OSTEOLOGY OF *PROLAGUS SARDUS*, A QUATERNARY OCHOTONID (MAMMALIA, LAGOMORPHA)

by

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Palæovertebrata, Montpellier, 1969, 2 : 157-190, 38 fig., 1 pl.

(*Accepté le 1er décembre 1968; publié le 21 juin 1969*)

SUMMARY

Prolagus sardus ist der letzte Vertreter der verschiedenen endemischen Europaischen Ochotoniden Ligien. Sie ist auch die meist reichliche aufbewahrte Art in den Sammlungen.

Der bis heute an dieser Art angewidmete Arbeit, erlaubt es, sein Gebiss, seine phylogenische Stellung, seine Verteilung in Raum und Zeit, seine individuellen intraspezifischen Variationen ziemlich gut zu befassen. Dagegen hat keine osteologische Beschreibung die merkwürdigen Sammlungen von Forsyth Major aus Korsika und Sardinien völlig ausgenutzt. In diese Sammlungen sind beinahe alle Teile des Skeletts vertreten; sie sind hier beschrieben und abgebildet.

Diese Art ist mit *Ochotona*, letzte überlebende Gattung der Familie, sowie als mit den heutigen Leporiden, besonders mit *Romerolagus, Oryctolagus*, und *Lepus*, vergliechen worden.

Eine kurze Untersuchung erlaubt es, beschränkte Deutungen über der Haltung, den Kauen, der Lokomotion und einigen anderen adaptativen Zügen vorzubringen.

Prolagus sardus erscheint als einen unbestreitbaren Ochotonid; weicht aber durch mehrere Merkmale die bei den Leporiden hervor kommen von *Ochotona* ab. Einige dieser Merkmale sind bei den Lagomorphen hier für primitiv gehalten. Die Gattung *Ochotona* kann also nicht mehr als Bild des primitiven Lagomorpen vorgestellt worden, weil sie, trotz dem Mangel an Anpassungen für das rennen, was sie den Leporiden gegenüberstellt, andere Anpassungen beweist, die ihr eingetümlich sind.

Prolagus sardus is the last representative of the diverse lineages of European endemic ochotonids. It is also the most abundant in the collections. The previous studies made of this species have established rather well its dental morphology, its phylogenetic position, its geographic and temporal distribution, and its intraspecific individual variation. On the other hand, no osteologic study has fully utilized the superb material from Corsica and Sardinia, collected by Forsyth Major.

Nearly all of the parts of the skeleton are represented in this material; they are here described and figured. Comparisons are made with *Ochotona*, the only surviving genus of the family, as well as with the living leporids, in particular *Romerolagus, Oryctolagus* and *Lepus*.

A brief examination of the dentition reveals some particular characters of the incisors.

The osteologic study allows limited interpretations to be advanced concerning the posture, mastication, locomotion and some other adaptive features of *P. sardus*.

P. sardus appears as an incontestable ochotonid, but it differs from *Ochotona* by some characters which are found in leporids. Certain of the characters are here judged primitive for lagomorphs. The genus *Ochotona* therefore can no longer be considered as the image of à primitive lagomorph, because in spite of the lack of cursorial adaptations which differentiate it from leporids, it presents other specializations which are common to it alone.

Prolagus sardus est le dernier représentant des diverses lignées d'ochotonides endémiques d'Europe. C'est aussi le plus abondant en collection. Les études consacrées jusqu'ici à cette espèce ont permis de fixer assez correctement sa morphologie dentaire, sa position phylogénique, sa distribution géographique et temporelle, et ses variations individuelles intraspécifiques. Par contre, aucune étude ostéologique n'a utlisé pleinement le superbe matériel de Corse et de Sardaigne récolté par Forsyth Major.

Presque toutes les parties du squelette sont représentées dans ce matériel; elles sont décrites et figurées ici. Des comparaisons sont faites avec *Ochotona*, unique genre survivant de la famille, ainsi qu'avec les léporides actuels, en particulier *Romerolagus, Oryctolagus*, et *Lepus*.

Un bref examen de la denture révèle des caractères particuliers des incisives.

L'étude ostéologique permet d'avancer des interprétations limitées concernant la posture, la mastication, la locomotion, et quelques-autres traits adaptatifs de *P. sardus*.

P. sardus apparaît comme un ochotonide incontestable, mais diffère d'*Ochotona* par quelques caractères qui se retrouvent chez les léporides. Certains de ces caractères sont ici jugés primitifs pour les lagomorphes. Le genre *Ochotona* ne peut donc plus être considéré comme l'image du lagomorphe primitif, car malgré le manque d'adaptation à la course qui l'oppose aux léporides, il présente d'autres spécialisations qui lui sont propres.

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INTRODUCTION

During the middle Tertiary several lines of endemic Ochotonidae occurred in Europe. These lines, probably derived from Asian ancestors, first appeared in the late Stampian (Coderet). The endemic ochotonids flourished during the Aquitanian, Burdigalian and Vindobonian in western Europe, being well represented at such localities as St.-Gérand-le-Puy, Wintershof-West, Manchones, and La Grive St.-Alban. None of them except the genus *Prolagus* persisted after the Pontian. *Prolagus* lived on through the Pliocene and Pleistocene, and the species *P. sardus* may even have been present during historic times on Corsica and Sardinia (Tobien, 1935, p. 262-263).

Not only is *Prolagus sardus* the last survivor from among the various endemic European ochotonids, but also it is the best represented by fossils, being known from numerous remains collected from cave and fissure deposits on the islands of Corsica and Sardinia. These remains have been known at least since 1807, when Rampasse reported on a bony breccia from Corsica. Various other collections were subsequently made, but the largest and most complete collections from Corsica and Sardinia were those made by C.I. Forsyth Major in 1922 and 1923, shortly before his death. The largest part of his collections went to the Basel Naturhistorisches Museum, and some excellent specimens, especially skulls, went to the British Museum (Natural History). This study is based primarily on Forsyth Major's collections in these two museums, although specimens in older collections in Paris and Lyon were also utilized.

The good fossil record of *Prolagus sardus* has led to a number of descriptive studies, including those of Cuvier (1823, v. 4, p. 199-204), Wagner (1832, p. 763-767), and Lortet (1876). Lortet (1876, pl. 8) presented a reconstruction of *Prolagus sardus* based on specimens from Bastia, Corsica, in the Muséum d'Histoire Naturelle of Lyon. The mounted composite skeleton has a good skull but is unfortunately misleading in the postcranial skeleton. The position of the scapula is too high relative to the vertebral column. The skeleton is restored with 13 thoracic and six lumbar vertebrae, which is near the number in leporids (12, 7) but quite different from that of ochotonids (usually 17, 5). The vertebral column is arched into an unnatural position. Lortet's illustration shows leporid-like transverse processes on the lumbar vertebrae, but these are absent in the specimen. The radii, carpals, tarsals, phalanges, and some vertebrae are restored (plaster or wood), and the metapodials are spread out unnaturally. The « left innominate » is actually a right ilium mounted upside down and with pubis and ischium restored. The total picture given by this specimen can thus not be regarded as accurate. Forsyth Major (1899) made a thorough study of the dentition of *P. sardus* and reviewed the nomenclature of the species. Comaschi Caria (1959) reported on new Sardinian materials of *P. sardus* and included a photograph of a mounted composite skeleton in the Basel Museum. The skull of this mount was restored from anterior and posterior parts joined by plaster and is flatter in the parietal region than is the case in more complete skulls. The leporid number of vertebrae is given in the composite, and the sacrum and pelvic girdle are mounted in an unnaturally high position.

The phylogenetic position of *Prolagus sardus* has been reasonably well established, representing as it does the last member of a group that started with *Piezodus* in the late Stampian. Several species of *Prolagus* are known from the Miocene and Pliocene. *Prolagus sardus* is surely close to these earlier species, although details of its ancestry have not yet been determined. The gradual dental changes in the *Piezodus-Prolagus* group have been well documented (Viret, 1950; Hürzeler, 1962; Tobien, 1963), although as Tobien (1963, p. 28-29) has suggested, as yet undescribed forms of *Prolagus* will broaden the morphological scope of this genus.

Still other studies of *P. sardus* have been aimed at problems related to geographic distribution (Depéret, 1902: Forsyth Major, 1905; Malatesta, 1951). The most comprehensive study of *Prolagus sardus* has been that of Tobien (1935), who analyzed distribution and variation of the Corsican and Sardinian populations. He came to the conclusion that the Pleistocene and post-Pleistocene *Prolagus* of Corsica and Sardinia should be regarded as referable to the species *P. sardus* but that several temporal and geographic races were represented. Tobien's study, like this one, was based largely on Forsyth Major's collections in Basel. Various ages within the Quaternary are represented by the different localities on Corsica and Sardinia but they have not yet been precisely correlated or dated.

Thus, at present *Prolagus sardus* is a relatively well known form, especially for dental morphology, phylogenetic position, distribution, and individual variation within the species. However, although skeletal material of this species has been figured and described to some extent, an osteological study has not previously been made on the superb materials that warrant such a study. It is, therefore, the purpose of the present work to present such an osteological description with comparisons to other Lagomorpha, and to utilize the osteological information in an attempt to determine something of the habits of *P. sardus*. In addition, the information will be used to evaluate the characteristic features of the family Ochotonidae. The first of these purposes — analysis of function — has proved difficult because *P. sardus* is not extreme in specialization. The second has provided interesting possibilities related to the interpretation of *Ochotona*, the only exant genus of ochotonid.

METHODS

The excelent collections from Corsica and Sardinia in the Basel Naturhistorisches Museum provided most morphological details for this study. Nearly all skeletal parts of *Prolagus sardus* are represented, of both adult and immature individuals. In most cases, however, these are isolated bones and not associated skeletal elements. There are a few associations, such as radius and ulna or radius, ulna, and humerus, but these are so few that it is necessary to base estimation of proportions of the limbs on averages from each locality. Nor do the collections indicate such things as the number of vertebrae of the different regions, which must thus be approximated based on morphology of individual vertebrae and comparisons with other lagomorphs. In estimating proportions of the limbs, measurements of Tobien (1935) were utilized. Size of the reconstructed composite skeleton (Fig. 38) is based on the size of individuals from Tavolara, a small island on the east coast of Sardinia. All figures are based on specimens in the Basel Naturhistorisches Museum.

As Tobien (1935) demonstrated, there is considerable size variation among the samples of *P. sardus* from different localities on Corsica and Sardinia. In morphology the samples are more homogeneous and specimens from the different localities are not differentiated in this osteological study. Morphological differences related to size were noted mostly in the cases of relative development of areas of muscle attachment, which tend to be better developed in larger and probably in older individuals.

In this study most comparisons of *Prolagus sardus* were made with the only Recent ochotonid, *Ochotona*, and with the leporids, *Romerolagus*, *Oryctolagus*, and *Lepus*. *Romerolagus*, a relatively primitive North American form, contrasts to the more advanced *Oryctolagus* and *Lepus*, and was chosen to give some breadth to the comparisons with leporids.

Attempts to interpret the osteological features of *Prolagus sardus* have been made difficult because of the lack of complete and thorough anatomical or functional studies of *Ochotona*. Camp and Borell's (1937) study is very useful but it deals with the hind limb only and emphasizes cursorial adaptations of the leporids. There is a real need for studies of *Ochotona* and comparisons of that genus with leporids. Anatomical terminology in this study is that of Craigie (1948) for the most part. In the osteological description, when no other species name is used *Prolagus* refers to *P. sardus*.

DESCRIPTION

Dentition.

The cheek teeth of *Prolagus sardus* have been well figured and discused since early studies on this species, and dental evolution from the *Piezodus* level through the species of *Prolagus* has been well documented (Forsyth Major, 1899; Viret, 1950; Hürzeler, 1962; Tobien, 1963). In *P. sardus* P_3 is relatively simple for the genus, lacking the accessory lobule of *P. bilobus*. P^2 is more advanced toward the level of P^{3-4} than in other ochotonids, and the molars have as the adult pattern only a long hypostria. Two lakes may occur on M^1 in young individuals but these are removed with wear. Although cheek tooth pattern and hypsodonty have been frequently discussed, the characters of the incisors have been largely overlooked, and here *P. sardus* has some highly individual features. Viewed laterally both the anterior upper incisor and the lower incisor appear to be dorsoventrally thick. A section of the anterior upper incisor shows the same condition — the lateral part protudes posteriorly, and the wear surface of the upper incisor has a lateral shelf at about the same level as the posterior incisor. Thus effectively the surface formed by the posterior incisor is widened. The groove is almost central in the anterior upper incisor, whereas it is more medial in *Ochotona*. The lower incisor is turned in the alveolus, so that the enamel covered surface faces ventrolaterally. The arc of the lower incisor is less concave dorsally than in *Ochotona*, but probably not greatly different from that in some leporids. A medial wear surface at the tip of the lower incisor shows that this tooth abraded against the lower incisor of the other side as in *Ochotona*, and thus shows that movement between the lower jaws was possible.

SKULL (Figs. 1-5).

The skull of *Prolagus sardus* gives a first impression of general similarity to those of leporids. This impression is related to 1) size, which is between that of *Romerolagus* and of *Ochotona;* 2) a large area of maxillary fenestration; 3) arching of the skull due to a larger basicranial-basifacial angle than in *Ochotona* and to doming of the parietals; 4) size and shape of the bullae; and 5) relatively large, dorsoventrally deep orbits. In detail, however, the skull shows many basic ochotonid features, especially in the structure of zygoma and maxilla, occiput, and palate. In addition to those basic characters in which *Prolagus sardus* resembles *Ochotona* and other characters of similarity to leporids, *P. sardus* has certain characters found neither in *Ochotona* nor in Recent leporids.

A dorsal view of the skull (Fig. 1) shows that the sides of the muzzle widen more posteriorly in *Prolagus* and *Ochotona* than in *Romerolagus*. In *Prolagus* the nasal bone is slightly narrower posteriorly than anteriorly but the bone does not narrow so much as in *Ochotona*. In contrast, in *Romerolagus* the nasal widens posteriorly. As in *Ochotona* the nasal is convex posteriorly at the frontal-nasal suture. The most conspicuous feature of the frontal in *Prolagus* is a ridge that starts near the premaxilla-frontal suture and extends along the dorsal border of the orbit. The ridge continues on the squamosal and parietal. Medial to the ridge the surface of the frontal is pitted. Length and elevation of the ridge and amount of pitting is individually variable, possibly with age. Neither *Prolagus* nor *Ochotona* have the supraorbital process of the frontal that characterizes leporids.

Along with the frontal, the parietal is important in forming the dorsal convexity of the skull roof that contributes, along with the basifacial-basicranial bending, to the arched appearance of the skull of *Prolagus* (Fig. 2). The skull is more flattened in *Ochotona*, with the closest approach to *Prolagus* being seen in the subgenus *Conothoa*. At the frontal-parietal contact the

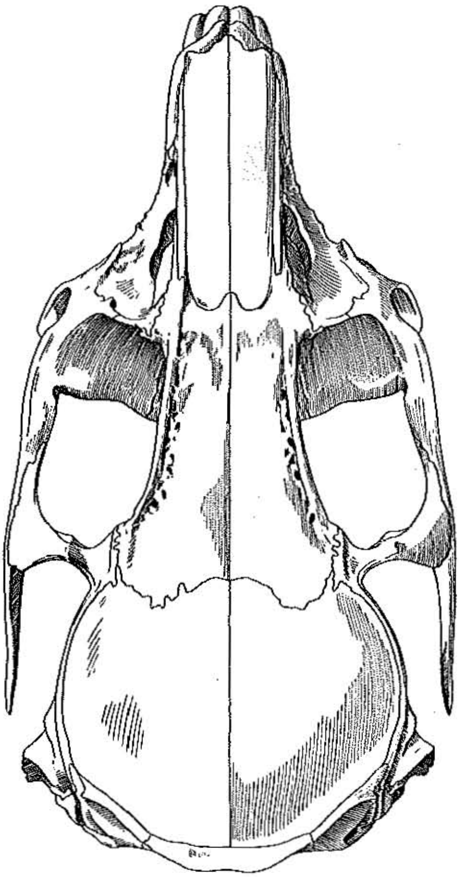

FIG. 1. — Dorsal view of skull, x 2.
Composite skull of figs. 1-5 based on : Grotto Nicolai-Ty. 11909, Ty. 11910, Ty. 11920; Toga-Ty. 1691; Dragonara-Ty. 7046; Tavolara-Ty. 8688, Ty. 8697.

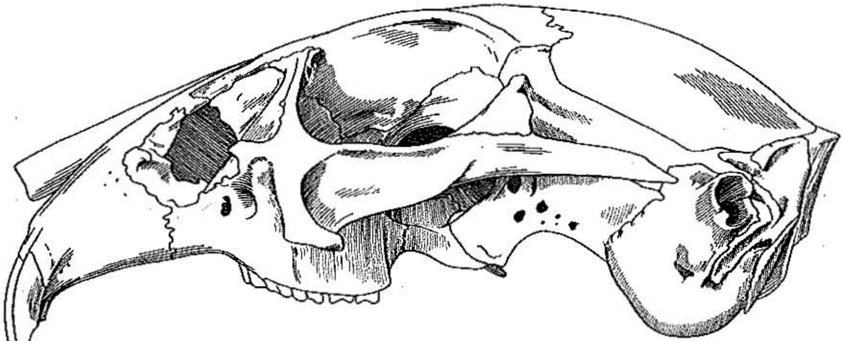

FIG. 2. — Lateral view of skull, x 2.

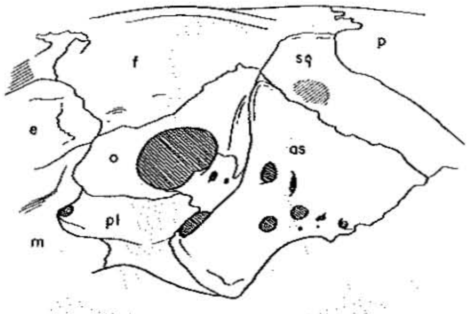

FIG. 3. — Lateral view of left orbit, zygoma removed, x 2.
as — alisphenoid, e — ethmoid (?), f — frontal, m — maxilla, o — orbitosphenoid, p — parietal, pl — palatine, sq — squamosal.

parietal reaches farther anteriorly in the midline in *Prolagus* than in *Ochotona*, in which the parietal extends farther anteriorly lateral to the midline. Posterior to the arch of the parietal that bone extends as a ledge to the contact with the occipital. There is a weak sagittal crest on the flattened ledge of the parietal but not extending anteriorly onto the domed area. No specimens of *Prolagus* showed a separate interparietal, such as occurs in young individuals of *Ochotona* and in some leporids.

The palate of *Prolagus* (Fig. 4) is basically similar to that of *Ochotona* in having the following features : two pairs of incisive foramina, the anterior of which is within the premaxilla, as in some species of *Ochotona;* a palatal bridge in which the maxillary component is reduced, as opposed to one as in leporids in which the palatine component is reduced; and a premolar foramen in the maxilla. The maxilla sends forward a process between the posterior pair of incisive foramina. None of the specimens of *Prolagus* have the palatine separating the maxillae anteriorly and forming part of the posterior border of the incisive foramina, such as occurs in some species of *Ochotona*. The internal nares are slightly expanded anteriorly in *Prolagus* and the palatine has a short posterior process into the narial opening. *Ochotona* has more nearly parallel narial walls and lacks the palatine process. In these two features of the internal nares *Prolagus* shows more similarity to *Romerolagus* than to *Ochotona*.

Like the palatine component of the maxilla, other parts of that bone show basic similarities to the maxilla of *Ochotona*, although there are differences in detail. Some of these similarities are related to the type of hypsodonty of ochotonids and accompanying development of the maxillary tuberosity. The strongly hypsodont cheek teeth extend into a maxillary tuberosity that contacts the zygoma along the entire length of the tuberosity. The teeth seem to be more hypsodont than in Recent *Ochotona*, which differs also in having that part of the tuberosity containing M^2 or sometimes M^1 and M^2 free of the zygoma. On its lateral surface the maxilla of *Prolagus* has a triangular opening in *Ochotona*. Well preserved specimens of *Prolagus* show that a well developed bony splint forms the ventral

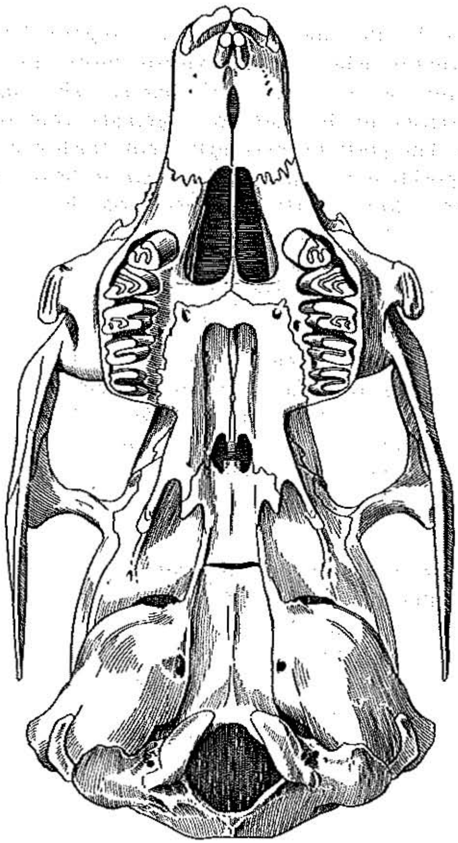

FIG. 4. — Ventral view of skull, x 2.

margin of this opening and that the maxilla below this splint is a lacework of fenestrated bone. Most specimens of *Ochotona* lack this ventral lacework, although some trace of it can be seen in a species such as *O. roylei*. The infraorbital foramen occurs in a line above P² and below the lacework of bone, in a more ventral position relative to the anterior zygomatic root than in *Ochotona*. Recent leporids have a more medially situated foramen that is dorsal to the anterior zygomatic root.

Development of the zygoma in *Prolagus* and *Ochotona* is related to its contact with the maxillary tuberosity and thus a basic similarity occurs. The zygoma of *Prolagus* resembles that of *Ochotona* anteriorly in having a deep anterolateral concavity and a well developed ventral process. In *Prolagus*, however, the anterior root is more verticaly oriented, and protudes farther laterally in its ventral part, with a more pronounced ventral hook than in *Ochotona*. The concavity on the zygoma for masseter attachment is more deeply concave than in *Ochotona*. Below the orbit the zygomatic arch, continued here by the jugal bone, has a slightly laterally protuding dorsal ridge. The ventral edge of the zygoma below the orbit does not bend upward abruptly as it does in *Ochotona*. The jugal has a long tapering process posterior to the posterior zygomatic root somewhat similar to that in *Ochotona*. The posterior zygomatic root, formed by the squamosal, resembles that in leporids more than in *Ochotona* in being relatively narrow anteroposteriorly. The dorsal surface of the root has a well developed groove, with a strong lateral process, for the temporalis muscle. The groove is not quite so well developed in *Ochotona*, and it is very shallow in Recent leporids. The glenoid fossa is similar to that in leporids and anteroposteriorly shorter than in *Ochotona*.

The expansion of the squamosal that forms the posterodorsal part of the zygoma below the orbit in *Ochotona* is lacking in *Prolagus*. Posterior to the zygomatic root the squamosal passes back and forks above the meatus into a spatulate ventral process and a short dorsal process. In *Ochotona* the squamosal is narrow posteriorly and lacks a division into two processes. Two processes, better developed than in *Prolagus*, occur in Recent leporids.

As a result of several structural differences, the orbit of *Prolagus* is relatively larger than that of *Ochotona*. In *Prolagus* the frontals are narrower at the anterior of the orbit and the sides of the frontal forming the dorsal orbital rim diverge only slightly toward the posterior of the orbit. Both anterior and posterior orbital walls diverge outward abruptly. The ventral orbital rim, formed by the jugal, is nearly horizontal. In *Ochotona* the frontals curve gradually outward both anteriorly and posteriorly, and the size of the orbit is further curtailed by the expanded process of the squamosal that forms the posterior zygomatic root and extends forward along the dorsal surface of the jugal. The orbit of *Prolagus* is thus more comparable in relative length to that in *Romerolagus*, although in *Romerolagus* and other Recent leporids the orbit is deeper in its anterior portion and is relatively deeper dorsoventrally in general.

The lacrimal bone, which is quite reduced in *Ochotona*, is not represented for *Prolagus*. As preserved, the ethmoid is visible in the anteromedial wall of the orbit. In the orbitosphenoid (Fig. 3) the optic foramen is large and confluent with that of the other side, as in other lagomorphs. The superior orbital fissure, which is between orbitosphenoid and alisphenoid, is separated by a narrow bony wall from the large, round anterior sphenoidal foramen in the alisphenoid. This foramen is relatively larger in *Prolagus* and *Ochotona* than in leporids; it is farther posterior in *Prolagus* than in *Ochotona* but farther anterior than in leporids, a series of positions probably related to the amount of basicranial-basifacial bending in these lagomorphs.

The lateral pterygoid lamina of the alisphenoid is less reduced than in leporids. The lamina and the alisphenoid posterior to it are penetrated by several, rather variable foramina as in *Ochotona*. The hamular process of the medial pterygoid lamina is better developed than in *Ochotona* but less so than in Recent leporids. The basisphenoid resembles that in leporids in having a shorter anterior process than in *Ochotona,* a difference probably related to the basifacial-basicranial bending. A ridge from the medial pterygoid lamina to the bulla is formed in part by the basisphenoid. Ventrally between the bulla and the alisphenoid all specimens show an open space, suggesting that the bone was delicate here as it is in Recent lagomorphs, and representing the opening of the foramen lacerum. The lateral margins of the basioccipital are essentially parallel as in *Ochotona* rather than constricted by the bulla as in Recent leporids.

The bulla is good sized, proportionately slightly larger than in *Romerolagus.* The axis of the bulla is anteromedially to posterolaterally oriented as in *Ochotona,* but in addition an anterolateral swelling contributes to a more rounded bulla than in *Ochotona.* Thus, the shape of the bulla shows some approach to that of leporids. The well developed, posterolaterally directed bony meatus is more leporid-like than like that in *Ochotona.* Lateral to the basioccipital the bulla is pierced by the external carotid foramen. A similar, although slightly more posterior foramen occurs in leporids, but *Ochotona* lacks the foramen. Within the bulla at least two and sometimes three bony septa extend inward, supporting the wall of the bulla. This condition is in contrast both to *Ochotona,* in which the wall of the bulla is a mass of spongy bone, and to Recent leporids, in which the bulla is thin walled and lacks septa. The surface of the mastoid is smooth as in *Ochotona* rather than being pitted as in Recent leporids. This bone is exposed between the two posterior processes of the squamosal and has a greater exposure on the occipital surface than in *Ochotona.* The mastoid has a dorsoventral ridge dorsal to the meatus and is also ridged at the paroccipital contact. It has a distinct mastoid process. *Ochotona* lacks these ridges as well as a distinct mastoid process. The mastoid thus has a tendency toward some leporid-like features.

The occiput of *Prolagus* (Fig. 5) is basically like that in *Ochotona,* lacking the extreme development of dorsal and lateral protrusions and ridges that is characteristic of Recent leporids and is associated with strengh of neck muscles. In *Prolagus* as in *Ochotona* the paroccipital processes are wide

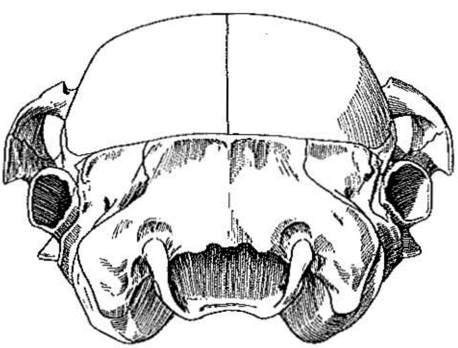

FIG. 5. — Occipital view of skull, x 2.

transversely. The supraoccipital is relatively higher than in *Ochotona* and forms a short shelf on the dorsal skull surface. The jugular foramen occurs between occipital and bulla. Lateroventral to the condyle the occipital is pierced by several foramina for the hypoglossal nerve.

LOWER JAW (Figs. 6-7).

The jaw presents a somewhat leporid-like appearance due in part to the upward bend at the diastema, which is similar to that in *Romerolagus*, and in part to the angle between horizontal and ascending rami, which is greater than in *Ochotona* although less than in *Romerolagus*. The ventrally protruding ridge for attachment of the masseter muscle is more anterior relative to the ascending ramus than in *Ochotona*. In addition to the ridge ventral to the

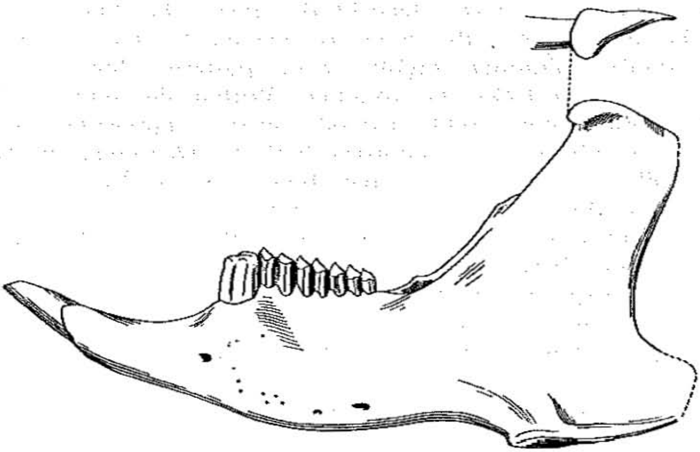

FIG. 6. — Lateral view of jaw and dorsal view of condyle, x 2.
Composite jaw of figs. 6-7 based on: Monte San Giovanni-Br. 359, Br. 363.

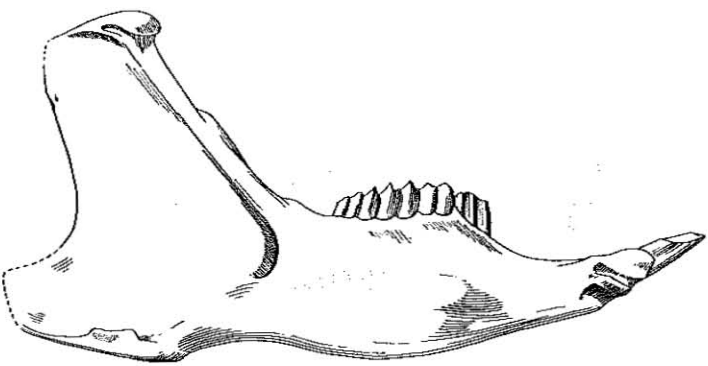

FIG. 7. — Medial view of jaw, x 2.

masseteric fossa there is a variably developed ridge extending into the fossa from posteroventral to anterodorsal. The comparable ridge in *Ochotona* is more anteroposteriorly oriented. Two distinct mental foramina are present, one below P_3 and the other lower and below M_1 or the trigonid of M_2. In this character *Prolagus* resembles more primitive lagomorphs such as the leporid *Palaeolagus* and the ochotonids *Sinolagomys* and *Kenyalagomys*. Between the two mental foramina and over the shaft of the incisor the bone is pitted. The swelling over the incisor on the medial side of the jaw extends to below P_4 where it is at about mid-depth of the jaw. In *Ochotona* the incisor is approximately as long but is closer to the ventral edge of the jaw, and the Recent leporids have a shorter swelling over the incisor. As in *Ochotona* the pterygoid fossa, which is set off by well developed anterior and ventral ridges, lacks the subdivision by a bony ridge into dorsal and ventral parts that occurs in Recent leporids. The anterior surface of the ascending ramus has a low but thickened, medially situated coronoid process similar to that in *Ochotona*. The condyle protrudes laterally in its anterior part and tapers posteriorly, thus resembling that of *Romerolagus* more closely than that of *Ochotona* in which the condyle has less anterolateral protrusion, tapers more gradually, and has a relatively longer articular surface.

VERTEBRAL COLUMN (Figs. 8-16, 38).

In Recent *Ochotona* the thoracic region is quite long, iwth 17 thoracic vertebrate usually present although some specimens show 16. The lumbar region usually has five vertebrae (four occasionally), and there are four fused sacral vertebrae (five occasionally). The trunk proportions of leporids are quite different, with 12 thoracic, seven lumbar, and four fused sacral vertebrae. *Prolagus* is here reconstructed as being more like *Ochotona*, with 16 thoracic vertebrae and five lumbar vertebrae. There is no really good evidence regarding this number in the absence of articulated specimens, and it may or may not approach the correct assignment. There were five vertebrae in the sacrum, the fifth of which is not completely fused to the fourth in young individuals but is in adults. Study of the vertebrae lacks precision due to the fact that in most specimens of *Prolagus* processes are broken away.

The cervical vertebrae (Figs. 8-11) do not differ greatly from those of *Ochotona*, although there are differences in detail, especiallty in development of transverse processes. Orientation of the transverse process of the atlas, which is less horizontal and more anterodorsal to posteroventral in inclination than in Recent leporids, may suggest a less upright posture for the neck in *Prolagus*. The spinous process of the axis is somewhat more robust than in *Ochotona*. In the third and sixth cervicals the transverse process is not elongated posteriorly so far as in *Ochotona*, and in the fourth cervical vertebra the ventral root of the transverse process is better developed than in *Ochotona*. The seventh cervical vertebra is variable in development of the vertebrarterial foramen, which may be absent completely or represented by a small foramen on one or both sides of the vertebra.

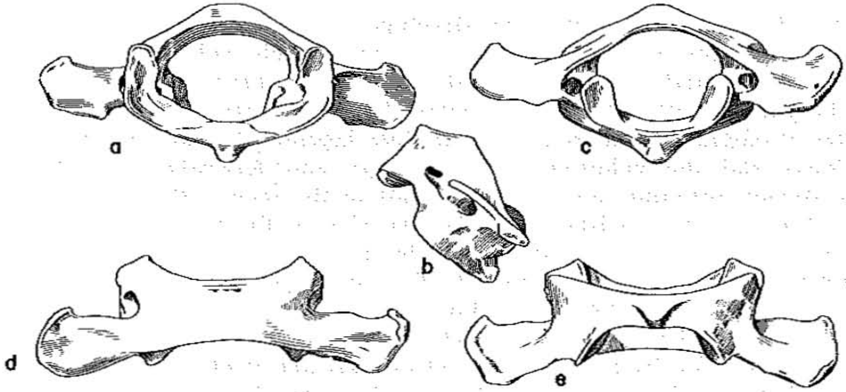

FIG. 8. — Atlas, a. anterior, b. lateral, c. posterior, d. dorsal, e. ventral, x 2. Tavolara-Ty. 7774.

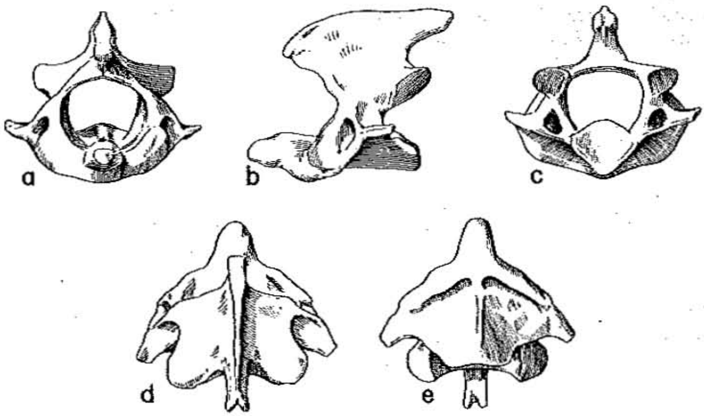

FIG. 9. — Axis, a. anterior, b. lateral, c. posterior, d. dorsal, e. ventral, x 2. Tavolara-Ty. 7788.

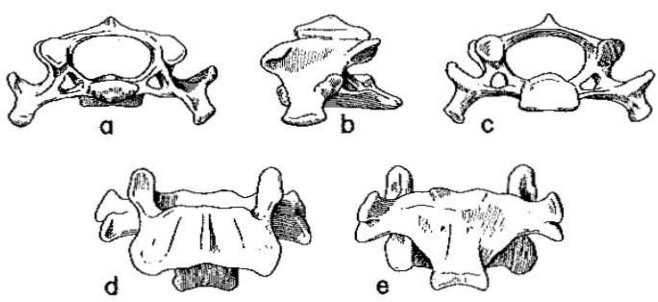

FIG. 10. — Cervical vertebra IV, a. anterior, b. lateral, c. posterior, d. dorsal, e. ventral, x 2. Tavolara-Ty. 7793, Ty 7779.

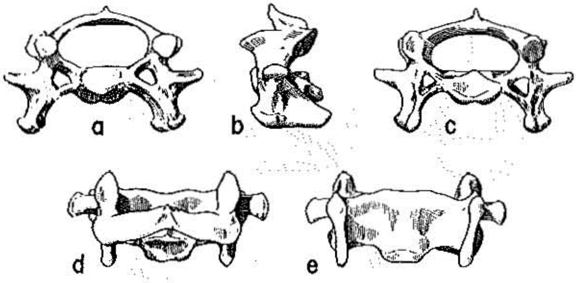

FIG. 11. — Cervical vertebra VI, a. anterior, b. lateral, c. posterior, d. dorsal, e. ventral, x 2
Tavolara-Ty. 7783.

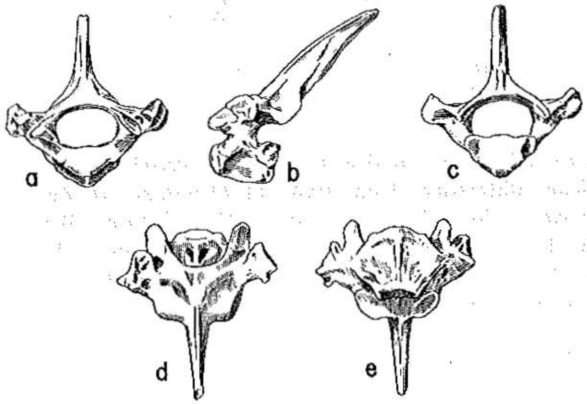

FIG. 12. — Thoracic vertebra, a. anterior, b. lateral, c. posterior, d. dorsal, e. ventral, x 2.
Tavolara-Ty. 7795.

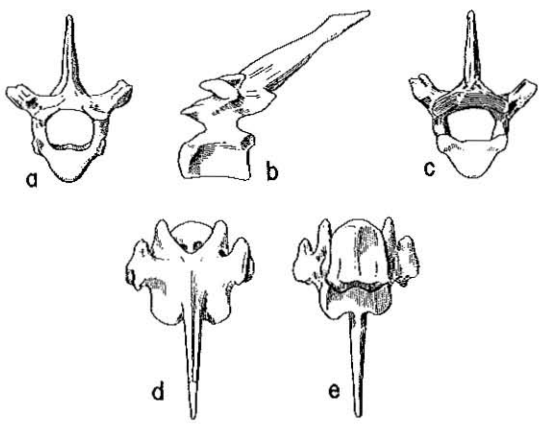

FIG. 13. — Thoracic vertebra, a. anterior, b. lateral, c. posterior, d. dorsal, e. ventral, x 2.
Tavolara-Ty. 8749.

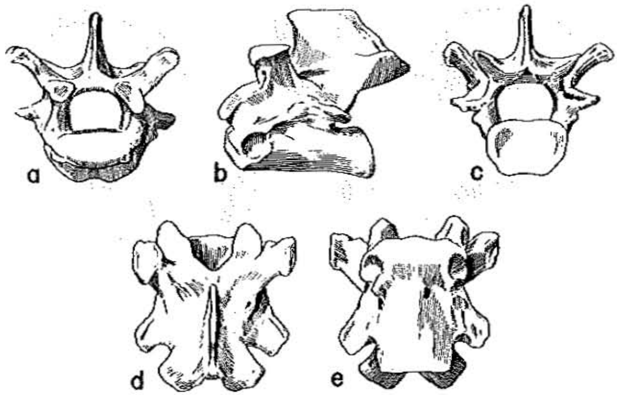

FIG. 14. — Thoracic vertebra, a. anterior, b. lateral, c. posterior, d. dorsal, e. ventral, x 2. Based on Tavolara — Ty. 7782, Ty 7784.

Except for differences in size, the thoracic vertebrae (Figs. 12-14) do not show significant differences from those of *Ochotona*. In the lumbar region, however, *Prolagus* does show some distinctive features. Basically a lumbar vertebra (Fig. 15) is similar to that in *Ochotona,* but on at least some lumbar vertebrae of *Prolagus* the anteroposteriorly elongated transverse process and the spinous process are relatively longer than in any lumbar vertebrae of *Ochotona,* and both of these processes show more anterior inclination than in *Ochotona*. The mammary processes seem to rise relatively higher than in *Ochotona*. Ventrally most lumbar vertebrae have a better developed keel than in *Ochotona* although none of them show the long keel of the anterior lumbar vertebrae that is characteristic of *Romerolagus* and other Recent leporids.

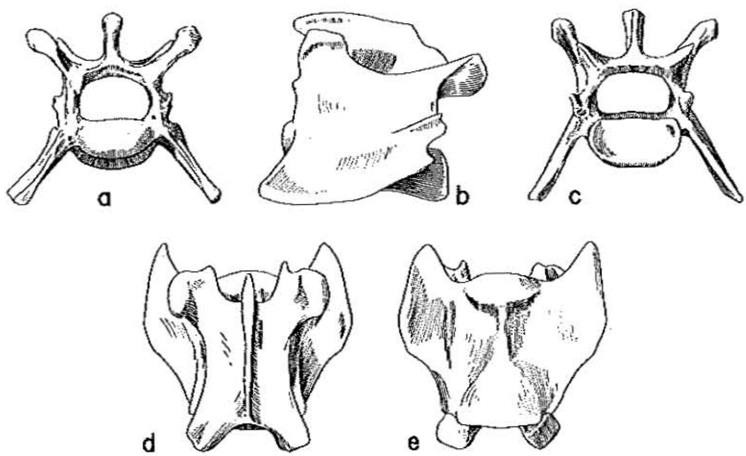

FIG. 15. — Lumbar vertebra, a. anterior, b. lateral, c. posterior, d. dorsal, e. ventral, x 2. Based on Tavolara-Ty. 8746, Ty. 7777.

Like the other vertebrae those of the sacrum (Fig. 16) have a basically *Ochotona*-like pattern with spinous processes and mammary processes fused anteroposteriorly into continuous ridges. The ridges thus formed are relatively higher than in *Ochotona*. The articular processes of the first sacral vertebra face more medially than in *Ochotona*, about as in *Romerolagus*. The greatest

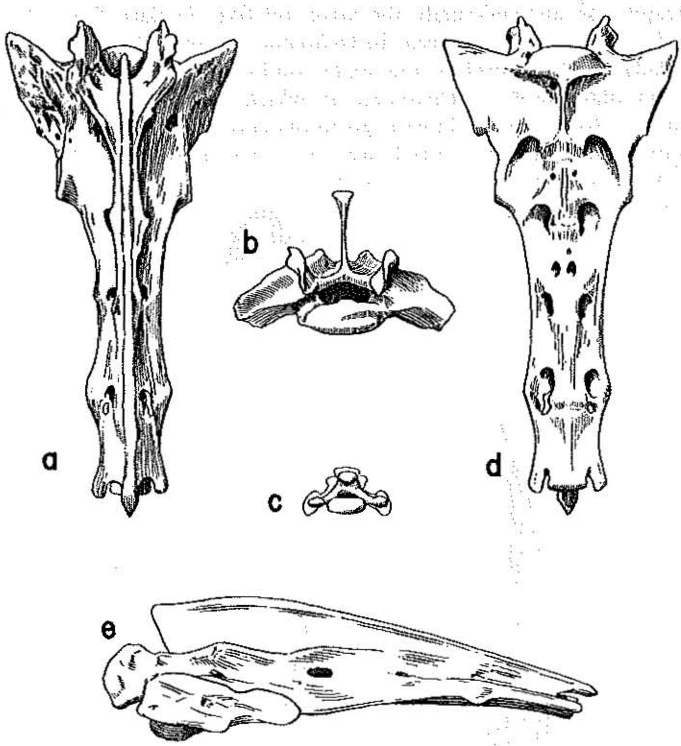

FIG. 16. — Sacral vertebrae, a. dorsal, b. anterior, c. posterior, d. ventral, e. lateral, x 1½. Based on Tavolara-Ty. 4142, Ty. 8739, T. 8741.

difference from the sacrum of *Ochotona* is in the much greater outward flare of the transverse processes of the first sacral vertebra. This expansion is less than in Recent leporids but tends toward that type of development rather than toward the essentially parallel processes of *Ochotona*. The auricular facet is similar in shape to that of *Ochotona*, having a long dorsal facet and shorter ventral facet. Correlated with the outward flare of the transverse processes the dorsal facet inclines outward anteriorly. The fifth sacral vertebra has better developed transverse processes than in *Ochotona*, possibly suggesting that more robust caudal vertebrae and thus perhaps more of a tail occurred in *Prolagus sardus*.

FORELIMB.

In proportions of supraspinous and infraspinous fossae the scapula (Fig. 17) is similar to that of *Romerolagus*, the supraspinous fossa being relatively larger than in *Ochotona*. The well developed spine becomes free of the body of the scapula at approximately the same relative distance from the glenoid cavity as in *Romerolagus*, whereas in *Ochotona* the spine becomes free farther up the blade. Both acromion and metacromion processes are present as in leporids but differing from *Ochotona*, in which the acromion is absent. The metacromion process bends inward posterolateral to the glenoid cavity in the one specimen in which this part is well preserved rather than having a more anteroposterior orientation as in leporids.

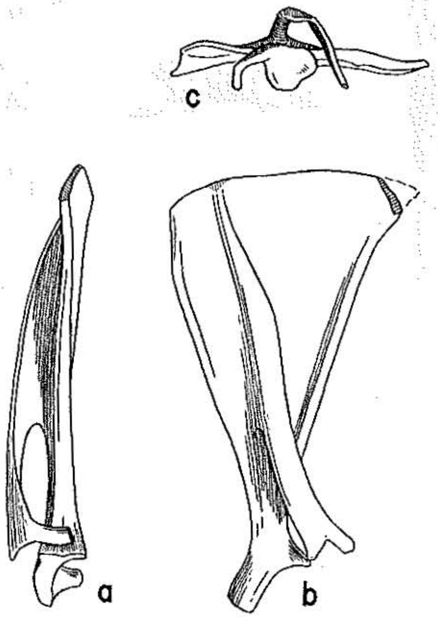

FIG. 17. — Left scapula, a. posterior, b. lateral, c. ventral, x 1½. Based on Tavolara-Ty. 8756, Ty. 8764.

The clavicle (Fig. 18) is approximately comparable in level of development to that of *Ochotona*. In this the two ochotonids contrast with the leporids, which have a relatively more reduced clavicle.

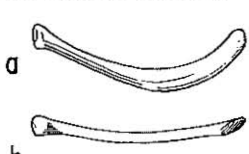

FIG. 18. — Left clavicle, a. anterior, b. anteroventral, x 1½. Funtaneddu-Ty. 2960.

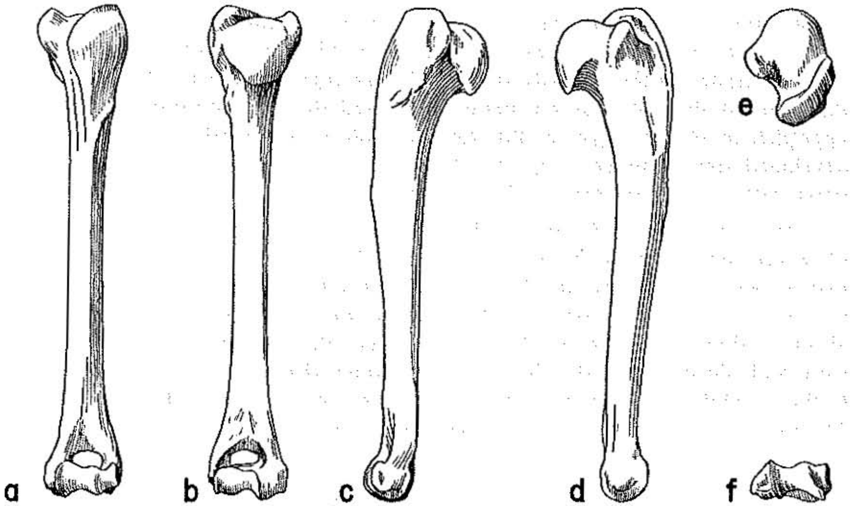

FIG. 19. — Left humerus, a. dorsal, b. posterior, c. lateral, d. medial, e. proximal, f. distal, x 1½.
Based on : Tavolara-Ty. 8776, Ty. 8780, Ty. 8788.

Like the scapula, the humerus (Fig. 19) has indications that the forelimb was strongly muscled. Its most characteristic feature is the strong, elevated greater tuberosity, which rises above the head and is slightly more transverse in orientation than in *Romerolagus*. Both greater and lesser tuberosities are better developed than in *Ochotona*. The head is more elongated anteropos-

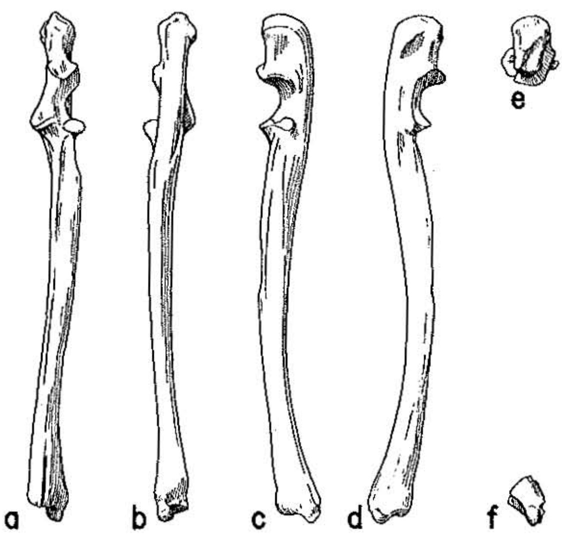

FIG. 20. — Left ulna, a. dorsal, b. posterior, c. lateral, d. medial, e. proximal, f. distal, x 1½.
Based on : Tavolara-Ty. 8806, Ty. 8812.

teriorly than in *Ochotona* but less so than in *Romerolagus*. The surface distal to the greater tuberosity for muscle insertion is wide proximally and the deltoid crest continues farther distally than in *Romerolagus* and *Oryctolagus*. Distally the keels of the humerus are better developed than in *Ochotona*, making an approach to *Romerolagus* in this feature. Lateral and medial epicondyles are developed approximately as in *Ochotona*, with the medial epicondyle especially being relatively larger than in Recent leporids.

The ulna (Fig. 20) has a less deeply grooved proximal end of the olecranon process than in Recent leporids. The bone is less reduced distally than in Recent leporids, and has a medial articular facet approximately equal in area to the styloid process. The styloid process protrudes distally more abrupt'y than in *Ochotona*. It appears likely that the muscles of the wrist were well developed. Like the ulna, the radius (Fig. 21) is generally similar to that in *Ochotona* in being a heavier element distally than in Recent leporids. The medial side of the distal end is especially well developed, extending farther distad than in leporids and is even somewhat stronger than in *Ochotona*.

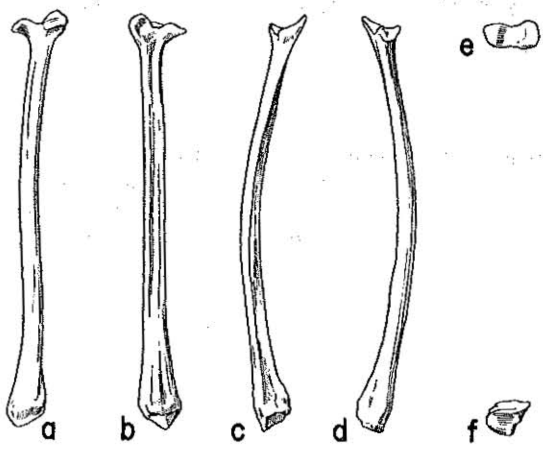

FIG. 21. — Left radius, a. dorsal, b. posterior, c. lateral, d. medial, e. proximal, f. distal, x 1½.
Based on : Tavolara-Ty. 8849, Ty. 8851.

The metacarpals (Figs. 22-26) resemble those of *Ochotona* in shape. On the proximal end of metacarpals II and III the lateral keel rises higher than the medial. In *Romerolagus* the medial keel of metacarpal II is higher than the lateral.

HIND LIMB.

In overall construction the innominate (Fig. 27) gives the impression of more similarity to that of *Ochotona* than to those of Recent leporids, the

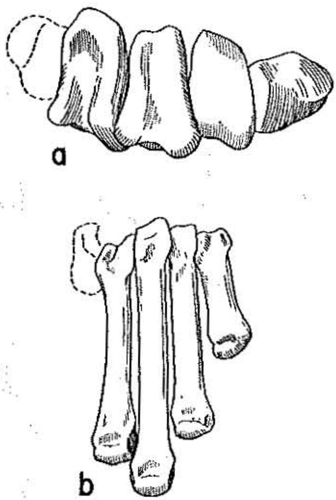

FIG. 22. — Composite left metacarpals, a. proximal, x 6, b. anterior, x 3. Based on specimens from Monte San Giovanni.

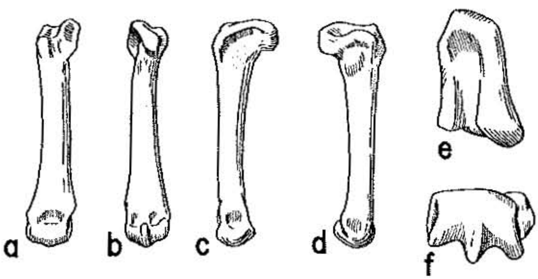

FIG. 23. — Left metacarpal II, a. anterior, b. posterior, c. lateral, d. medial, x 3, e. proximal, f. distal, x 6.

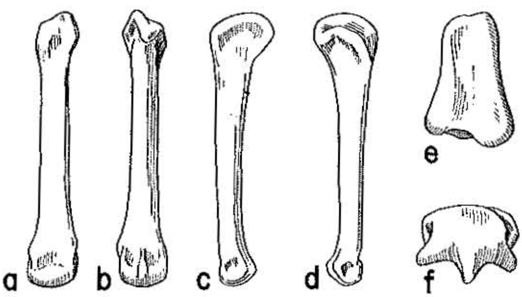

FIG. 24. — Left metacarpal III, positions and magnification as in Fig. 23.

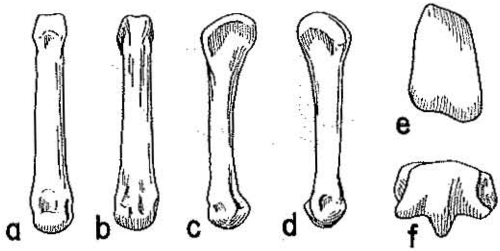

FIG. 25. — Left metacarpal IV, positions and magnification as in Fig. 23.

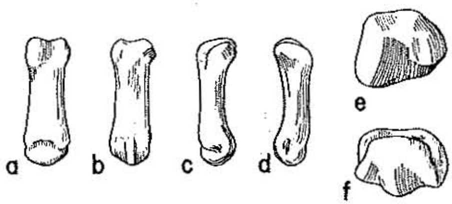

FIG. 26. — Left metacarpal V, positions and magnification as in Fig. 23.

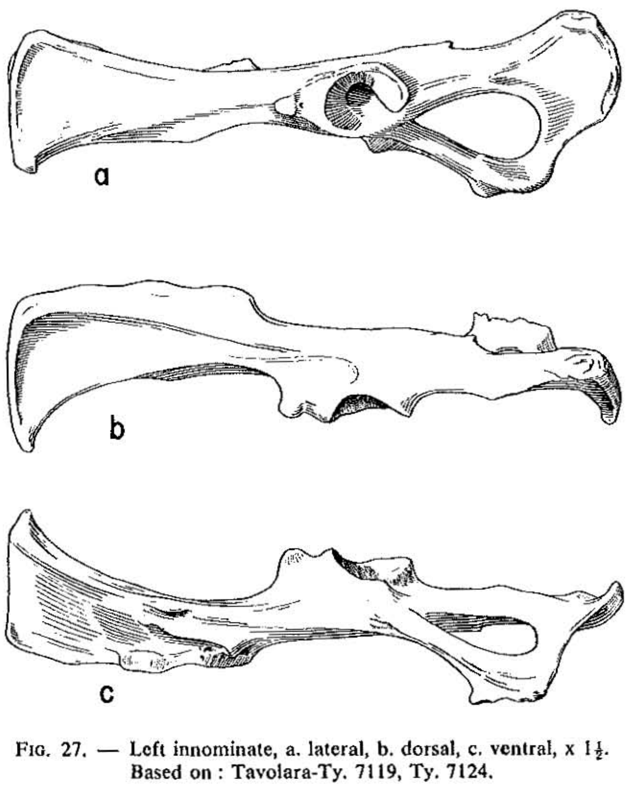

FIG. 27. — Left innominate, a. lateral, b. dorsal, c. ventral, x 1½.
Based on : Tavolara-Ty. 7119, Ty. 7124.

similarity being especially noticeable in the angle between pubis and ischium, shape of the obturator foramen, and the lack of a leporid-like posterior expansion of the ischium. In detail, however, the innominate of *Prolagus* has several distinctive features, especially in the iliac blade and the ischial tuberosity. Two well marked anteroposterior ridges divide the lateral surface of the ilium into three parts, one facing ventrolaterally, one laterally, and the third dorsally. The ventral ridge runs anteriorly from the iliac tubercle (inferior anterior spine of Craigie) and bends laterally to form a prominent hook. The dorsal ridge runs dorsoanteriorly to the thickened anterodorsal border of the ilium. The iliac surface is concave between the two ridges. An early stage in the development of these ridges occurs in the late Miocene species *Prolagus oeningensis,* in which a ventral ridge extends forward from the tubercle into the ventral fossa, not quite contacting the main, more anteriorly commencing ventral ridge. The dorsal ridge is present but weak, and the iliac blade is only slightly convex between the two main ridges. In *Ochotona* the iliac blade has only one prominent anteroposterior ridge that begins farther anteriorly than the ventral ridge in *Prolagus,* extends anteriorly and forms a more prominent laterally projecting hook. In the fossa ventral to this ridge a faint line extends forward from the iliac tubercle marking the dorsal margin of attachment of the iliacus muscle. The ilium of Recent leporids has a faint ridge from the tubercle across the ventral fossa, but basically the iliac blade forms a wide, laterally convex surface. The iliac tubercle is more prominent in *Prolagus* than in *Ochotona,* and quite different in both ochotonids from the more flattened tubercle of Recent leporids. Posterior to the tubercle is a roughened area, probably for muscle attachment. The pubis is thickened at the symphysis, and some large and possibly old individuals show that there was interlocking and perhaps some fusion, making this a stronger joint than in *Ochotona.* The ischial tuberosity is thick dorsally and ventrolaterally, with the ventrolateral thickening extending farther ventrad than in *Ochotona.* The tuberosity does not protrude dorsally as markedly as that in *Romerolagus* but has a shape more similar to that in *Romerolagus* than to that of *Oryctolagus.* The structure suggests stronger flexors of the thigh than in *Ochotona.*

The femur (Fig. 28) is a sturdy element with a shaft that is straight in side view as in *Ochotona.* The femoral shaft in Recent leporids is convex anteriorly. The greater trochanter rises relatively farther above the head than in *Ochotona* and even somewhat farther than in *Romerolagus.* The most characteristic feature is the relatively low position of the strong third trochanter, which is farther distad than in *Ochotona* or in Recent leporids.

The shaft of the stoutly built tibiofibula (Fig. 29) is slightly convex medially as is that of *Romerolagus.* It is straighter than in *Ochotona* but more bowed than in such Recent leporids as *Oryctolagus* and *Lepus.* As in *Ochotona* the cnemial crest is relatively longer than that in Recent leporids. This crest seems to lack the distal protrusion found in *Ochotona.* The free part of the fibula is relatively more robust proximally than in *Romerolagus.* The distal end of the tibiofibula is especially massive relative to that in Recent leporids. Facets for articulation with astragalus and calcaneum are well developed, approximately as in *Romerolagus* although the astragalar articulation is relatively wider transversely than in Recent leporids. *Ochotona* has somewhat weaker grooves for astragalar contact.

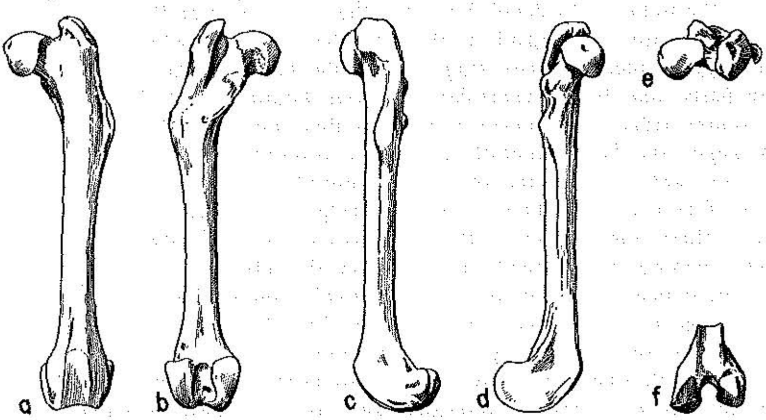

FIG. 28. — Left femur, a. anterior, b. posterior, c. lateral, d. medial, e. proximal, f. distal, x 1.
Based on : Tavolara-Ty. 7131, Ty. 7139, Ty 7140.

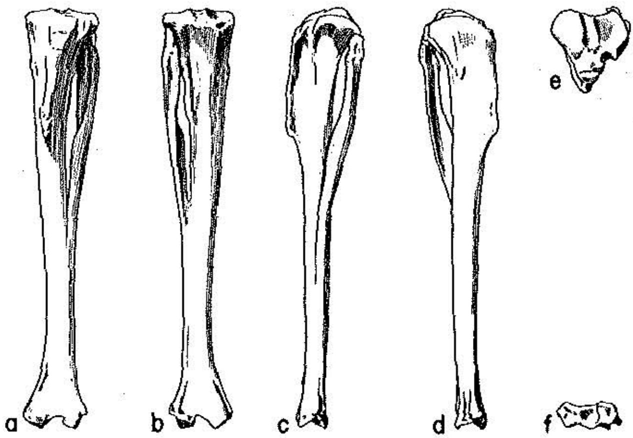

FIG. 29. — Left tibiofibula, a. anterior, b. posterior, c. lateral, d. medial, e. proximal, f. distal, x 1.
Based on : Tavolara-Ty. 7152, Ty. 7155, Ty. 7158.

The tarsals are basically similar to those of *Ochotona* but with a few differences suggesting an approach to a more leporid-like tarsus. On the astragalus (Fig. 30) the neck is relatively longer than in *Ochotona,* approaching the relative proportions of *Romerolagus.* The medial malleolus rises somewhat higher than in *Ochotona* although less high than in Recent leporids. A distinct groove and ridge on the anterolateral surface of the neck is more distinct in *Prolagus* than in either *Ochotona* or leporids. The facet on the plantar surface

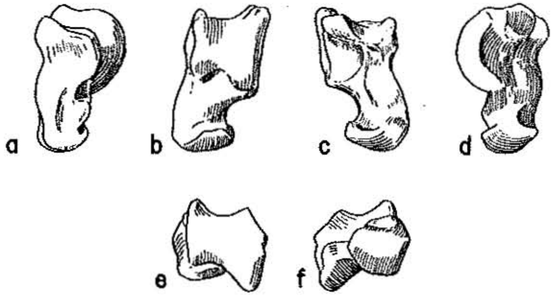

Fig. 30. — Left astragalus, a. medial, b. anterior, c. posterior, d. lateral, e. proximal, f. distal, x 3.
Based on specimens from Monte San Giovanni.

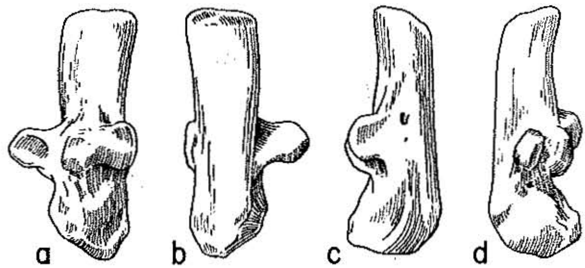

Fig. 31. — Left calcaneum, a. anterior, b. posterior, c. lateral, d. medial, x 3.
Based on specimens from Monte San Giovanni.

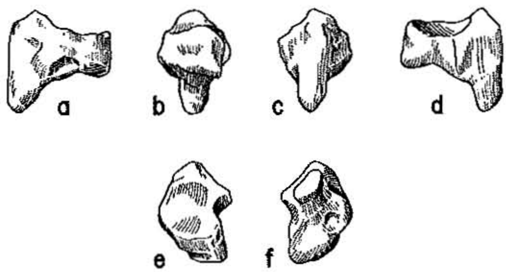

Fig. 32. — Left navicular, a. medial, b. anterior, c. posterior, d. lateral, e. proximal, f. distal, x 3.
Based on specimens from Monte San Giovanni.

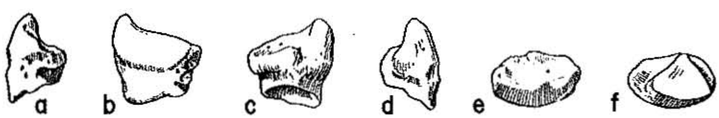

Fig. 33. — Left cuboid, a. medial, b. anterior, c. posterior, d. lateral, e. proximal, f. distal, x 3.
Based on specimens from Monte San Giovanni.

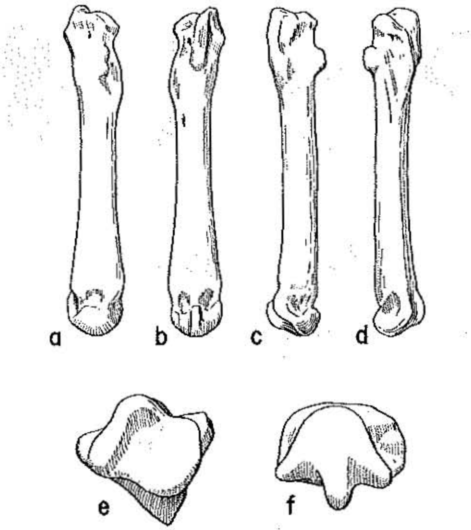

FIG. 34. — Left metatarsal II, a. anterior, b. posterior, c. medial, d. lateral, x 3, e. proximal, f. distal, x 6.
Based on specimens from Monte San Giovanni.

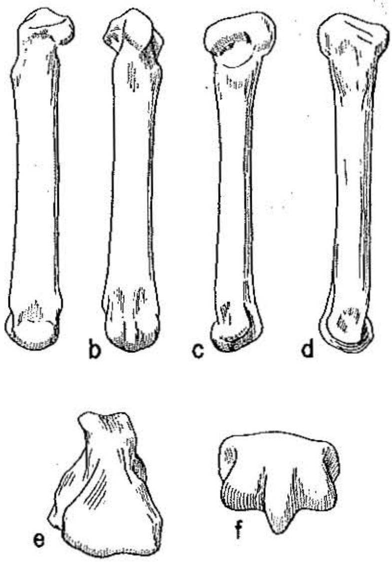

FIG. 35. — Left metatarsal III, a. anterior, b. posterior, c. lateral, d. medial, x 3, e. proximal, f. distal, x 6.
Based on specimens from Monte San Giovanni.

for articulation with the sustentaculum tali is more deeply concave than in *Ochotona*. The head resembles that in *Romerolagus* in width, being transversely narrower than in *Ochotona*. On the calcaneum (Fig. 31) the knob for

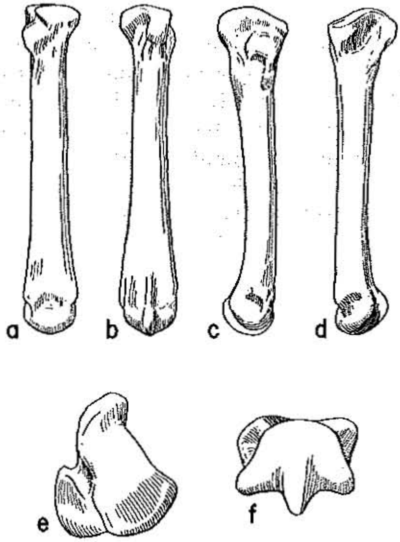

FIG. 36. — Left metatarsal IV, a. anterior, b. posterior, c. medial, d. lateral, x 3, e. proximal, f. distal, x 6.
Based on specimens from Monte San Giovanni.

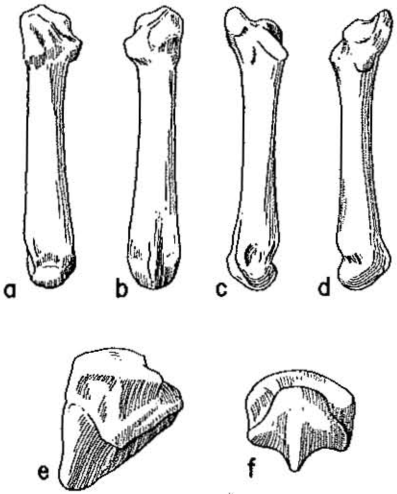

FIG. 37. — Left metatarsal V, a. anterior, b. posterior, c. medial, d. lateral, x 3, e. proximal, f. distal, x 6.
Based on specimens from Monte San Giovanni.

astragalar and fibular articulation resembles that in *Romerolagus* in having two distinct facets for the astragalus rather than one continuous facet as in *Ochotona*. The tuber is transversely wider than in *Ochotona*. The shape of the navicular (Fig. 32) is more like that in *Romerolagus* than in *Ochotona* in that the posterior process is long, relatively even longer in *Prolagus* than in *Romerolagus*. The notch for cuboid articulation is relatively deeper than in *Romerolagus*. As in *Ochotona* there is no navicular-calcaneum contact such as occurs in Recent leporids. The bodies of both navicular and cuboid (Fig. 33) are relatively shorter proximodistally than in *Romerolagus*. No third cuneiform is represented. As in *Ochotona* the second cuneiform is fused to the proximal end of metatarsal II. The metatarsals (Figs. 34-37) are similar to those in *Ochotona* in most features, although metatarsal II does not protrude medially so much at its proximal end and metatarsal V does not have such a marked proximal protrusion.

DISCUSSION

ADAPTIVE FEATURES OF *Prolagus sardus*.

There are relatively few features in which *Prolagus sardus* shows strong indications of what its mode of life and adaptations might have been. However, *P. sardus* does have some characters that can be interpreted with a degree of certainty. In the skull the basicranial-basifacial bending indicates that the head was held somewhat more upright than in *Ochotona*, though less so than in *Romerolagus*. Another line of evidence favoring this posture comes from some expansion of the supraoccipital onto the skull roof, which suggests strengthened neck muscles. However, the muscles were not developed nearly so well as in Recent leporids, in which the posterior part of the skull is much more greatly modified in this direction. The slightly widened internal nares of *Prolagus* might suggest greater endurance than in *Ochotona*. The somewhat leporid-like condyle of *P. sardus* suggests that chewing motions affecting the cheek teeth may have had an important transverse component as in leporids. The incisors of *P. sardus* are highly characteristic. The lateral thickening of upper and lower incisors and position of the lower incisor provide relatively well developed lateral cutting edges, and it may be that movements of the incisors transversely were important in *Prolagus*. The adaptive significance of this incisor specialization is not known at present.

In the postcranial skeleton some of the differences from *Ochotona* in degree of development of various structures are difficult to access because they might reflect differences related to size, *Prolagus* being larger than *Ochotona*. However, morphological differences from *Ochotona* that seem to be especially significant occur in the scapula and humerus, and in the lumbar vertebrae, sacral vertebrae, innominate, and femur. Scapula and humerus have characters indicating a greater muscular development than in *Ochotona*. This is shown especially by the subequal supraspinous and infraspinous fossae, by presence of acromion as well as metacromion processes of the scapula, by very prominent greater tuberosity for insertion of the supraspinatus and infraspinatus muscles and for origin of the triceps brachii, and by expanded area for muscle attachment below the greater tuberosity and on the long deltoid crest.

Enlargement of processes of the lumbar vertebrae and outward flare of the transverse processes of the first sacral vertebrae suggest strengthening of the hind limb. The latter character is somewhat reminiscent of the progressively developed flare in leporids that seems to have accompanied increased thrust of the hind limb as the typically leporid cursorial modifications developed. *Prolagus sardus* has not developed in the direction of cursorial specialization but possibly the flare can be interpreetd also as a response to strong hind limbs. The characteristically ridged ilium is not found in any living lagomorphs and thus cannot be compared directly for adaptive significance. However, the dorsal ridge of the ilium may indicate strengthened origin for part of the gluteal musculature, especially the gluteus maximus and gluteus medius. The separation of the iliac surface into distinct parts suggests that the different parts of the gluteal group had more independent action resulting in a greater range of movements than in leporids, in which the gluteal mass is concentrated toward action resulting in retraction of the thigh. The strong, relatively distally situated third trochanter of he femur, serving for insertion of the gluteus maximus, suggests that this muscle was strong, and the well developed greater trochanter might indicate a similarly strong gluteus medius.

When proportions of the limbs are compared, specimens of *Prolagus sardus* from different localities show considerable variation (Table 1). The most significant difference from *Ochotona* seems to be in the shorter forelimb relative to hind limb, the humerus shorter relative to length of femur but radius longer relative to length of humerus. In these proportions *Prolagus* approaches *Romerolagus* more closely than *Ochotona*.

TABLE 1

Relative lengths of limb bones of *Romerolagus diazi*, *Ochotona princeps*, and *Prolagus sardus*.

	Romerolagus	*Prolagus* * Tavolara	*Prolagus* * Monte San Giovanni	*Ochotona*
humerus + radius / femur + tibia	.72	.71	.74	.65
radius / humerus	.87	.89	.87	.77
femur / tibia	.90	.89	.92	.89
radius / tibia	.64	.64	.66	.62
humerus / femur	.81	.80	.83	.91

* Based on means from Tobien (1935).

In total, the structural features that can be interpreted adaptively are not many, nor do they show extreme developments. Indications of well muscled fore- and hind limbs point toward an interpretation of *Prolagus sardus* as a

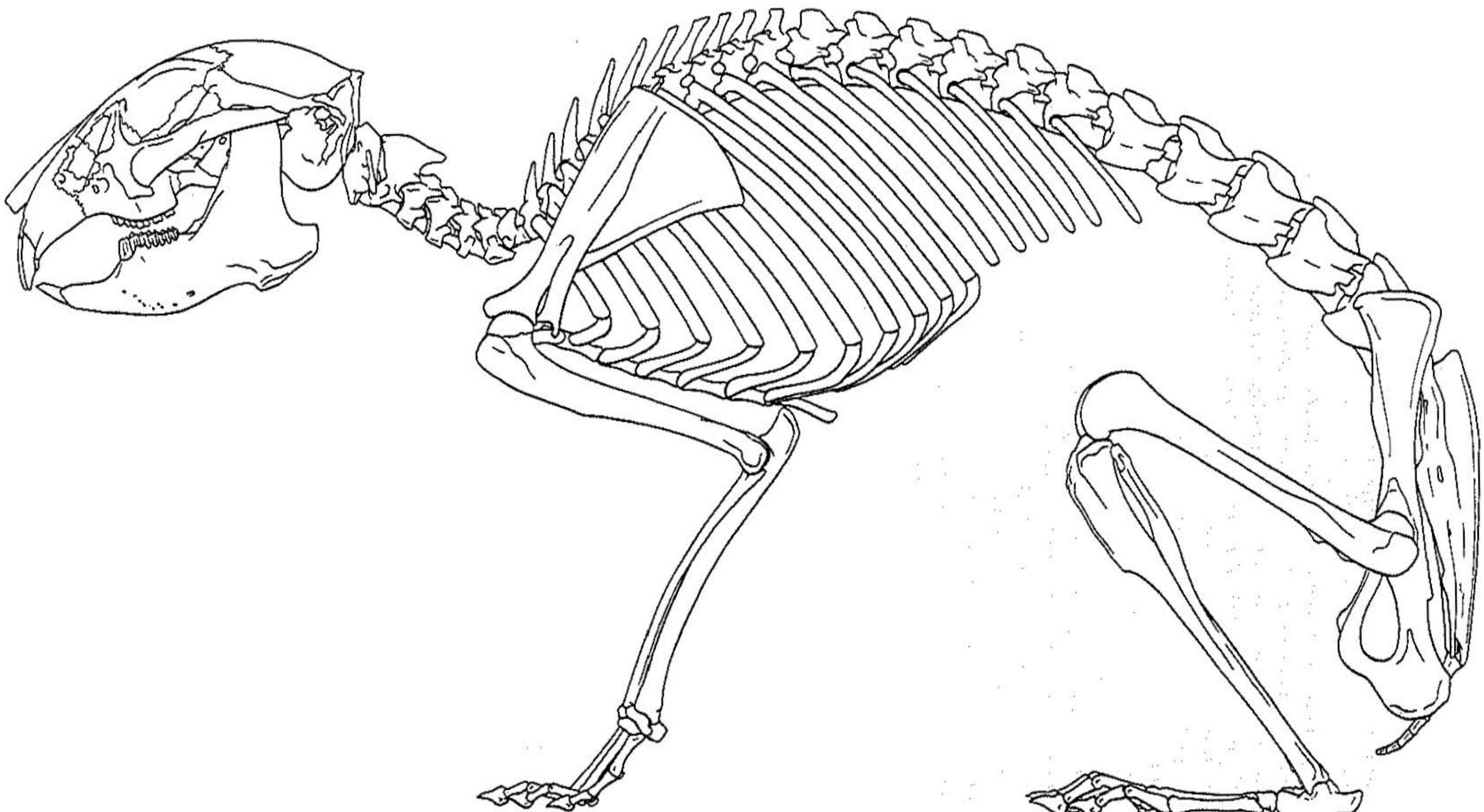

FIG. 38. — Composite skeleton of *Prolagus sardus*, size based on specimens from Tavolara, x 1.

small, well muscled quadruped with a somewhat upright position of the neck and with the capability of a wider range of limb movements than in Recent leporids. The range of movments was probably more comparable to that in Oligocene leporids such as *Palaeolagus* and *Megalagus*. *Prolagus* was probably not suited for speed over any great distance but was probably fairly adept at digging and well adapted for climbing and scrambling in the rough terrain that characterizes much of the Corsican and Sardinian countryside. The reconstructed skeletons of *Prolagus sardus* (Fig. 38, Pl. 1) are presented in what seem to be reasonable resting positions for this ochotonid.

Characters of the Ochotonidae and of primitive lagomorphs.

Comparisons of *Prolagus sardus* with such Tertiary ochotonids as *Sinolagomys* (Bohlin, 1942, 1946) and *Kenyalagomys* (MacInnes, 1953) on the one hand and with Recent *Ochotona* on the other reveal structures that can be regarded as characteristically ochotonid in nature. Dental features characterizing the ochotonids include the non-molariform P^3, tendency toward separate trigonid and talonid columns of P_4-M_2, and reduction or loss of M_3^3. In addition, the following characters of skull and jaw seem to be basically features of fossil and Recent ochotonids: 1) zygoma sturdily constructed anteriorly and contacted by maxillary tuberosity; 2) palate with premolar foramen and shortened maxillary component of the bony palatal bridge; 3) distinct groove on posterior zygomatic root suggesting well developed temporalis muscle relative to that in leporids: 4) symphysis of jaw without posterior buttress that occurs in leporids. One of these four characters occurs in known leporids. The postcranial skeleton of *Prolagus sardus*, though having a number of features of general similarity to *Ochotona*, has fewer features that can be regarded as definitely basic to the ochotonids. However, the anteroposteriorly wide transverse processes of the lumbar vertebrae, fused spines and processes of the sacrum, and shape of ischium and pubis are probably characteristically ochotonid features.

Prolagus sardus also has a number of features in which it differs from *Ochotona* and approaches conditions found in some leporids. Some of these may represent features that are primitive for lagomorphs in general while others may be developed in parallel within the two families. Interpretation of some of these features is difficult because relatively few Tertiary ochotonid remains other than jaws and dentitions have been described, thus making difficult determination of whether primitive characters of adaptive parallelizations are concerned. An arched appearance of the skull, due in part to bending at the basicranial-basifacial angle and in part to doming of the braincase, is characteristic of the Leporidae but is much less distinctly developed in Oligocene and early Miocene leporids than in Recent members of the family. Presence of a similar sort of arching in *Prolagus sardus* may suggest that the primitive condition for lagomorphs was a somewhat more arched skull than in Recent *Ochotona*. However, the ochotonid *Kenyalagomys* of the African Miocene (MacInnes, 1953) seems to have had a relatively flat skull with little bending at the basifacial-basicranial angle. Thus, the arched condition of *Prolagus* may have developed in parallel to the arching of leporids. Both *P. sardus* and *Kenyalagomys* show some expansion of the supraoccipital onto the dorsal skull roof, although much less than in Recent leporids. Early leporids are variable in this character, the supraoccipital having less expansion in *Palaeolagus haydeni* than in *P. hypsodus,* for example (Dawson, 1958, p. 25). Development of the supraoccipital is tied in closely to development of the neck muscles. It seems likely that muscle strengthening has occurred in *Prolagus* and *Kenyalagomys* in parallel to strengthening of those muscles in leporids, among which the strengthening reached a greater development than in any known ochotonid. Other features of the skull of *Prolagus sardus* somewhat reminiscent of leporids are : 1) the relatively large orbit; 2) fenestration of the maxilla below the dorsal, typically ochotonid, opening; 3) relatively well developed squamosal above the auditory meatus and dorsal exposure of the mastoid; 4) relatively long auditory meatus; 5) presence of an external carotid foramen. *Prolagus sardus* shares with primitive leporids and ochotonids presence of two mental foramina of the jaw. The shape of the condyle resembles that in leporids more closely than that of *Ochotona.* Of these leporid-like characters, the relatively large orbit, maxillary fenestration, and two mental foramina are found in *Kenyalagomys* as well as in *Prolagus sardus.* It seems reasonable that these characters were found in primitive lagomorphs though lost in *Ochotona. Prolagus* and *Palaeolagus* are similar in having a well developed process of the squamosal dorsal to the auditory meatus, dorsal exposure of the mastoid, and a longer auditory meatus than in *Ochotona.* This may represent the primitive condition for lagomorphs, differing both from the posteriorly low skull of *Ochotona* and from the highly modified posterior end of the skull of Recent leporids, with its attachments for strong neck muscles. The external carotid foramen occurs in *Palaeolagus,* Recent leporids, and *Prolagus.* Again, lack of evidence from Tertiary ochotonids prohibits certainty, but the evidence available suggests that this foramen occurred in primitive lagomorphs. In the postcranial skeleton the sub-equal supraspinous and infraspinous fossae of the scapula and development of the scapular spine of *P. sardus* are found also in primitive leporids and probably represent the ancestral condition.

Frequently the genus *Ochotona* is cited as a primitive lagomorph. Certainly it does lack the specializations of Recent leporids for a cursorial mode of life. However, this does not prove that *Ochotona* is primitive — that is, closer to the ancestral condition — in all regards. Indeed, several of the features mentioned above as probably representing truly ancestral conditions are not present in Recent *Ochotona.* It has been suggested by others (Bohlin, 1942, p. 82, and references cited there) on other grounds that the skull of primitive lagomorphs may have been more like that of *Lepus* than of *Ochotona.* Certainly the evidence presented here does not give rise to an image of the primitive lagomorph as being *Lepus*-like. It does suggest, however, that such a primitive lagomorph would also not be entirely *Ochotona*-like and that it would probably have some features that are now associated with the Recent

Leporidae and lost in the Ochotonidae. Characters of *Ochotona* such as the bulla filled with spongy bone, maxillary tuberosity with M^2 free, and single mental foramen are probably specializations of the line of *Ochotona*. *Ochotona* does not simply show a primitive lagomorph state but has its own specializations for its own particular adaptive niche.

ACKNOWLEDGEMENTS

Sincere thanks are due to the two colleagues in Basel who made this study possible — Otto Garraux and Johannes Hürzeler. Mr. Garraux turned his abilities as a superb artist to the task of figuring and reconstructing *Prolagus sardus*. Dr. Hürzeler provided access to the excellent collections and libraries of the Basel Naturhistorisches Museum. His own extensive studies on European fossil lagomorphs contributed greatly to our discussions of the problems of *P. sardus*. I appreciate also access to collections in their care provided by Drs. E.I. White and A.J. Sutcliffe, British Museum (Natural History), Prof. J.-P. Lehman and Abbé R. Lavocat, Muséum National d'Histoire Naturelle, Paris, and P. Mein, Faculté des Sciences, Lyon. J.-P. Gasc was most helpful in sharing with me his extensive knowledge of Corsican forms of *Prolagus*. A successful collecting expedition to Sardinia, which contributed to the understanding of *Prolagus*, would not have been possible without the splendid cooperation of Dr. Annalisa Berzi, Istituto di Geologia, Florence, and B. Piredda and other members of the Nuoro Gruppo Grotto. This study was supported by a grant from the Penrose Fund of the American Philosophical Society.

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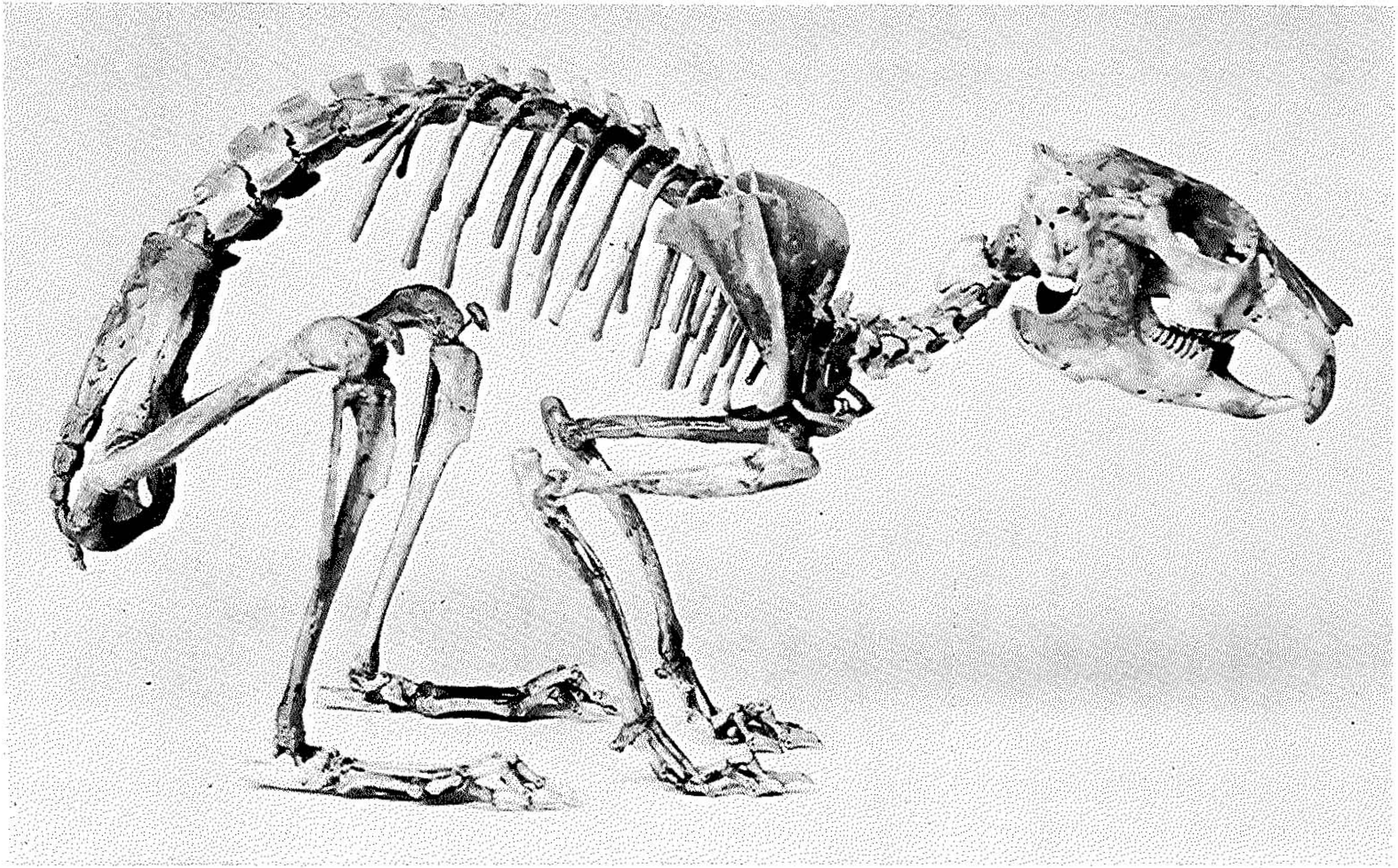

PLATE I

Reconstructed skeleton of *Prolagus sardus* from Corbeddu Cave, Sardinia, mounted by Daniel Oppliger. × 1.