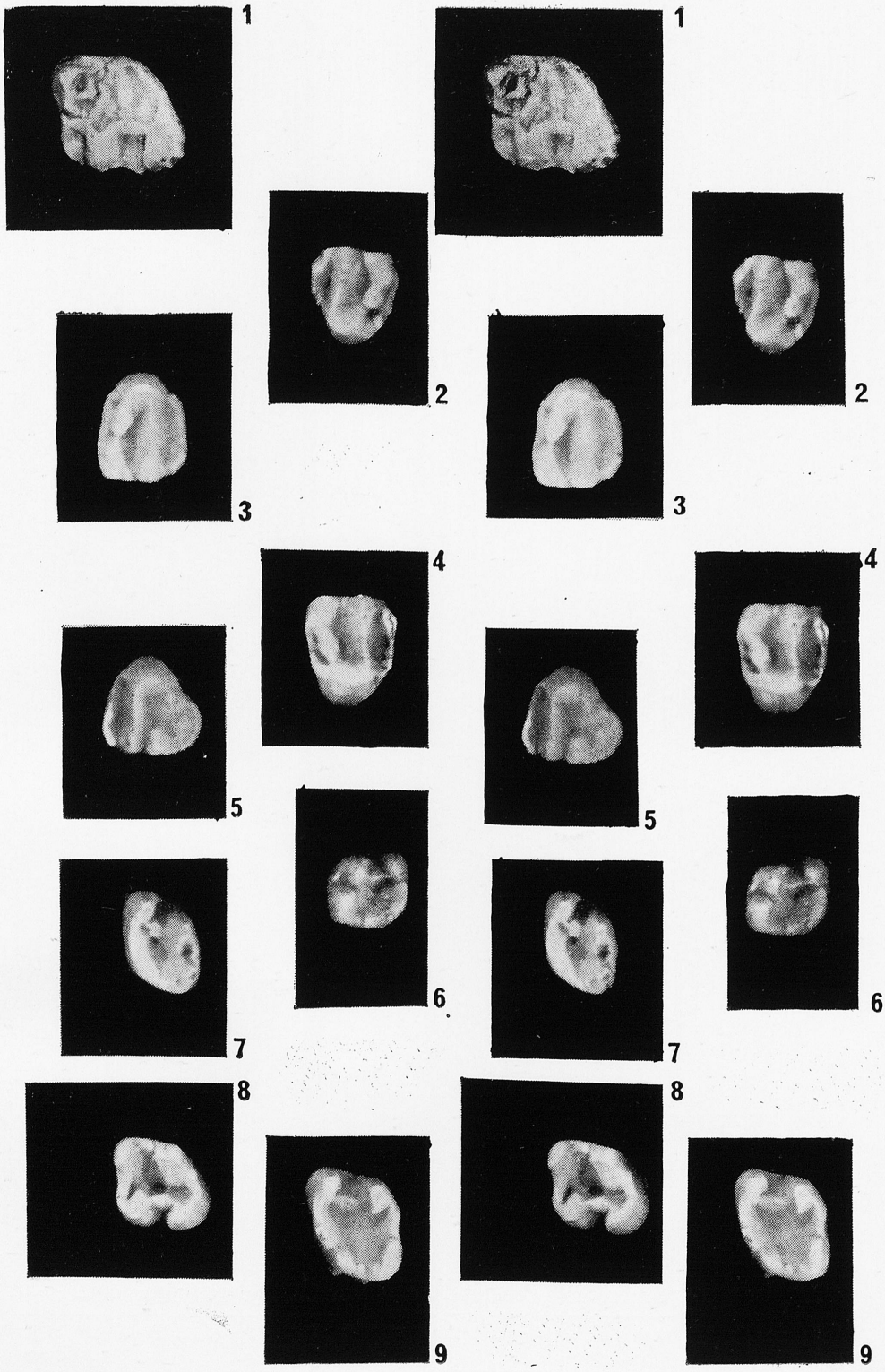


Fig. 1. *Petauria* sp. Kozi Grzbiet. No. MF/1112/1. LM_{1-2}. × 5
Fig. 2. *Citellus polonicus* GROMOV. Kamyk. No. MF/83/1. LP^4. × 5
Fig. 3. *Citellus polonicus* GROMOV. Kamyk. No. MF/83/2. LM^{1-2}. × 5
Fig. 4. *Citellus polonicus* GROMOV. Kamyk. No. MF/83/2. RM^{1-2}. × 5
Fig. 5. *Citellus polonicus* GROMOV. Kamyk. No. MF/83/4. RM^3. × 5
Fig. 6. *Citellus polonicus* GROMOV. Kamyk. No. MF/83/5. RM_{1-2}. × 5
Fig. 7. *Citellus polonicus* GROMOV. Kamyk. No. MF/83/6. LM^{1-2}. × 5
Fig. 8. *Citellus polonicus* GROMOV. Kamyk. No. MF/83/7. LM_{1-2}. × 5
Fig. 9. *Citellus polonicus* GROMOV. Kamyk. No. MF/83/8. LM . × 5



C. Black, K. Kowalski

Redaktor zeszytu: prof. dr M. Młynarski

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