The giant erinaceid insectivore, *Deinogalerix* Freudenthal, from the Upper Miocene of Gargano, Italy

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Butler, P. M. The giant erinaceid insectivore, *Deinogalerix* Freudenthal, from the Upper Miocene of Gargano, Italy. — Scripta Geol., 57: 1 - 72, 17 figs., 3 pls., Leiden, June 1981.

A detailed description of *Deinogalerix* is provided. In addition to the type species, four new species are distinguished: *D. freudenthali, D. minor, D. brevirostris,* and *D. intermedius.* There were two lineages, which differed in size. *Deinogalerix* was not directly derived from any of the Galericinae known from Europe but was probably an immigrant from Asia. It is interpreted as a predator which captured prey by a snapping action of the jaws.

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Introduction

In 1972 Freudenthal published a preliminary description of *Deinogalerix koenigswaldi,* a giant erinaceid insectivore from fissure deposits on the Gargano Peninsula of Italy. The deposits are considered to be Late Miocene (Late Vallesian - Turolian) in age (Freudenthal, 1971). The peculiar fauna shows that the area was at that time an island on which evolution proceeded in isolation from the European mainland. The numerous fissure deposits represent a range of time which is reflected in their fossil content (Freudenthal, 1976; Ballmann, 1973). The holotype of *D. koenigswaldi* comes from San Giovannino, a fissure deposit regarded as one of the latest. The material consists of a skull and most of the bones of a skeleton, probably from a single individual. Further collecting at San Giovannino has resulted in the discovery of the remains of at least ten other individuals, including some that are much larger than the holotype. Five metres lower in the same fissure (distinguished as San Giovannino Low) have been found specimens representing at least four more individuals. *Deinogalerix* is represented in 40 other fissures, but specimens are less abundant and for the most part more fragmentary than at San Giovannino. They are mostly smaller in size than the holotype. Of particular interest is the material from Biancone 1, the oldest deposit, which includes the smallest teeth and postcranial bones.

In this paper the material belonging to *Deinogalerix* is first described morphologically at the generic level, noting variations but without dividing the genus into species. Specific distinctions are then considered, followed by discussions of relationships and mode of life. All the specimens are housed in the Rijksmuseum van Geologie en Mineralogie, Leiden (catalogue numbers beginning RGM).

I am most grateful to Dr M. Freudenthal for inviting me to study this material, and for helpful discussions in the course of the work. I also thank the staff of the Mammal Section of the British Museum (Natural History), and Mr J. J. Hooker of the Palaeontology Department of the Museum, for facilities to study comparative material. Much of the work was done at Royal Holloway College, where Professor C. T. Lewis kindly provided accomodation and Mr M. H. Colthorpe photographed the specimens. Thanks are also due to Professor W. A. Clemens for allowing me to examine *Lanthanotherium* material during a visit to Berkeley, California, to Dr J.-Y. Crochet for access to fossil erinaceids at Montpellier, and to Professor G. T. MacIntyre for help with interpretation of the middle ear.

General description

DENTITION

The dental formula is I $\frac{3}{2}$, C $\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{3}{3}$. The holotype skull contains all the upper teeth or their alveoli. I^1 is enlarged and the canine is premolariform. The mandibles of this individual are incomplete anteriorly; other specimens, e.g.

RGM 179 148, show that the enlarged tooth that Freudenthal (1972) interpreted as an incisor is the canine, and that it was preceded by two procumbent incisors. As in *Echinosorex,* the lower canine did not meet I^1, but bit into a diastema between I^3 and C^1.

There are 8 examples of I^1. It is a vertical tooth, separated from its fellow on the opposite side by a small gap. In the holotype the crown measures 17 mm in height and 8.5 mm in anteroposterior length. There is a strong posterobuccal ridge and a lingual ridge that does not quite reach the tip. The anterior surface is convex, the posterior surface flattened. In the holotype, wear is confined to the posterior surface near the tip, but in RGM 179 199 and 179 230 the whole of the posterior side of the tooth shows wear, and in heavily worn specimens, e.g. RGM 179 231, the top of the crown has been removed by abrasion. Isolated teeth show that the root curves posteriorly and is compressed mediolaterally; its medial surface is flat or shallowly grooved.

I^2 and I^3 are small teeth placed closely behind I^1; in some cases the alveoli of I^1 and I^2 are confluent. I^2 has fallen out on both sides of the holotype, but isolated crowns of right and left teeth (RGM 177 783, 177 784) probably belong to this skull. I^2 is in place on the left side of the skull RGM 179 192, and RGM 179 120 is an isolated specimen. I^2 is triangular in crown view, and has a single root; there is a low, blunt cusp, provided with a posterobuccal ridge and a lingual ridge; the base of the posterobuccal ridge forms a convexity, or shoulder. I^3 is preserved in place in the holotype, in the skull RGM 179 192, and in the premaxilla RGM 179 237. It is similar to I^2 but somewhat larger. A premaxilla from Chiro 20 D (RGM 177 997) shows the broken root of I^2 close to the alveolus of I^1, but I^3 is absent. Posterior to I^3 the premaxilla is excavated to receive the lower canine.

C^1, P^1 and P^2 are similar one-cusped teeth, oval in outline with two roots. They are preserved together in situ in five specimens (the holotype, RGM 177 918, 179 192, 179 146, and 179 221); RGM 179 194 and 260 978 have C^1 and P^1; RGM 179 134 has P^1 and P^2. Owing to the similarity of the three teeth, identification of isolated specimens, of which there are eight, is open to some doubt. Teeth in situ show that P^1 resembles the canine in shape but is slightly smaller, while P^2, though of similar length to the canine, differs in its lower cusp and in the presence of a posterior basal shoulder. The teeth are spaced: the longest space is between the canine and P^1, the shortest between P^2 and P^3. Spacing varies with the length of the face: the total distance between the canine and P^3 ranges from 39.5 mm in RGM 179 192 to 19.5 mm in RGM 179 134; in the holotype it is 29 mm. Corresponding lengths of the C^1 - P^1 diastema are 16.5, 2.5 and 10 mm respectively.

P^3, of which there are 15 specimens, is much larger than P^2. Its outline approximates to an equilateral triangle, but the lingual apex is broadly rounded and the buccal edge is convex. Isolated specimens, e.g. RGM 178 084, show that there are three roots, of which the anterobuccal is the longest and the lingual root is broadened; interradicular crests are present. On the crown, the paracone is the highest cusp. It has a rounded posterior ridge on which an elevation representing the metastyle is variably developed. The parastyle is merely a shoulder low on the anterior profile of the paracone. The lingual part of the crown is occupied by the blunt protocone and the somewhat lower hypocone. Wear facets develop in the shallow valley between these cusps, and also on a ridge that arises on the posterior surface of the hypocone and is con-

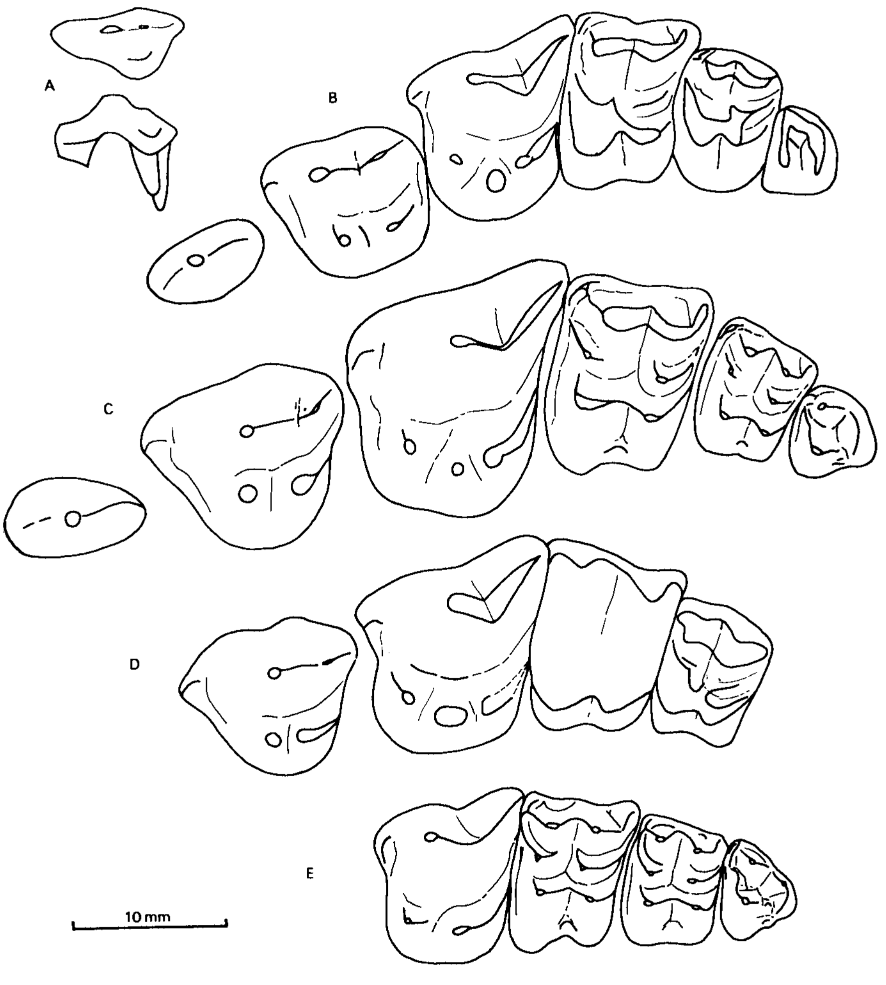


Fig. 1. Left upper cheek teeth; A: dP^3, *Deinogalerix minor* (?), RGM 178 149, crown and lingual views; B: P^3 - M^3, *D. brevirostris*, RGM 179 134 (holotype); C: P^2 - M^3, *D. koenigswaldi*, RGM 177 777 (holotype); D: P^3 - M^2, *D. intermedius*, RGM 177 982 (paratype, reversed); E: P^4 - M^3, *D. freudenthali*, RGM 178 101 (paratype), RGM 178 100 (holotype, reversed), RGM 178 098 (paratype, reversed), RGM 178 104 (paratype).

tinuous with the cingulum that follows the posterior border of the crown.

P^4 is present in 13 specimens. It is the largest of the upper cheek teeth. Its outline is trapezoidal, with the posterobuccal apex most acute and the anterior and posterior edges nearly parallel. There are three roots, of which the lingual one has the largest diameter and is grooved to a variable extent on its lingual surface. From the paracone, the highest cusp, arises a posterior crest which dips to a notch and then continues nearly horizontally and partly buccally to form the metastylar crest. A well-marked shearing facet forms on the lingual surface of the crest near the notch, and in old individuals the edge of the crest in this region becomes worn from the top, exposing dentine. There is a low, rounded parastyle, not connected by a crest to the paracone. The lingual cusps are also low and rounded. The protocone, situated more anteriorly than the paracone, is worn on its anterior surface. The hypocone occupies a larger area than the protocone, and it is worn horizontally at the tip. It is continuous with the posterior cingulum. In RGM 178 101 (Biancone 1) the hypocone is simple, but in specimens from younger localities it is divided by a shallow groove into anterior and posterior cusps.

M^1 is known from 10 individuals. It is about one-third wider than long, and it is placed obliquely in the jaw so that the anterior edge inclines forward lingually. The posterobuccal corner is not drawn out as in *Parasorex* (= „*Galerix*", see p. 47). The lingual margin is divided by a bay into two lobes, of which the anterior, bearing the protocone, is the more prominent. The bay is continued up the lingual root as a groove, and alveoli in RGM 179 194 and 179 221 show that the root is divided near the tip. Interradicular crests are clearly visible in the isolated specimen RGM 177 990. Details of the crown are best seen on this specimen, which is very lightly worn, and on an unerupted tooth from Biancone 1 (RGM 178 100). The paracrista runs directly forward from the paracone and ends at the lingual side of the parastyle. The metacone is slightly higher than the paracone. Between paracone and metacone is a deep groove, demarcated by the anterior metacone crest and the posterior paracone crest, which are diverted towards the buccal side. The buccal cingulum is most distinct above the paracone; it merges into a mid-buccal swelling that represents an incipient mesostyle. The metacrista runs at first directly posteriorly and then turns buccally to form a short metastylar crest. Paraconule and metaconule are both distinct and of nearly equal height. The anterior crest of the paraconule connects with the parastyle, and the short posterior crest ends on the lingual surface of the paracone. The metaconule has an anterior crest which turns buccally to merge into the base of the metacone, and a posterior crest which varies in length. In most specimens there is a continuous posterior cingulum from the hypocone to below the metastyle, and the posterior metaconule crest is short, but in the Biancone specimen RGM 178 100 the crest continues to the margin of the cingulum, which is consequently broken into two parts. The protocone stands directly lingually to the paraconule, with which it is connected by a short crest. The posterior protocone crest does not connect with the metaconule, but joins the anterior hypocone crest, so that the trigon basin opens posteriorly by a valley between the hypocone and the metaconule. The hypocone is slightly lower than the protocone. Its posterior crest continues buccally as the posterior cingulum. There is an anterior cingulum above the protocone, and a fragment of lingual cingulum between the bases of the protocone and the hypocone. Wear takes place on the sides and floor of the groove bounded by the paracone and paraconule anteriorly, and by the metacone and metaconule posteriorly. This wear was due to the hypoconid of M_1, which moved across in a direction parallel to the anterior edge of M^1, i.e. the movement had an anterior component. The groove persists even after most of the enamel has been worn off, e.g. RGM 177 918.

M^2 is known from 8 individuals, including a pair of unerupted tooth-caps from Biancone 1 (RGM 178 102, 178 106). It is much smaller than M_1; it is less transverse; the anterior lingual lobe is less prominent, and the bay in the lingual margin is shallower; the metastyle is relatively smaller and the posterobuccal angle of the outline is obtuse. In the unerupted teeth from Biancone and in RGM 179 076, from Chiro 14 A, the posterior cingulum is interrupted by the metaconule crest, but in the holotype and in another Biancone specimen (RGM 178 098) the cingulum is continuous. RGM 178 098 shows that interradicular crests are present and that the lingual root is divided at its tip.

M^3, the smallest upper molar, is present in 7 specimens. It resembles *Lanthanotherium.* The outline is triangular: the anterior margin is nearly straight, the posterobuccal margin convex and the posterolingual margin straight or slightly concave. The tooth is only a little broader than long. There are three roots (preserved in RGM 177 970), of which the anterobuccal is the shortest and the posterior root is slightly bifid at the tip. Three interradicular crests meet in the centre of the base. The anterior part of the crown resembles M^1 and M^2, except that the paraconule is less distinct. The posterior part is occupied by a large, transversely extended metacone, equal in height to the paracone. The anterior surface of the metacone wears against the posterior side of the talonid of M_3. Between the protocone and the metacone is a fragment of cingulum.

The only probable milk tooth is RGM 178 149, from Fina D, identified as dP^3. It is smaller than any known specimen of P^3, measuring 8.3 mm in buccal length and 4.7 mm in posterior width. It is much worn. The outline is triangular, with a short posterior side and a very prominent anterior apex. There is a centrally placed paracone, with a smaller cusp on its posterior ridge. If present, the lingual cusp must have been small, and there may have been a small anterior parastyle, now removed by wear. There is a root at the anterior end and two posterior roots that are connected by a high crest, from which a lower crest runs to the anterior root.

There are three examples of I_1, one in a jaw (RGM 179 148) and two isolated. The tooth is fairly large (mediolateral diameter 8.0 - 8.8 mm), procumbent, and placed close to the symphysis. The crown is compressed labiolingually and it is divided into two subequal lobes by grooves on the labial and lingual surfaces. The straight root is compressed laterally. On all three specimens the top of the crown has been worn off, presumably against the posterior side of I^1.

I_2 is not preserved in situ, but the alveolus, present in several specimens, shows that it was much smaller than I_1 and was situated somewhat more laterally. There are two isolated specimens, one (RGM 177 782) found near the holotype skull and the other (RGM 178 087) from Fina A/N. They are similar in size to I^2, but the outline in crown view is ovoid rather than triangular, and there is a wear facet at the tip, facing labially. Between the alveolus of I_2 and the canine is a short gap of 2 - 4 mm.

Right and left lower canines, found separately, are referred to the holotype skull. Only two specimens have been found in jaws (RGM 179 148, 179 224). There are 6 other isolated teeth, a broken fragment from Chiro 5 A and the tip of a tooth germ from Biancone 1. In the holotype the total length from root tip to cusp tip is 38 mm and the height of the enamelled crown is 16 mm. The root passes posteriorly below P_1, but owing to the curvature of the tooth the crown is fairly upright. There is a weak ridge on the anterior surface of the cusp, and a slight posterior convexity near the base of the crown. The root has the same diameter as the base of the crown; it has a shallow groove on the lingual surface, and near the tip it is flattened labiolingually. The canine becomes worn at the tip, and it also develops wear polish on its posterior surface.

As in the maxilla, the teeth between the canine and P_3 are spaced, the amount of spacing being greatest in the largest specimens. The longest diastema, between P_1 and P_2, ranges from 5 mm in RGM 179 232 to 17.5 mm in RGM 179 193.

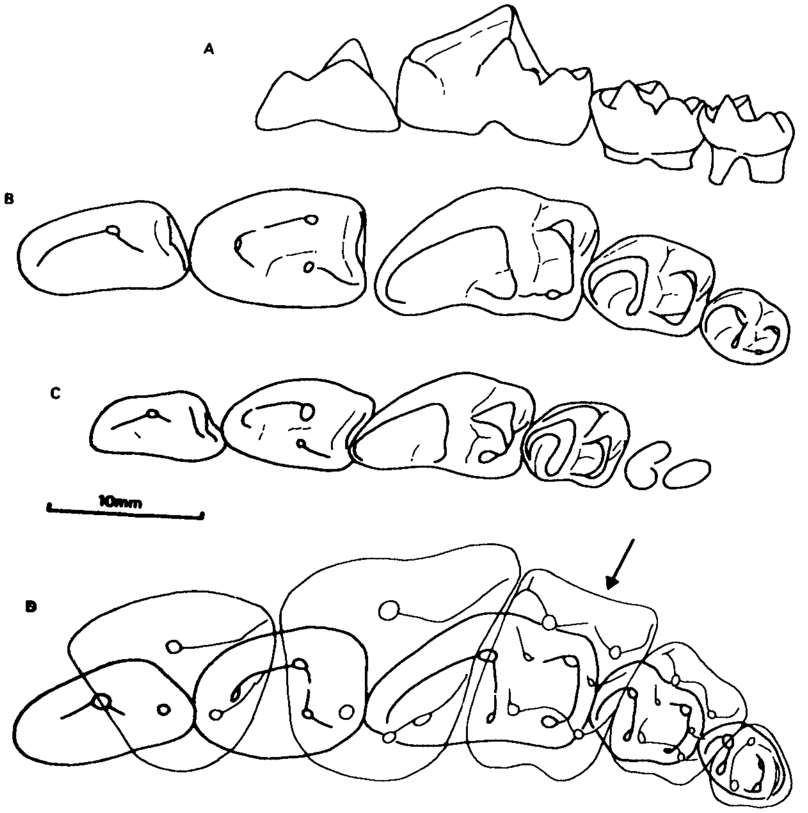


Fig. 2. A - C: right lower cheek teeth; A: P_4 - M_3, *D. koenigswaldi,* RGM 179 238, lingual view; B: P_3 - M_3, *D. koenigswaldi,* RGM 177 779 (holotype), crown view; C: P_3 - M_2 and alveoli of M_3, *D. minor,* RGM 178 184 (holotype), crown view; D: occlusal diagram of cheek teeth, *D. koenigswaldi.* The arrow indicates the direction of the power stroke.

P_1 is known from only 4 examples, but several specimens show the alveolus or root. It is a small, somewhat procumbent tooth, with a single root that is grooved laterally near the tip. There is a single, obtuse cusp and a weakly developed posterior shoulder.

There are 6 specimens of P_2 in situ, and an isolated crown which has not developed roots (RGM 178 148). It resembles P^1 and P^2 in having a single cusp and two roots, but it is smaller and its cusp is more obtuse. A posterior shoulder represents the talonid. In RGM 179 174 there are no alveoli for P_2, which presumably was lost during life.

P_3 is known from 16 individuals. It is much larger than P_2. Its outline is somewhat triangular owing to a prominence of the buccal margin near the posterior end. There is only one well developed cusp, the protoconid; an anterior shoulder represents the paraconid, but there is no metaconid. The talonid is represented by a low, rounded, posterior cusp situated midway across the crown. There are two roots but no interradicular crest can be seen in isolated specimens.

P_4 is known from 19 individuals, and is thus the best represented tooth in the collection. It is subequal in length to P_3 but much wider. Its cusps and ridges are rounded and obtuse. The highest cusp is the protoconid; the paraconid is a stout anterior cusp, about half the height of the protoconid; the metaconid is higher than the paraconid and is situated directly lingually to the protoconid. On the posterior surface of the metaconid there develops to a variable degree a shoulder, representing a metastylid; in an unerupted tooth (RGM 179 242) a small cusp is present in this position. The talonid is a cingulum-like structure that rises towards the lingual side where it bears a small cusp, seemingly equivalent to the entoconid of the molar.

There are 18 examples of M_1; the best preserved is RGM 179 238, where it is associated with an incompletely erupted P_4. M_1 is the largest lower postcanine tooth, its length being only a little less than the combined lengths of M_2 and M_3. It is remarkable for its massive trigonid which occupies about two-thirds of the length of the crown. From the protoconid runs a strong anterior crest, which curves lingually to end abruptly at the anterolingual extremity of the crown. This crest is not notched as in carnivore carnassials, and no paraconid elevation can be distinguished. The metaconid is a small cusp, rapidly removed by wear and no longer visible in most specimens. It is situated rather more posteriorly than the protoconid, to which it is joined by a crest. In RGM 179 238 there is a swelling low on the posterior side of the metaconid, representing a metastylid. The talonid is narrower and much lower than the trigonid. Even on little-worn teeth the entoconid is slightly higher than the hypoconid. A transverse crest connects the hypoconid to the posterior side of the entoconid, and there is no hypoconulid. A cingulum, of variable distinctness, arises from the middle of the talonid crest and occupies the posterior edge of the tooth behind the hypoconid. The anterobuccal cingulum is indistinct or absent, but some specimens have a trace of cingulum between the protoconid and the hypoconid. The top of the trigonid shows considerable abrasion, dentine being exposed even in the subadult holotype. There is also an attrition facet on the buccal side of the anterior crest of the protoconid, caused by shearing against P^4. On the talonid wear affects mainly the upper surface of the hypoconid. There are two roots, of which the anterior is the larger; they are joined by an interradicular crest.

M_2, known from 18 individuals, is much smaller than M_1. Its trigonid is less specialized. The anterior crest of the protoconid curves lingually, to join the anterior base of the metaconid; there is no paraconid elevation. The metaconid stands directly opposite the protoconid, and equals or slightly exceeds that cusp in height on unworn specimens. The talonid resembles that of M_1. The buccal cingulum varies in distinctness, but it is better developed than on M_1 of the same jaw. There are two equal roots, with an interradicular crest.

M_3 resembles M_2 but it is smaller and its talonid is proportionately narrower. The posterior root, narrower than the anterior root, is inclined posteriorly. M_3 is known from 10 individuals.

SKULL

The most complete specimens are from San Giovannino. In the holotype skull M^3 is only lightly worn and the premolars are practically unworn: the animal must have died soon after replacing its milk dentition. The skull RGM 177 918 is crushed. It was probably of similar size to the holotype, but measurements of the snout anterior to P^3 are about 6% greater. The molars are heavily worn. The skulls RGM 179 192 and 179 194 are respectively 13% and

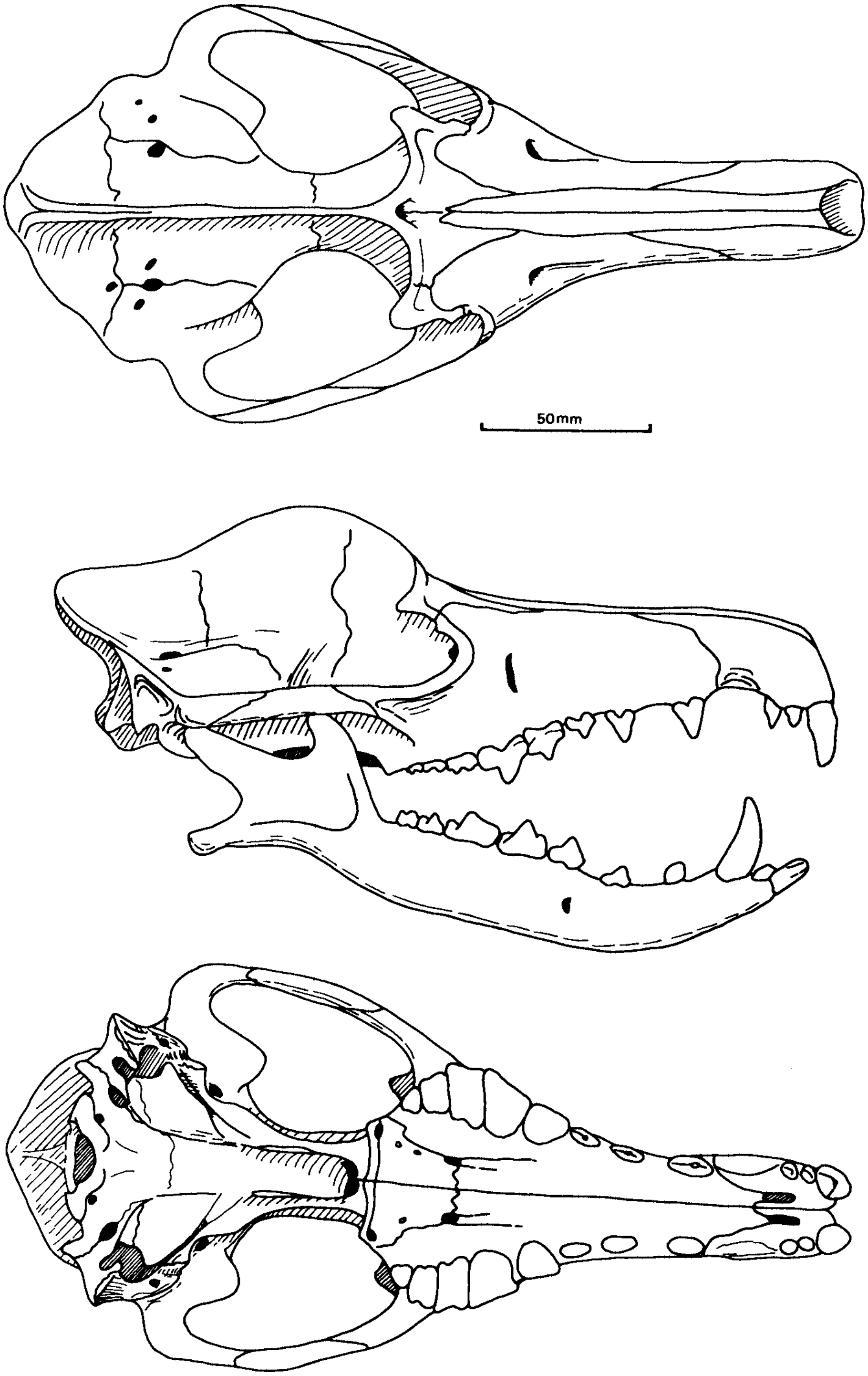


Fig. 3. Male skull of *D. koenigswaldi*, based on RGM 179 192, 179 194 and (mandible) 179 147.

10% longer than the holotype, and measurements of their teeth are about 9% greater. The snout anterior to P^3 is proportionately longer than in the holotype (22% and 17% respectively). M^3 is worn. These specimens are regarded as mature males, the holotype as a young female and RGM 177 918 as a mature female. RGM 179 146, the facial part of a skull, and RGM 179 155, a cranium, are both larger than the holotype. There is also a small skull (RGM 179 134) which has an estimated length only 78% of that of the holotype. The premaxilla is missing, but an isolated premaxilla (RGM 179 237) may belong to a skull of this size. The teeth of RGM 179 134 are smaller than those of the holotype; the molars are heavily worn, indicating maturity. From San Giovannino Low there is a palate (RGM 179 221), lacking the premaxilla and broken into right and left pieces; its teeth are comparable in size with the holotype. From other localities the skull is known only by four maxillary fragments: RGM 177 945 (Chiro 5 A), RGM 177 982 (Chiro 20 C), RGM 177 975 (Chiro 18), and RGM 178 208 (Pepo 1 A).

One of the most striking features of the skull is the elongation of the face. This increases with skull size: the length anterior to P^3, expressed as a percentage of the total basal length of the skull, ranges from about 31% in RGM 179 134 to 40% in RGM 179 192. In *Echinosorex gymnurus* the proportion is 23 - 24%.

The narrow, parallel-sided nasals extend farther back than in *Echinosorex,* ending above the orbits, on a level with the facial extensions of the maxillae. The nasal process of the premaxilla reaches to above P^1, but does not meet the frontal. The infraorbital foramen is above the anterior end of P^4, as in most erinaceids, but in *Echinosorex* it is farther back. A prelachrymal crest arises in front of the lachrymal foramen and continues along the lower border of the orbit to become the dorsal edge of the zygomatic arch. Below this crest, the zygomatic process of the maxilla is deeply excavated for the origin of the m. zygomaticus. The dorsal edge of the orbit is defined by a supraorbital ridge on the maxilla, ending in a stout postorbital process on the frontal. The postorbital process stands at the lateral end of a strong transverse frontal crest which joins its fellow to form the sagittal crest. In the large skull RGM 179 194 a deep pit lies immediately anterior to the junction of the frontal crests, but it is not present in the other specimens. The postorbital process and frontal crest, which provide origin for the most anterior fibres of the m. temporalis, are much more strongly developed than in other erinaceids.

The sagittal crest is exceptionally well developed in the large skulls. In RGM 179 194, where it is fully preserved, it rises to its greatest height in the parietal region, anterior to the level of the jaw articulation. Here it stands about 26 mm above the cranial roof. Farther back, where it is formed from the interparietal, its profile dips, rising again towards the posterior end. There it unites with the nuchal crests on a supraoccipital prominence which projects posteriorly beyond the level of the condyles. The supraoccipital prominence is also preserved in RGM 179 192 and 177 918, but it is incomplete in the holotype and missing from RGM 179 155. The sagittal crest of the holotype is less high (about 10 mm over the parietals), perhaps partly due to immaturity. On the small skull RGM 179 134 the crest is also lower (9 mm), and the supraoccipital prominence, though incompletely preserved, seems to have been much less salient.

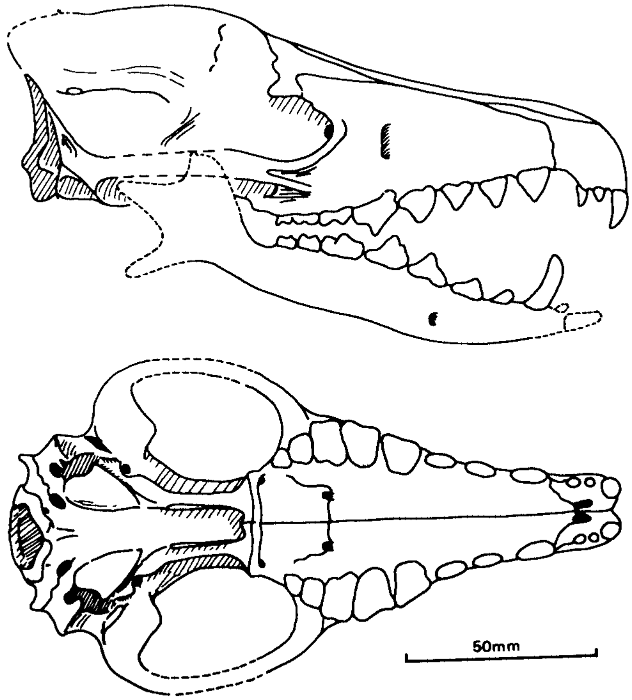


Fig. 4. Skull of *D. brevirostris*, RGM 179 134 (holotype); premaxilla added from RGM 179 237; mandible RGM 179 232 (paratypes).

In RGM 179 194 the surface of the parietals, on either side of the sagittal crest, is sculptured with irregular ridges, trending posterolaterally; they extend onto the adjacent surface of the squamosals. Similar sculpturing occurs in *Gymnurechinus* and other erinaceids (Butler, 1956). A large postparietal foramen opens in the parietal-squamosal suture; in RGM 179 194 it is accompanied by two smaller foramina in the parietal and one in the squamosal, and in RGM 179 192 there is a supplementary foramen in the squamosal.

The nuchal crest is strongly developed. It leans backwards, overhanging the occipital surface of the skull, whereas in *Echinosorex* it is upright. At its ventral end it is continuous with a crest that crosses the squamosal to become the dorsal edge of the zygomatic arch. A posterior branch (corresponding to the anterior lambdoid crest of other erinaceids) runs vertically along the posterior edge of the squamosal to end in the mastoid process. A deep concavity in the squamosal lies between these two crests. The posterior lambdoid crest, which crosses the mastoid to reach the paroccipital process, is very weakly developed; as a result, the lambdoid area faces posteriorly, rather than laterally as in other erinaceids. The zygomatic arches, completely preserved in RGM 179 192, are a little more divergent than in *Echinosorex*. The arch is horizontal in lateral view, and does not possess an anterior ventral process. The zygomatic process of the maxilla arises opposite M^2 and the anterior part of M^3. As in other erinaceids, the jugal is confined to the middle of the arch, extending laterally to the maxilla and squamosal.

The palate differs from that of *Echinosorex* in being relatively longer and narrower anterior to P^3, while its posterior portion is shorter owing to the relatively smaller molars. As in *Echinosorex*, the anterior end of the palate is bent downwards, so that the incisors stand at a lower level than the canine and anterior premolars. The maxillae reach the posterior edges of the incisive foramina, opposite I^3. The palatines extend to the level of the posterior part of M^1. There are no palatal vacuities. From the anterior palatine foramen, near the palatine suture, a shallow groove runs forward to fade opposite P^3. There are some smaller foramina behind the anterior palatine foramen. The transverse crest, situated about 7 mm posterior to M^3, is pierced at either end by a posterior palatine foramen (in most specimens represented by a notch, probably due to breakage). The hard palate ends almost immediately behind the crest.

The mid-cranial region is long and narrow. The ectopterygoid processes are narrow, as in *Echinosorex.* The orbitonasal (sphenopalatine) and sphenorbital foramina are far apart, and the orbitosphenoid is elongated anteroposteriorly, though not as much as in *Echinosorex.* As in erinaceids generally, there is an extensive orbital wing of the maxilla which has a long suture with the frontal, and the lachrymal is fused with the maxilla. The optic foramen opens posteriorly to the centre of the orbitosphenoid; it is immediately dorsal to the suboptic foramen, as in *Neurogymnurus* and *Lanthanotherium.* Above the optic foramen is a pit for the rectus eye-muscles, and above this again, in the orbitosphenoid-parietal suture, is the anterior opening of the lateral cerebral sinus (ethmoid foramen). Some vascular foramina open near the dorsal edge of the orbitosphenoid and the adjacent part of the frontal.

The posterior part of the cranial base is comparatively short, so that the jaw articulation is situated farther back on the skull than in other erinaceids. The glenoid surface is broad and flat, extending onto the root of the zygoma. Its anterior edge projects forward as a semicircular process. The postglenoid process is an elevated ridge, orientated at an angle of about 40° to the long axis of the skull. The small postglenoid foramen opens on its posteromedial surface. In *Echinosorex* the postglenoid process is proportionately less high and the foramen is larger. The exit of the ramus superior of the stapedial artery from the tympanic chamber (fissura glaseri) is marked by a notch on the posterior surface of the ridge, lateral to the squamosal-alisphenoid suture. The ridge is continued medially across the alisphenoid to join the ectopterygoid process. Behind the foramen ovale a groove in the anterior surface of the ridge marks the course of the mandibular nerve. An alisphenoid canal is present.

The bullae are elongated, divergent posteriorly and extended anteriorly. A groove marks the course of the eustachian canal which opened into the pharynx anterior to the level of the foramen ovale as in *Echinosorex.* The basisphenoid contribution to the bulla is extensive; posteriorly there is a small tympanic process of the petrosal. RGM 179 155 shows what appears to be a narrow tympanic bone attached to the edge of the bulla or partly overhung by it as in *Echinosorex.* The meatal groove is deeply concave and directed posterolaterally. A sharp ridge of the squamosal (post-tympanic process) borders the meatus posteriorly and merges laterally into the mastoid process.

The interior of the tympanic chamber may be seen best in the holotype and RGM 177 918. It is of typical erinaceid structure. The anterior half of the roof is formed by the (ali)sphenoid. The fenestra rotunda is covered from behind by the tympanic process of the petrosal. The carotid artery entered the bulla between the tympanic processes of the petrosal and the basisphenoid. Its

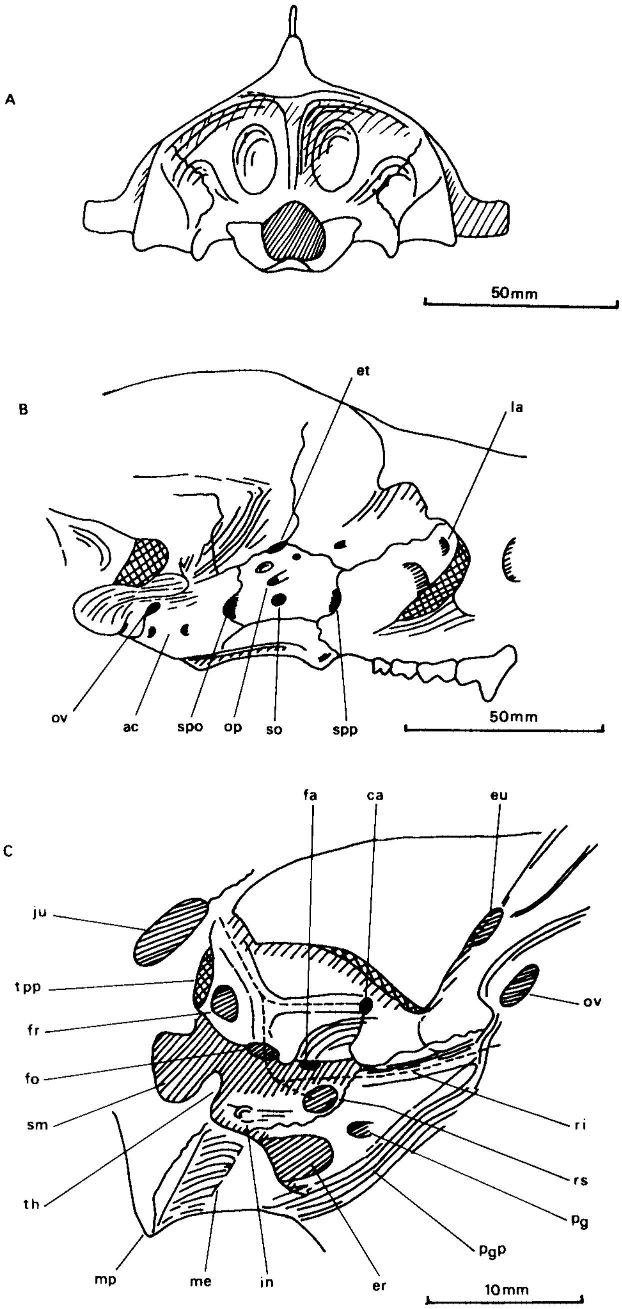


Fig. 5. Skull of *D. koenigswaldi.* A: Posterior view of male skull. B: Medial wall of orbit; zygomatic arch removed. Abbreviations: ac, alisphenoid canal; et, ethmoid foramen; la, lachrymal foramen; op, optic foramen; ov, foramen ovale; so, suboptic foramen; spo, sphenorbital foramen; spp, sphenopalatine foramen. C: Tympanic region; tympanic process of basisphenoid cut back. Dotted line shows the course of branches of the carotid artery. Abbreviations: ca, carotid foramen (for promontorial artery); er, epitympanic recess; eu, eustachian foramen; fa, exit of facial nerve; fo, fenestra ovalis; fr, fenestra rotunda; in, fossa incudis; ju, jugular foramen; me, auditory meatus; mp, mastoid process; ov, foramen ovale; pg, postglenoid foramen; pgp, postglenoid process; ri, groove for ramus inferior; rs, foramen spinosum (for ramus superior); sm, stylomastoid foramen; th, tympanohyal; tpp, tympanic process of petrosal (broken off).

course can be followed as a shallow groove which runs immediately ventral to the fenestra rotunda, after which it divides: one branch (stapedial artery) continues towards the fenestra ovalis, and the other runs forwards along the promontorium to a foramen in the petrosal-sphenoid suture. The ramus superior of the stapedial artery entered the braincase by a large foramen near the suture with the squamosal. The ramus inferior ran forward in a groove in the squamosal close to its suture with the sphenoid, to the fissura glaseri. A concavity in the roof of the tympanic chamber, between the promontorium and the squamosal suture, was occupied by the m. tensor tympani. The facial nerve entered the chamber shortly anterior to the fenestra ovalis. It ran in a groove and left the skull posteriorly to the tympanohyal. A medial expansion of the posterior end of the facial groove held the m. stapedius. The lateral part of the roof of the chamber, above the meatus, is excavated to form an epitympanic recess, deeper than in *Echinosorex*. A concavity between the epitympanic recess and the facial groove received the head of the incus. Broken remains of ear ossicles can be seen in RGM 179 155 and 179 194. The malleus appears to resemble that of *Echinosorex* but it is about twice as large.

In comparison with other erinaceids, the post-meatal region is very short, so that the anterior edges of the condyles are almost in line with the mastoid processes. In shape the condyles resemble those of *Echinosorex,* but they are more prominent ventrally. The condylar foramen is single, whereas in *Echinosorex* it is usually doubled. The small paroccipital processes resemble those of *Echinosorex.* The foramen magnum is about as high as wide, rising a little above the top of the condyles. A median ridge on the occipital surface separates concavities for the insertion of the rectus capitis muscles. These concavities are particularly deep in RGM 179 194.

BRAIN-CAST

A cast was made by Dr L. Radinsky of the cranial cavity of the holotype, and he kindly allows me to describe it. It is incomplete anteriorly, where it does not include the olfactory lobes. Some features of the internal surface of the cranial cavity are visible in RGM 177 918.

The brain resembled in shape that of *Echinosorex* (figured by Dechaseaux, 1964; measurements given by Butler, 1956), but is was about 40% larger in linear dimensions. The rhinal fissure appears to be situated more dorsally than in *Echinosorex,* resembling *Neurogymnurus* (Dechaseaux, 1964) in that it was not covered by the lateral cerebral sinus. If this interpretation is correct, the neopallium was small: on the cast its width is 70% of the width of the cerebrum, compared with 85% in *Echinosorex.* A concavity of the dorsal surface, near the fronto-parietal suture, represents the sulcus orbitalis, and there is a longitudinal sulcus more posteriorly; these occur in *Echinosorex* and in *Gymnurechinus* (Butler, 1956). There is a well developed subarcuate fossa in the periotic, seen in RGM 177 918. In the cast the pituitary fossa is hardly indicated.

Owing to the small size of the postglenoid foramen, most blood leaving the skull must have passed dorsally to the periotic in the lateral jugular sinus, to exit by the jugular foramen. The lateral jugular sinus received blood from

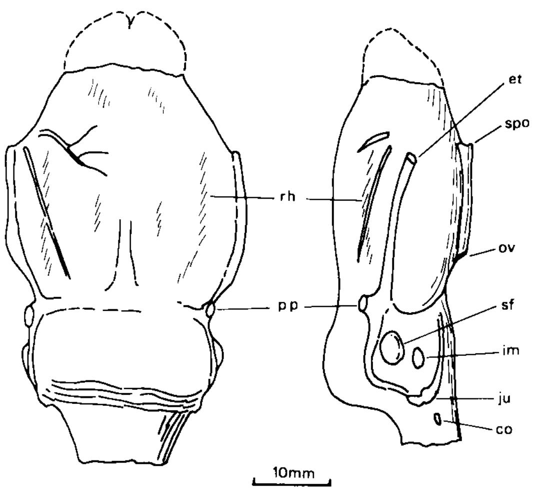


Fig. 6. Braincast of *D. koenigswaldi.* Abbreviations: co, condylar foramen; et, ethmoid foramen; im, internal auditory meatus; ju, jugular foramen; ov, foramen ovale; pp, postparietal foramen; rh, rhinal fissure; sf, subarcuate fossa; spo, sphenorbital foramen.

three main sources: the transverse sinus, near the parietal-interparietal suture; the lateral cerebral sinus, from the orbit via the ethmoid foramen; and from the m. temporalis, via the postparietal foramina.

MANDIBLE

There are 24 mandibular specimens, counting as one right and left jaws that are probably from the same individual. The most complete are RGM 179 193 (belonging to the skull 179 192) and 179 147 (a right jaw associated with the slightly less complete left jaw 179 145). These are larger than the holotype and are regarded as mature males. RGM 179 148, the only specimen with I_1 in situ, is broken off posteriorly at the level of M_2; it is also male. RGM 179 149 is another male specimen, lacking the condyle and the extreme anterior end. In the holotype both jaws are incomplete anteriorly, and the right jaw lacks the coronoid process (restored in Freudenthal, 1972, pl. 2). RGM 179 224, complete except for the incisor portion, is regarded as a mature female. All these are from San Giovannino. From the same site there is also a smaller jaw (RGM 179 232), lacking the extreme anterior end and all the posterior processes, which fits the small skull RGM 179 134. RGM 179 206, from San Giovannino Low, is complete except for the condyle; it is of the size of the holotype, and fits the maxilla RGM 179 221. The best preserved specimens from other fissures, all smaller than the holotype, are RGM 179 170 (Gervasio; lacks the condyle, and is broken off at the level of P_4), RGM 179 174 (Gervasio; coronoid and condyle broken off, otherwise complete), RGM 178 184 (Fina H; coronoid and angle incomplete, and broken off at the level of P_1), RGM 179 092 (Fina H; coronoid and angle incomplete, and broken off anterior to P_4), and RGM 179 063 (Nazario 4; lacks the coronoid and the anterior end beyond P_1).

The horizontal ramus is divided into a posterior region that bears the cheek teeth (P_3 - M_3) and an anterior symphyseal region. The symphysis ex-

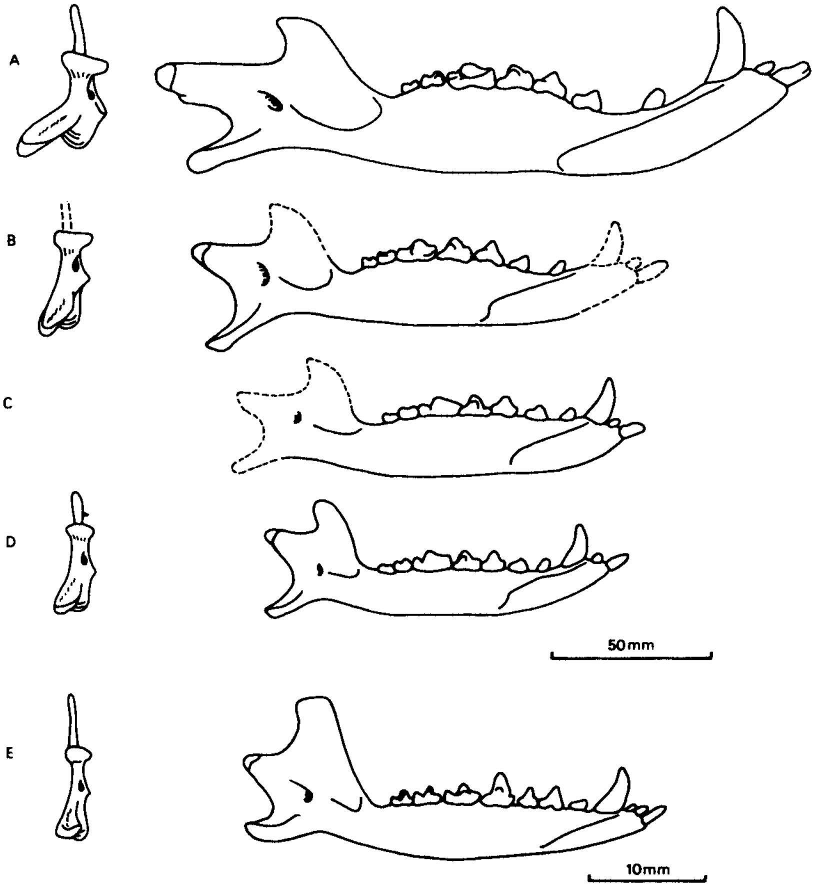


Fig. 7. Left mandibles, posterior and medial views. A: *D. koenigswaldi,* based on RGM 179 147. B: *D. intermedius,* RGM 179 063 (holotype); teeth partly restored. C: *D. brevirostris,* RGM 179 232 (paratype); teeth partly restored. D: *D. minor,* restoration based on RGM 178 184 (holotype) and RGM 179 174 (paratype). E: *Galerix stehlini,* BMNH M15810.

tends as far back as the anterior end of P_3, as in *Echinosorex.* The symphysis is relatively longest in the largest specimens: expressed as a ratio to the total length of P_3 - M_3, its length is 1.37 in RGM 179 147, about 1.0 in the small jaw RGM 179 174 and about 0.6 in *Echinosorex.* Lengthening takes place mainly between P_3 and the canine, and it is accompanied by spacing of the teeth. The symphyseal region is tilted upwards in relation to the posterior region, and it is less deep, due to a fall in the alveolar border in the region of P_2. Distinction between the two regions is most noticeable in the larger specimens that have a long diastema between P_2 and P_1. The mental foramen is below P_3; in *Echinosorex* it is usually below P_4.

Depth of the ramus increases with age; it is less in RGM 179 238 and 179 242, in which P_4 is incompletely erupted, than in other specimens with teeth of similar size, and it is less in the holotype than in mature specimens from San Giovannino. Ramus depth, relative to tooth length, is also less in the smaller specimens, and much less in *Echinosorex.*

The ascending ramus, measured from the posterior side of the condyle to the anterior base of the coronoid process, is much longer than P_3 - M_3 in the large mature specimens (ratio, 1.29 to 1.36), but in the holotype it is less elongated (ratio 1.00); it probably lengthens with age. It is also proportionately shorter in small specimens (1.18 in RGM 179 063, and 0.91 in RGM 178 184), and much shorter in *Echinosorex* (0.71 to 0.85).

The condyle is very low in position, in line with the tooth row in the larger specimens but slightly higher in RGM 178 184. In shape it resembles *Echinosorex:* it is transversely widened, with a cylindrically curved articulatory surface that extends down the posterior side.

The coronoid process is remarkably small, both in length and height. It is situated at some distance forward from the condyle, anterior to the mandibular foramen. Its anterior edge rises at a smaller angle from the tooth row than in *Echinosorex* and other erinaceids; this angle is somewhat greater in the small specimens RGM 178 184 and 179 170 than in larger specimens. On the medial side of the jaw, a ridge running from the anterior base of the coronoid process towards the mandibular foramen marks the ventral edge of the insertion of m. temporalis; it is present, though less strongly developed, in *Echinosorex.*

The angular process is long and stout, and it projects laterally out of the plane of the rest of the jaw, more so in large specimens. Medially there is a strong crest for m. pterygoideus internus, and the dorsal surface is hollowed out as a gutter. The angular process is truncate and somewhat club-shaped at the tip in the larger specimens, due to deposition of bone on its ventral surface; in the small specimen RGM 179 174 the process is shallower and more pointed. In RGM 179 063 (Nazario 4) the angular and condylar processes diverge more widely than in large specimens from San Giovannino, and this is probably true also of the other small specimens. On the lateral side, between the coronoid and angular processes, the jaw is hollowed out for the deep part of m. masseter.

VERTEBRAL COLUMN

The best preserved atlas is from the holotype (RGM 177 785), which lacks only the right side of the neural arch. There are also two fragments, both smaller than the holotype: RGM 179 141 from San Giovannino and RGM 179 296 from Chiro 28A. The neural arch is broader anteroposteriorly than in *Erinaceus,* and it differs from *Echinosorex* in the presence of a rudimentary neural spine. The right transverse process of the holotype, which is the best preserved, is incompletely ossified at the tip; the left process is partly preserved in RGM 179 296 but its tip is broken. These specimens indicate that the transverse process was less expanded anteroposteriorly but more stoutly constructed than in *Echinosorex.* A strut of thickened bone, continuous with the posterior edge of the neural arch, runs dorsally to the posterior opening of the vertebrarterial canal to reach the posterodorsal surface of the transverse process. The glenoid fossa (for the condyle of the skull) is overhung dorsally by a process of the anterior edge of the arch, more developed in the holotype than in the smaller specimens and in *Echinosorex.* The ventral surface of the atlas differs from that of *Echinosorex* in having no hypapophyseal spine.

The axis (epistropheus) of the holotype is represented only by the centrum and a fragment of neural arch. RGM 179 302 (from San Giovannino) is a

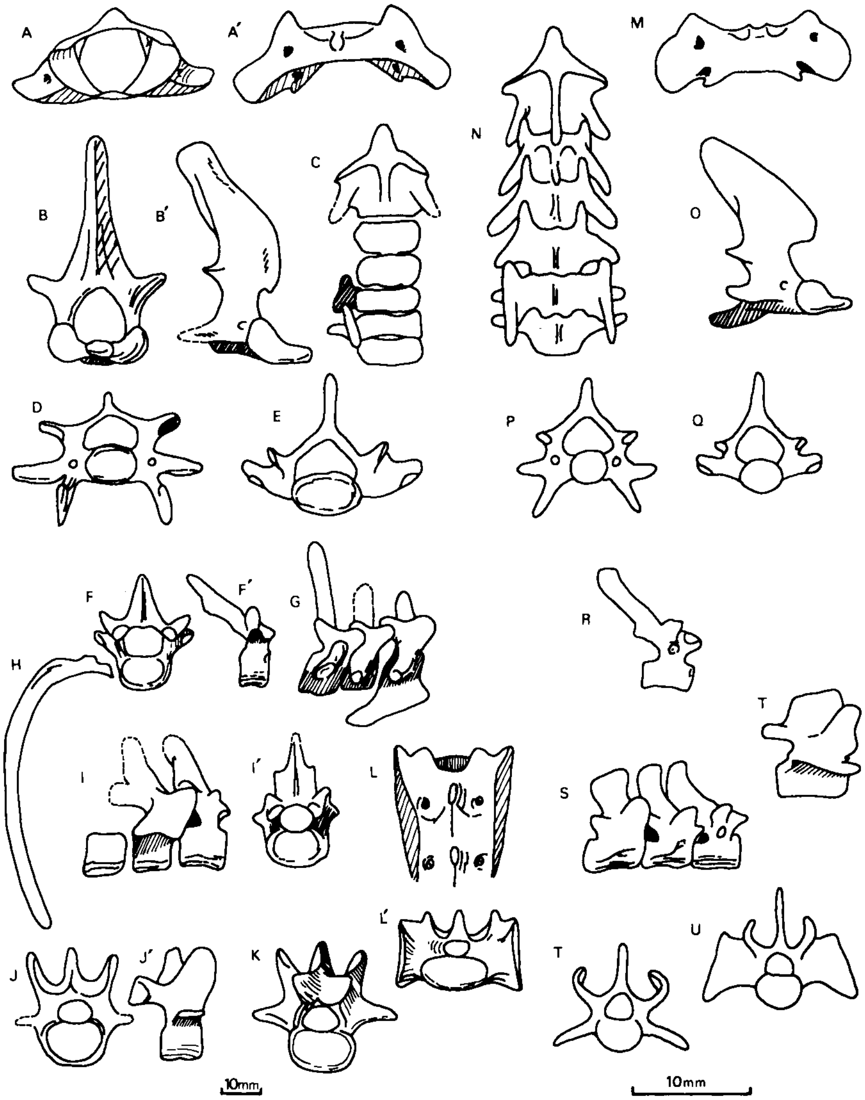


Fig. 8. Vertebrae of *Deinogalerix* and *Echinosorex*.

Deinogalerix, A, A': atlas, RGM 177 785 (holotype of *D. koenigswaldi),* anterior and dorsal views; B, B': axis, RGM 179 302, anterior and lateral views; C: cervicals 2 - 7, holotype of *D. koenigswaldi,* ventral view; D: cervical 6, RGM 179 138, posterior view; E: thoracic 1, RGM 179 142, posterior view; F, F' : a middle thoracic, RGM 177 798 (holotype of *D. koenigswaldi),* anterior and lateral views; G: associated C 6 - Th 1, RGM 179 138, 143, 142, lateral view; H: rib 10, RGM 177 810 (holotype of *D. koenigswaldi);* I: associated posterior thoracics, RGM 179 135 - 137; I' : anterior view of RGM 179 135; J, J' : lumbar, RGM 177 835 (holotype of *D. koenigswaldi),* anterior and lateral views; K: lumbar, RGM 179 064, posterior view; L, L' : anterior part of sacrum, based on RGM 178 049 and RGM 179 294, dorsal and anterior views.

Echinosorex gymnurus, BMNH 67.1480: M: atlas, dorsal view; N: cervicals 2 - 7, ventral view; O: axis, lateral view; P: cervical 6, posterior view; Q: thoracic 1, posterior view; R: thoracic 8, lateral view; S: thoracics 11 - 13, lateral view; T, T' : lumbar 3, anterior and lateral views; U: sacrum, anterior view.

complete specimen, a little larger than the holotype, and RGM 177 961 (from Chiro 11 A), slightly smaller than the holotype, lacks the neural spine. There are also three very small, incomplete specimens from Biancone 1. The neural spine in RGM 179 302 is high, inclined at an angle of about 60° to the floor of the spinal canal, and broader at the tip than in *Echinosorex* but shorter at the base. The tip seems to be incompletely ossified. The centrum is proportionately shorter and broader than in *Echinosorex.* Two of the Biancone 1 specimens (RGM 178 116, 178 121) are particularly short, probably due to immaturity. Unlike *Echinosorex,* there is no hypapophyseal spine, but a prominent median longitudinal ridge separates a pair of concavities for m. longus cervicis superior. The short pleurapophyses point posterolaterally as in *Echinosorex,* but they are flattened rather than rodlike, and have a shallow concavity on their anterolateral surfaces.

The remaining cervicals of the holotype (RGM 177 787 - 791) are represented by their centra, showing in addition on the right side the zygapophyses of C 5 and broken pleurapophyses of C 6. Better preserved is a series of the last three cervicals (RGM 179 140, 179 138, 179 143) associated with the first thoracic (179 142), from San Giovannino; these are larger than the holotype. There are also two examples of C 6: RGM 179 220, larger than the holotype, from San Giovannino Low and RGM 177 976, a smaller specimen from Chiro 20 A. Both of these lack the neural arch, but RGM 177 976 retains the zygapophyses. Finally, RGM 178 128 is a centrum from Biancone 1. In all these vertebrae the centrum is broader in comparison with its length and height than in *Echinosorex.* It is approximately equal in width to the spinal canal, as in *Erinaceus,* whereas in *Echinosorex* it is narrower. The laminae of the neural arch, seen in RGM 179 138, are less steeply inclined, and the neural spine is smaller. The lateral pleurapophysis, preserved on C 5 (RGM 179 140), C 6 (RGM 179 138, 179 220) and C 7 (RGM 179 143), is long, directed laterally and blunt at the tip, as in *Echinosorex.* The ventral pleurapophysis is preserved only on C 6, where it forms a flange that extends back under C 7, as in *Echinosorex.* Its broken base is visible on RGM 179 140 (C 5). C 7 of *Deinogalerix,* like that of other erinaceids, has no ventral pleurapophysis and no vertebrarterial canal. The centra of C 3 - 7 lack the median ventral ridge that occurs in *Echinosorex,* but a pair of pits for muscle insertion is present on C 5 -7; these are indistinct in the holotype. A pair of nutritive foramina opens on the dorsal surface of each centrum.

Ten thoracic vertebrae were found near the holotype skull, a series of three (RGM 177 792 - 794) and a series of seven (RGM 177 795 - 801). The series of three are probably anterior: their centra are flattened dorsoventrally like cervicals. Only one neural arch belonging to this series is preserved. The series of seven are more complete. Their centra are deeper and more convex ventrally. The penultimate member of this series has a more upright neural spine than the vertebrae in front of it, indicating an approach towards the anticlinal vertebra (T 12 in *Echinosorex).* Twelve pairs of ribs are preserved in association with these vertebrae. They represent nos. 2 - 13, for comparison with *Echinosorex* shows that the first rib is not included. As the last rib is still long the supposition that there were 15 thoracic vertebrae (Freudenthal, 1972) is reasonable. Besides the holotype there are from San Giovannino a well preserved T 1 (RGM 179 142), associated with posterior cervicals, an incomplete vertebra from the middle of the series (RGM 179 139), and three posterior thoracics in articulation (RGM 179 135 - 137). There is also a small anterior thoracic from Biancone 1 (RGM 178 129).

The neural arch of T 1 is narrow anteroposteriorly, as in the cervicals. The neural spine is rod-like and nearly vertical, and proportionately as high as in *Echinosorex.* Whether the spine of T 2 was higher as in *Echinosorex* is unknown. On the middle thoracics the arches become broader and the spines are inclined posteriorly. In the holotype skeleton the spines are small, triangular in section and keeled on their anterior sides. They thus differ from those of *Echinosorex* which are higher and laterally flattened, but the difference may be partly due to incomplete ossification in the immature holotype. Towards the posterior end of the thoracic series the spine becomes more upright, as may be seen on the 7th vertebra of the series of 8 (the 8th is poorly preserved), and also on RGM 179 135. This specimen, which comes from a larger individual, unfortunately lacks the top of the spine; it corresponds to T 12 of *Echinosorex,* which also has a more upright spine. On the anterior thoracics the anterior edge of the neural arch, when seen in dorsal view, is broadly concave; further back in the series the concavity becomes a deep indentation in the middle line.

A mammillary process is present on T 1, projecting laterally beyond the facet for the tubercle of the rib. On more posterior vertebrae the mammillary process becomes progressively more separated from the small transverse process. RGM 179 135 resembles T 12 of *Echinosorex* in that the anterior zygapophysis faces dorsally but the posterior zygapophysis is of lumbar type, facing laterally. On the next vertebra (RGM 179 136) the anterior zygapophyseal articulation has shifted to the medial surface of the mammillary process. On these vertebrae there appears to be only one rib facet.

The centra of the thoracic vertebrae are broader in proportion to their height and length than in *Echinosorex,* and also broader relative to the spinal canal. There is no ventral keel, such as occurs on the anterior thoracics of *Echinosorex,* but the ventral surface is evenly rounded, becoming more convex in the more posterior thoracics.

All the ribs are much larger and stouter than in *Echinosorex.* As in the living form, rib 2 is broad throughout its length, and rib 3 is broadest proximally, near the angle; this proximal broadening diminishes in the succeeding ribs. From rib 5 backwards the cross-section of the middle part is oval but the distal end is flattened. Ribs 10 - 12 are of nearly equal length and probably the longest; in *Echinosorex* the longest ribs are 9 and 10. The head, visible in ribs 4 - 10, 12 and 13, is broader anteroposteriorly than in *Echinosorex,* and the neck is also broadened. The tubercle approaches the head on rib 12, and the articular surfaces are contiguous on rib 13. The dorsal process, lateral to the tubercle, for insertion of m. levator costarum, is less distinct than in *Echinosorex.* RGM 178 117 is the proximal part of a rib from Biancone 1. It agrees best with rib 10 but is much smaller. The head is less broadened than in the holotype, resembling *Echinosorex.*

Three associated lumbars belong to the holotype skeleton (RGM 177 835 - 837) and there is an isolated lumbar (RGM 177 838) from the same site. From Chiro 24 there is a specimen smaller than the holotype (RGM 179 072) and a larger specimen (RGM 179 064). The spinal canal is smaller than in the thoracics. The neural spine, best preserved in RGM 177 835, is upright, and shorter anteroposteriorly than in *Echinosorex.* Its anterior edge forms a keel which extends to the top of the spinal canal. The spine was probably not much higher than the metapophyses. These are large, vertical processes, carrying the anterior zygapophyseal facets on their medial surfaces. In *Echinosorex* the metapophyses curve medially. The lumbar centra are larger than those of the thoracics; they are relatively shorter and broader than in *Echinosorex* or *Erinaceus.* The ventral surface has a blunt keel. The transverse processes are broken in all the specimens, but to judge from their bases they appear to have been smaller than in *Echinosorex,* though not as reduced as in *Erinaceus.* Anapophyses are absent. No lumbar intercentra have been found.

The sacrum of the holotype skeleton has not been preserved, but there are two other specimens: RGM 179 294 (Chiro 28A) fits a lumbar of the holotype, and RGM 178 049 (San Giovannino) is larger. Both specimens are incomplete posteriorly, but RGM 179 294 shows that there were at least three sacral vertebrae. In *Echinosorex* the number of sacrals varies from 4 to 7 (Leche, 1902). The first two sacrals of *Deinogalerix* are much wider in proportion to length and height than in *Echinosorex.* The first neural spine, which is the only one preserved, is much smaller, not rising above the level of the metapophyses. The ilium articulated with the first two sacrals as in *Echinosorex.* The ventral surface of the centra is damaged, but it was evidently less convex transversely than in *Echinosorex.*

Eight caudal vertebrae (RGM 177 876 - 883), found at San Giovannino but at different spots, probably do not belong to the same individual (Freudenthal, 1972). Three more vertebrae (RGM 179 246 - 248) were found on a subsequent occasion. These specimens have been compared with the caudal vertebrae of a skeleton of *Echinosorex* with four sacrals (BMNH 67. 1480). RGM 177 876 is poorly preserved but shows a large, laterally extended transverse process; it may represent Cd 1. RGM 177 877, possibly Cd 2, is also poorly preserved; it lacks the neural arch and transverse processes but retains the left anterior zygapophysis. RGM 177 878 and 179 248 resemble Cd 3 of *Echinosorex.* The neural arch has broken away but it seems to have been confined to the anterior half of the vertebra. The transverse process (complete on the left side of 177 878) is situated anteriorly and points somewhat forward. RGM 177 878 is a little smaller than 179 248 and its epiphyses are distinct. Cd 4 is represented by RGM 179 247 and 177 879, the latter being somewhat smaller. The spinal canal is open, the neural arch being represented by a pair of anterior dorsal processes. The transverse processes are near the anterior end and point somewhat forward. A lateral ridge connects the transverse process with a small process at the posterior end. On RGM 179 246 the transverse process and posterior lateral process are of equal size. This vertebra probably represents Cd 5 or 6, although on these vertebrae in *Echinosorex* the transverse process remains more prominent than the posterior lateral process. The remaining vertebrae (RGM 177 880 - 883) are simplified, with rudimentary processes, like Cd 7 - 13 of *Echinosorex.* RGM 177 880 is the longest; in *Echinosorex* the longest caudals are Cd 9 - 11, and the total number is 23 to 27.

All the caudal vertebrae of *Deinogalerix* are relatively shorter and broader than the corresponding vertebrae of *Echinosorex.* The ventral surface of Cd 1 - 3 has a median ridge separating a pair of lateral concavities; on Cd 4 and backwards the ridge is slightly indicated or absent, whereas in *Echinosorex* it remains distinct much farther along the tail. A median dorsal ridge is

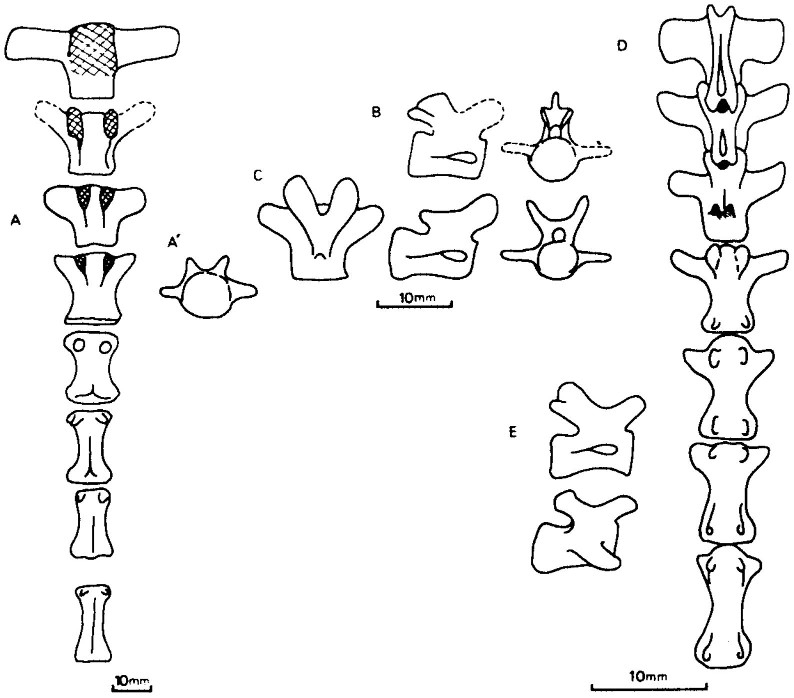


Fig. 9. Caudal vertebrae; A: *D. koenigswaldi,* dorsal view: RGM 177 876, 177 877, 177 878, 179 247, 179 248, 177 880, 177 881, 177 883; A' : anterior view of RGM 179 247; B, C: *D. freudenthali,* B: RGM 178 130, lateral and posterior views; C: RGM 178 125, dorsal, lateral and anterior views; D: *Echinosorex gymnurus,* BMNH 67.1480, caudals 1 - 7, dorsal view; E: caudals 2 and 3, lateral view.

present near the posterior end on RGM 179 246 and 177 880 - 882, as on Cd 6 and subsequent vertebrae of *Echinosorex,* but on RGM 177 883 the ridge is absent. No chevron bones have been found.

Two small vertebrae from Biancone 1 (RGM 178 125, 178 127) resemble Cd 3 of *Echinosorex,* with which they agree in length but differ in their greater width. The anterior zygapophyses are well developed, but the neural arch does not reach the posterior end of the centrum and there are no posterior zygapophyses. The neural spine is less developed than in *Echinosorex.* The anteriorly situated transverse processes have broken off. Another Biancone specimen (RGM 178 130) has closely approximated posterior zygapophyses like Cd 2 of *Echinosorex.* The anterior part of the neural arch is not preserved, but the neural spine, lower than in *Echinosorex,* is visible. A fourth specimen (RGM 178 123) apparently represents Cd 4. In all these specimens from Biancone 1 the centrum, though broader than in *Echinosorex,* is not so broad in comparison with its length as in specimens from San Giovannino.

PECTORAL GIRDLE AND FORE-LIMB

The clavicle is known from both sides in the holotype (RGM 177 824 - 825). The clavicle closely resembles that of *Echinosorex,* except that the middle part is more flattened dorsoventrally. At the medial end there is a concavity for ar-

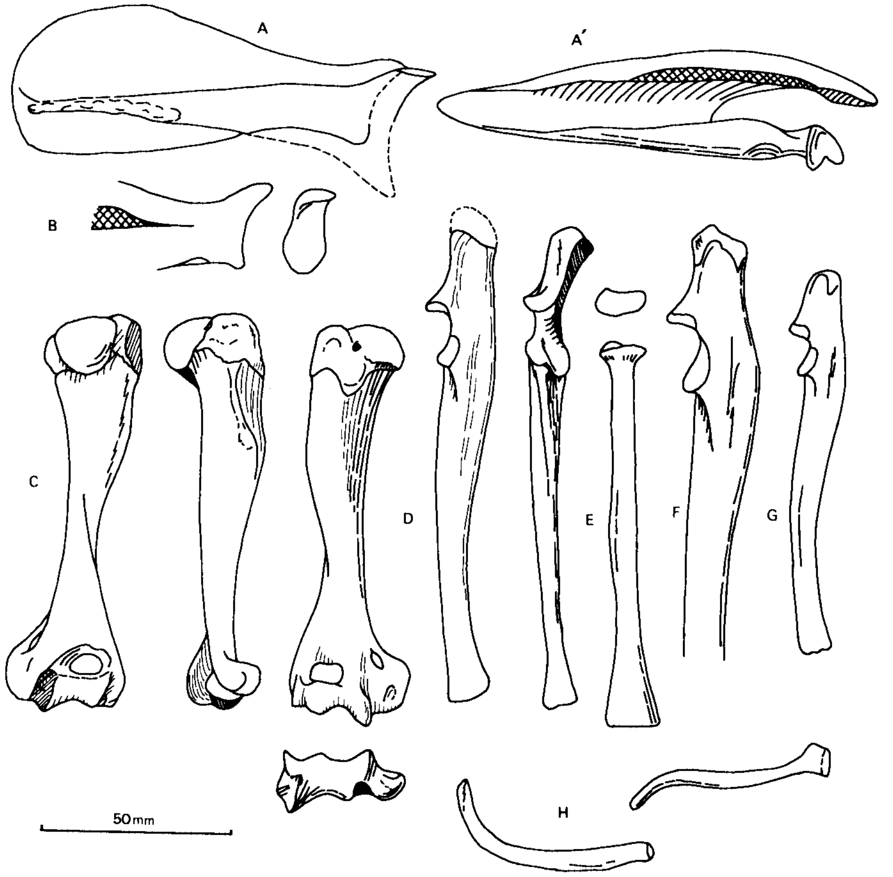


Fig. 10. Right pectoral girdle and fore-limb; A, A' : scapula, RGM 179 285, lateral and posterior vieuws; B: scapula, RGM 177 828 (holotype, of *D. koeningswaldi),* lateral and distal vieuws of humeral end; C: humerus, RGM 177 829 (holotype of *D. koenigswaldi,* reversed), posterior, lateral, anterior, and distal views; D: ulna, RGM 177 833 (holotype of *D. koenigswaldi,* reversed), medial and anterior views; E: radius, RGM 177 831 (holotype of *D. koenigswaldi,* reversed), anterior and proximal views; F: ulna, RGM 179 176, *D. intermedius,* medial view; G: ulna, RGM 179 177 *(D. minor,* reversed), medial view; H: clavicle, RGM 177 825 (holotype of *D. koenigswaldi),* anterior and dorsal views.

ticulation with the sternum, and a dorsal process for ligamentary attachment. The bone curves posteriorly towards its lateral end, where the tip turns ventrally. The lateral end is tapered, with a flat joint surface for the acromion.

RGM 177 826, interpreted by Freudenthal (1972) as possibly part of the sternum, shows little resemblance to *Echinosorex* or *Erinaceus,* and probably does not belong to *Deinogalerix.*

The most complete scapula is RGM 179 285, found at San Giovannino near the large skull RGM 179 194. The scapulae of the holotype skeleton are represented only by their humeral ends, which are smaller than the corresponding part of RGM 179 285. In most respects the scapula resembles that of *Echinosorex.* The width of the blade is about 2/5 of its length. The anterior margin is bent laterally more than in *Echinosorex,* so that the supraspinous fossa is more concave. The edge of the spine turns backwards as a flange overhanging the infraspinous fossa; the metacromion process is not preserved. The dorsal third of the spine is roughened for m. trapezius. There is a well developed acromion process, which bends anteriorly and medially. On the posterior and medial side of the neck is a pit for m. triceps. The glenoid cavity is oval, about 1.5 times as long as wide, with a slight inflection in the lateral margin.

The only complete humerus is from the left side of the holotype (RGM 177 829). Its epiphysis has not united with the shaft, and the isolated epiphysis of the right humerus was found separately. There are four other specimens, all incomplete, including a fragment of the distal end of a small example from Biancone 1 (RGM 178 122). In proportion to its length the humerus is thicker than in *Echinosorex,* resembling *Erinaceus.* The proportions of the head and tuberosities resemble *Echinosorex,* but the bicipital groove is shallower, as in *Erinaceus.* There is a pit in the bicipital groove for the superior glenohumeral ligament, present also in the living genera. The deltoid crest arises on the lateral side below the greater tuberosity and passes obliquely to reach the anterior edge about halfway down the bone. Medially to the crest is a scar for m. pectoralis. On the posterior surface a ridge arises medially below the lesser tuberosity and crosses the shaft obliquely to reach the ectepicondyle. The humerus is perforated near its distal end by a supracondylar fenestra. The ectepicondyle is small; the entepicondyle is larger than in *Echinosorex,* but as in the living genus it is pierced by an entepicondylar foramen. Most details of the distal end resemble *Echinosorex:* the medial trochlear keel is prominent distally and the lateral keel is prominent posteriorly. There is a ligamentary pit, deeper than in *Echinosorex,* on the posterior side between the trochlea and the entepicondyle. Another pit is present in the distal end of the bone, near the capitulum.

The left ulna of the holotype (RGM 177 833) lacks the distal epiphysis and the olecranon process is incompletely ossified; the right ulna is fragmentary. There are seven other specimens, in all of which the distal end is broken but the olecranon is more complete. They differ in size: RGM 179 176 (Gervasio) and RGM 179 269 (San Giovannino Low) are larger than the holotype, while RGM 178 192 (Fina H) and RGM 177 979 (Chiro 20 A) are much smaller, though mature. Resemblance to *Echinosorex* is very close. The olecranon is strongly developed, concave medially, and with a posterointernal tubercle for m. flexor carpi ulnaris. The anconeal process projects laterally beyond the surface of the ulna, but medially it is continuous with the anterior edge of the olecranon. The articulatory surface for the radius is only very slightly concave; it is divided by a ridge on the coronoid process from the facet for the capitulum of the humerus. For the proximal two-thirds of its length the ulna is flattened mediolaterally, widening towards the distal end, where it curves posteriorly. The anterior (interosseous) edge is ridged, and there is a longitudinal ridge on the middle part of the lateral surface. The coronoid process is less salient than in *Echinosorex.* It is buttressed distally on the medial side by a ridge that forms the margin of a deep groove into which the nutrient foramen opens. In *Echinosorex* this ridge is weaker, and it arises more proximally in relation to the articulatory surface. The anteroposterior diameter of the ulna varies relatively to other measurements, probably increasing with individual age.

The radius is complete in the holotype except for the distal epiphysis (RGM 177 831 - 832). The only other example is the proximal end of a much smaller specimen from Biancone 1 (RGM 178 111). The radius again resem-

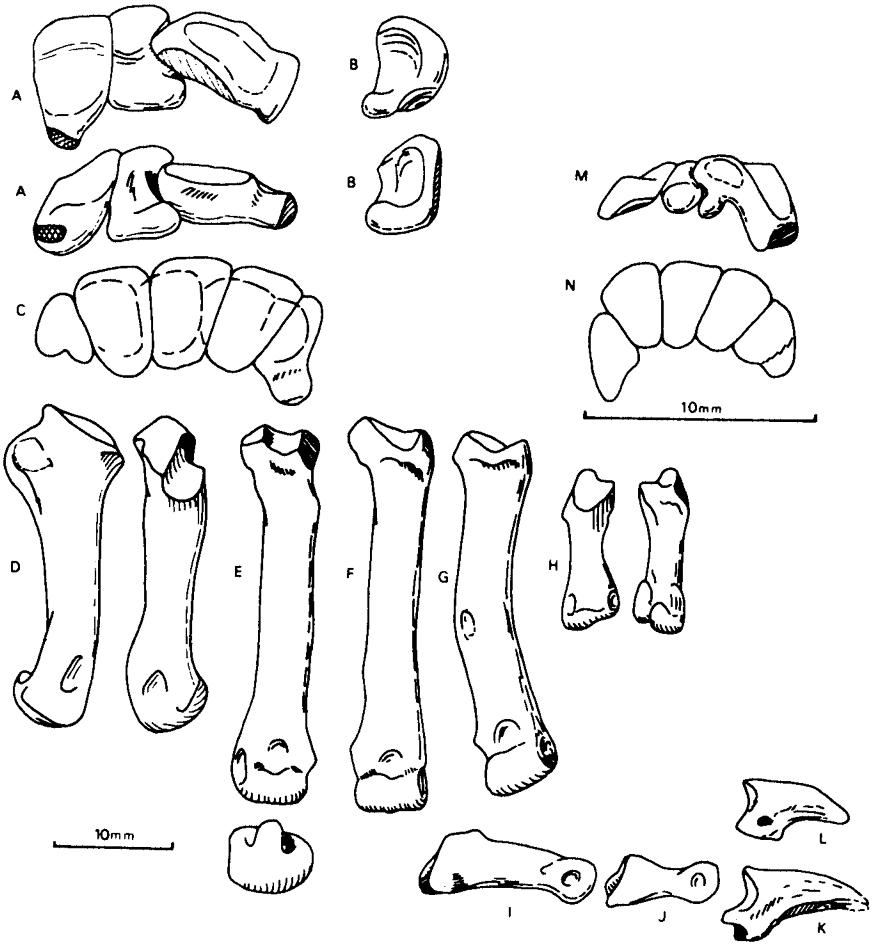


Fig. 11. Bones of right manus of holotype of *D. koenigswaldi* and (M, N) *Echinosorex gymnurus*, BMNH 67.1480.

A: proximal carpals, RGM 177 873-875, proximal vieuw A′ : the same, palmar vieuw, B, B′ : lunate, lateral and distal views; C: proximal ends of metacarpals in articulation; D: metacarpal V, RGM 177 859, lateral and dorsal views; E: metacarpal IV, RGM 177 858, dorsal and distal views; F: metacarpal III, RGM 177 857, dorsal view; G: metacarpal II, RGM 177 856, dorsal view; H: metacarpal I, RGM 177 860, dorsal and palmar views; I, J, K: phalanges of toe III, RGM 177 863, 177 867 and 177 869; L: ungual phalanx of toe ?V, RGM 177 871; M: proximal carpals of *Echinosorex*, palmar view; N: proximal ends of metacarpals of *Echinosorex*.

bles *Echinosorex*. It is more slender than the ulna, except at the distal end. The head is approximately rectangular in end view, broadened mediolaterally. The neck is oval in cross-section. The middle part of the shaft is flattened, its lateral edge sharpened and its posterior surface grooved longitudinally for the interosseous ligament. In the holotype there is no process for insertion of m. biceps, but an indistinct convexity represents this in the Biancone specimen.

Three basal carpals (scaphoid, lunate, cuneiform) from the right side are represented in the holotype skeleton (RGM 177 873 - 875). The scaphoid and lunate are separate, as in *Echinosorex*, and not fused as they usually are in *Erinaceus*.

The scaphoid resembles that of *Echinosorex*. It is compressed proximodistally. The proximal surface is mainly occupied by the articulation for the radius, concave over most of the area but cylindrically convex dorsally. The lunate fitted closely against the scaphoid by a flat lateral facet that makes an angle of about 45° with the proximal surface. On the distal surface is a concave facet for the trapezoid, situated towards the dorsal side. The palmar tubercle and the facet for the trapezium have not been preserved.

The proximal surface of the lunate is convex, for articulation with the radius. On the medial surface there is a large, flat facet for the scaphoid. A concave facet for the cuneiform occupies the proximal part of the lateral surface. On the distal surface there is a large concave facet for the magnum and a smaller, slightly convex facet for the trapezoid. Unlike *Echinosorex,* the palmar process is a transverse flange which projects laterally behind the cuneiform.

The cuneiform (triquetral) is a transversely extended bone, with a groove on its proximal surface for articulation with the ulna. The pisiform facet is an elongated area at the proximal edge of the palmar surface. Distally to this the palmar surface is pitted for a ligament. The medial surface, which articulates with the lunate, is convex. A concave facet for the unciform covers most of the distal surface. The palmar process, present in *Echinosorex* and *Erinaceus,* is not developed, being apparently replaced by the extended palmar process of the lunate. Laterally, where the bone extends beyond the ulna facet, there is an oval facet for a sesamoid, which also exists in *Echinosorex.*

The five metacarpals of the right manus of the holotype are preserved. When fitted together it is seen that the metacarpus as a whole is proportionately shorter and broader than in *Echinosorex,* resembling *Erinaceus* in proportions except that MC V is relatively larger. As in *Echinosorex,* MC III is the longest, and MC IV is only slightly shorter; however, MC II and MC V are relatively less short, especially MC V which has 70% of the length of MC III, compared with 45% in *Echinosorex.* MC I is one-third as long as MC III, both in *Deinogalerix* and *Echinosorex.* There are some metacarpals from Biancone 1 that resemble the holotype but are much smaller. A MC II (RGM 178 119) is two-thirds as long as that of the holotype. The other specimens from Biancone are still smaller, about half the size of the holotype and probably immature: RGM 178 118 (MC III), 178 131 (distal end of MC ?IV), and 178 137 (MC V).

MC I of the holotype (RGM 177 860) is less flattened than in *Echinosorex,* especially proximally. The proximal surface, which articulated with the trapezium, is broader, and it is extended as a palmar process, situated towards the lateral side. The palmar process is rudimentary in *Echinosorex.* The bone is less twisted along its axis than in *Echinosorex:* the plane of bending at the metacarpo-phalangeal joint is displaced about 40° from that at the proximal metacarpal joint, compared with about 60° in *Echinosorex.* MC I seems to be placed more to the side of MC II than in *Echinosorex,* where it is partly behind MC II and its dorsal surface faces medially.

MC II (RGM 177 856) is bent in a medial direction about midway along its length, where there is a scar on the lateral side for m. extensor carpi radialis longus. Proximally to the bend the bone is thickest anteroposteriorly; distally it is widened mediolaterally. The proximal end has a grooved facet for the trapezoid, a medial facet for the trapezium, and a flat lateral facet for the magnum. MC III fits into a hollow on the lateral side below the magnum facet. In *Echinosorex* MC II is more slender and nearly straight.

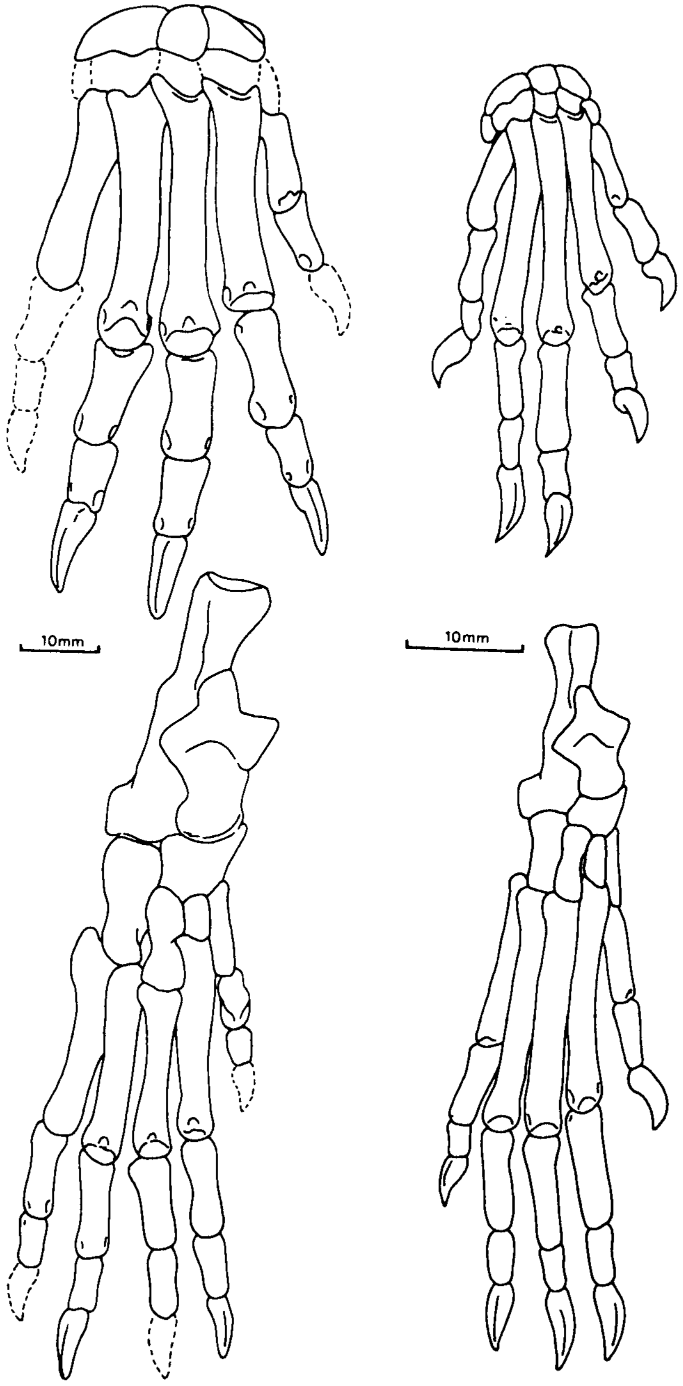


Fig. 12. Right manus and pes of *Deinogalerix koenigswaldi* (on left) compared with *Echinosorex gymnurus* (on right). Manus of *Deinogalerix* reconstituted from bones of the holotype; pes drawn from the articulated foot (reversed).

MC III (RGM 177 857) resembles *Echinosorex* except that it is proportionately shorter. The anteroposterior diameter of the shaft is greatest towards the proximal end. Distally there is a very slight medial curvature. The proximal end has a grooved facet for the magnum; laterally to this there is a prominence which articulates with the unciform and overhangs a concavity for MC IV. MC IV (RGM 177 858) resembles MC III. Its proximal end has a grooved facet for the unciform, divided by keels from a medial facet for MC III and a lateral, second unciform facet.

MC V (RGM 177 859) is placed partly behind MC IV so that its dorsal surface faces partly laterally. The facet for MC IV is confined to the dorsal side of the bone. Proximally there is a convex facet for the unciform. A prominent palmar process near the proximal end bears a facet for a sesamoid. On the medial side, distal to the facet for MC IV, there is an extensive roughened area for ligamentary attachment. MC V differs from that of *Echinosorex* in having a proportionately longer shaft.

Five proximal phalanges probably belong to the same manus (RGM 177 861 - 865). Four are complete; one, believed to belong to digit V, lacks the distal end. The four complete bones are proportionately shorter and thicker than in *Echinosorex,* having more resemblance to *Erinaceus.* In *Echinosorex* the phalanx of digit III is much longer than those of digits II and IV, but in *Deinogalerix,* as in *Erinaceus,* the basal phalanges of the three middle digits are nearly equal in length. The basal phalanx of digit I is the shortest and most slender, as in the living forms.

Three middle phalanges (RGM 177 866 - 868) are relatively broader than in *Echinosorex* and resemble *Erinaceus.* Three ungual phalanges (RGM 177 869 - 871) form compressed claws like those of living erinaceids. Two specimens have larger claws than the third; in *Echinosorex* the claws of digits II - IV are larger than those of digits I and V.

PELVIS AND HIND-LIMB

The pelvis of the holotype (RGM 177 839 - 840) is incomplete on both sides. The right side lacks the tip of the ilium, most of the pubis and the descending ramus of the ischium; on the left side the ischium is complete, but much of the ilium and most of the pubis are missing. There are eight additional specimens, all more or less fragmentary. Two from San Giovannino (RGM 179 125, 179 315) and two from San Giovannino Low (RGM 179 222 - 223) are larger than the holotype.

The anterior part of the ilium is unknown. When RGM 177 839 is fitted to the sacrum RGM 179 294 it is seen that the ilium has been broken across at the level of the posterior end of the first sacral vertebra. The broken surface is triangular, approaching *Erinaceus,* and less compressed mediolaterally than in *Echinosorex.* The ventral surface, for m. iliacus, is proportionately broader than in *Echinosorex.* The posterior iliac spine, preserved in RGM 179 258 (San Giovannino Low) and 178 018 (Chiro 20 E), stands relatively closer to the acetabulum than in *Echinosorex.* The process for m. rectus femoris, anterior to the acetabulum, is well developed as in *Echinosorex.*

The spine of the ischium, situated dorsally to the posterior border of the acetabulum, is more distinct than in *Echinosorex.* The ischial tuberosity rises

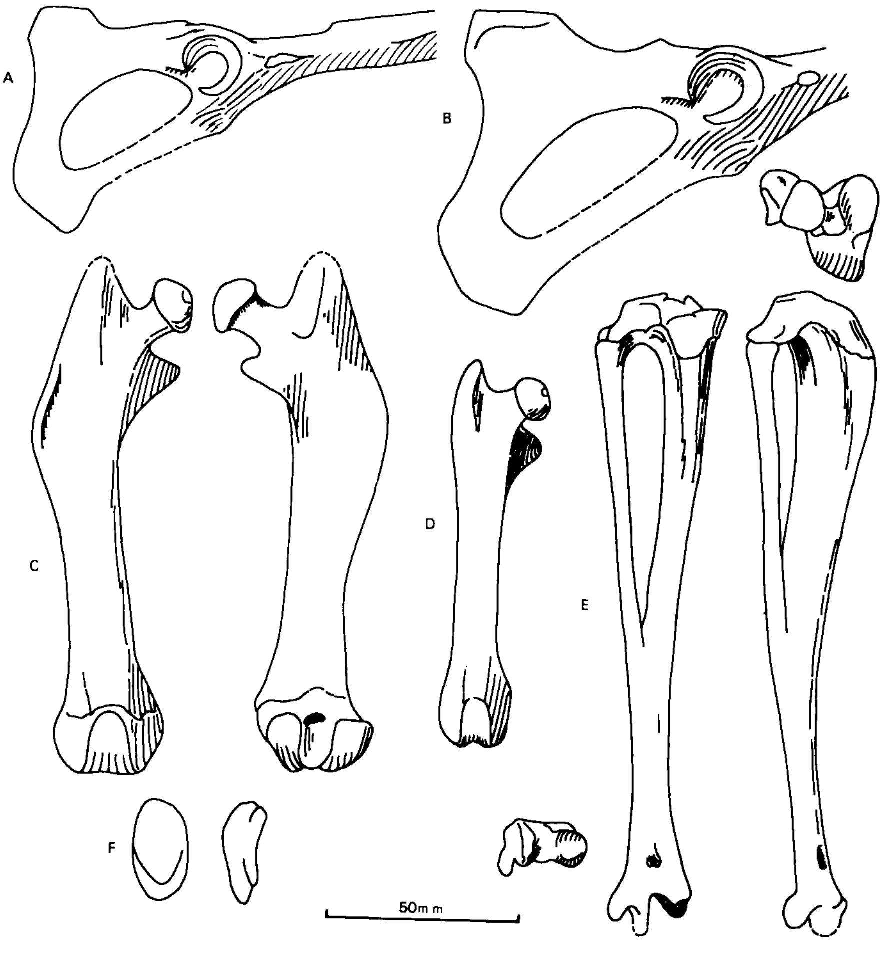


Fig. 13. Right pelvis and hind limb; A: pelvis, based on RGM 177 839 and 177 840 (holotype of *D. koenigswaldi),* B: pelvis, RGM 179 125; C: femur, RGM 177 919, anterior and posterior views; D: femur, RGM 179 283 *(D. brevirostris),* anterior view; E: tibiofibula, RGM 178 056, anterior, lateral, proximal and distal views; F: patella, RGM 178 057, posterior and lateral views.

more sharply than in *Echinosorex* from the dorsal edge of the ischium, but as in the living form it projects posteriorly, so that the posterior edge of the descending ramus is concave. The pubis is incompletely known. It was directed posteriorly at an angle of about 30° to the ischium, and the obturator fenestra must have been narrow, as in *Echinosorex* rather than *Erinaceus*. Ventral to the acetabulum there is an obtuse prominence of the edge of the pubis, associated with a scar for m. pectineus. The junction of the pubis and ischium is preserved in RGM 179 222 and 179 125. There is no ventral extension of the pubis such as occurs in *Echinosorex,* but the posteroventral extremity of the bone has a roughened surface and was probably incompletely ossified. The symphysis was presumably cartilaginous, as in living erinaceids.

The acetabulum is best preserved in RGM 179 125, 178 018, and 179 315. Its rim is interrupted posterolaterally by the rather wide cotyloid notch. The walls converge inwards rather more than in living erinaceids, so that the floor occupies a smaller proportion of the area. The medial surface of the pelvis, internally to the acetabulum, has a deep concavity for coccygeal muscles as in *Echinosorex;* it is much shallower in *Erinaceus.*

The best preserved examples of the femur are RGM 177 841, the left femur of the holotype, RGM 177 919, a larger specimen from San Giovannino, and RGM 179 283, smaller than the holotype but mature, from San Giovannino Low. RGM 179 316, another large specimen from San Giovannino, is broken at the proximal end. RGM 177 953 (Chiro 6), 179 105 (Pizzicoli 1), 178 203 (Fina H), and 179 286 (Fina D) lack the distal epiphysis; they are similar in size to the holotype. There are also three isolated distal epiphyses and some smaller fragments. One of the epiphyses (RGM 177 842), from the right side, and included in the holotype by Freudenthal (1972), is somewhat smaller than the epiphysis of RGM 177 841, which probably belongs to the femur of another individual.

The femur is a little longer than the humerus, as in *Echinosorex;* in *Erinaceus* the two bones are of equal length or the femur is slightly the shorter. The femur is relatively broader and thicker in *Deinogalerix* than in *Echinosorex,* but it is not flattened as in *Erinaceus.* The head is proportionately larger than in *Echinosorex.* In agreement with *Echinosorex* rather than *Erinaceus,* the neck is comparatively slender, the trochanteric fossa is deep, and the greater trochanter projects proximally beyond the head. The third trochanter has the form of a crest that reaches to about halfway down the bone. This crest is particularly prominent in the large specimen RGM 177 919 and probably increases with age. The trochlea for the patella is narrower than in *Erinaceus,* resembling *Echinosorex.* It seems that fusion of the distal epiphysis takes place rather late in life, for in most specimens the epiphysis is either unfused or missing. The suture is still visible in the two large femurs from San Giovannino (RGM 177 919, 179 316); only in the small specimen (RGM 179 283) is the union complete.

There are four examples of the patella: the pair from the holotype (RGM 177 843 - 844), a large specimen (RGM 178 057) that would fit the femur RGM 177 919, and one of intermediate size (RGM 179 250). All are from San Giovannino. The patella is more elongated proximodistally than in the living genera. It tapers at the distal end, where it extends beyond the articular facet.

Both tibiofibulae of the holotype are well preserved (RGM 177 845 - 846), and there is also a complete and larger example from San Giovannino (RGM 178 056). Despite its large size, this specimen has the proximal epiphysis unfused; an equally large isolated epiphysis (RGM 179 236) was found in the same fissure. Eight more specimens, from various localities, show only the distal portion; several of them are smaller than the holotype. The tibiofibula is more elongated than in *Erinaceus* and differs little from *Echinosorex.* The anterior tibial crest is less sharp than in *Echinosorex,* and it is gradually reduced in prominence towards its distal end, instead of ending abruptly. The groove for m. tibialis anterior is correspondingly less deep. In these respects *Deinogalerix* resembles *Erinaceus.* The groove in the lateral malleolus for the peroneal tendons is deep; laterally to the groove there is a flattened, posteriorly projecting, semicircular process, much weaker in *Erinaceus.* The processes of the tibia that overhang the astragalus anteriorly and posteriorly are also better developed than in *Erinaceus.* On the other hand, the medial malleolus resembles *Erinaceus* rather than *Echinosorex:* it is weaker, and the groove on its posterior side for flexor tendons is faint.

The following bones of the pes belong to the holotype: astragalus and calcaneum from both sides, right navicular, mesocuneiform and metatarsals II and V, left metatarsal III, and a middle phalanx (RGM 177 847 - 855, 177 872). Most important is an almost complete articulated left pes from San Giovannino (RGM 177 885 - 907), the bones of which are a little smaller than those of the holotype. There are also a number of isolated bones from various fissures: two astragali (San Giovannino Low, Chiro 11 B), calcanea (San Giovannino, Chiro 24, Chiro 20 D, Chiro 28, Biancone 1), two cuboids (Rinascita 1, Biancone 1), two MT II (Rinascita 1, Biancone 1), five basal phalanges (Biancone 1, Cantatore 3 A), and three middle phalanges (Rinascita 1). The bones from Biancone 1 and Rinascita 1 are only about 60% as long as those of the holotype.

The astragalus (talus) is very similar to that of *Echinosorex.* It differs from *Erinaceus* in the proportionately longer neck, which projects medially beyond the head, and also in the deeper groove and the more prominent lateral keel of the trochlea. The astragalar foramen is well developed. The calcaneum also resembles that of *Echinosorex* rather than *Erinaceus,* in which it is less elongated. Near the dorsal edge of the tuber, proximal to the thalamic facet, is a small facet for the fibula, absent in *Erinaceus.* On the lateral side of the distal end a ridge-like peroneal tubercle projects beyond the cuboid contact; this tubercle is rudimentary in *Erinaceus.* The articulated foot shows that the calcaneum almost touches the proximolateral corner of the navicular, but no facets can be seen on the bones; the calcaneum and navicular are well separated in living erinaceids.

The distal ends of the astragalus and calcaneum are nearly at the same level, as in *Erinaceus.* In *Echinosorex,* however, the calcaneum reaches more distally, and as a result the cuboid is situated more distally in relation to the navicular, reducing the contact between them. The cuboid facet on the navicular of *Echinosorex* is at the end of a lateral process; in *Deinogalerix* and *Erinaceus* it is situated directly on the body of the bone. In all three genera the proximal surface of the navicular is occupied by a concave facet for the astragalus that extends onto a plantar process on the medial side (broken off from the navicular of the articulated foot). The medial plantar process forms the medial wall of a groove for flexor tendons, and in *Deinogalerix,* but not in *Echinosorex* or *Erinaceus,* the groove is partly enclosed by a hook at the tip of the process. The lateral wall of the groove is formed by a lateral plantar process, which in *Deinogalerix* and *Echinosorex* is elongated proximodistally and projects distally beyond the facets for the meso- and ectocuneiforms; in *Erinaceus* it is hemispherical.

The entocuneiform is a flattened, elongated bone which articulates with the medioplantar surface of the navicular. It resembles *Echinosorex* in being much longer proximodistally than in *Erinaceus.* The mesocuneiform is a small, laterally flattened, quadrate bone, relatively somewhat shorter than in *Echinosorex* but not as short as in *Erinaceus.* The ectocuneiform is laterally flattened, trapezoidal in lateral view, and similar in proportions to *Echinosorex;* it is much longer than in *Erinaceus.* It widens distally, where a slightly convex facet for MT II occupies about half of the medial side. Near the proximal end there is a dorsomedial prominence for a ligament to the mesocuneiform, more strongly developed than in *Echinosorex.* On the lateral side, proximal and distal facets articulate with the cuboid.

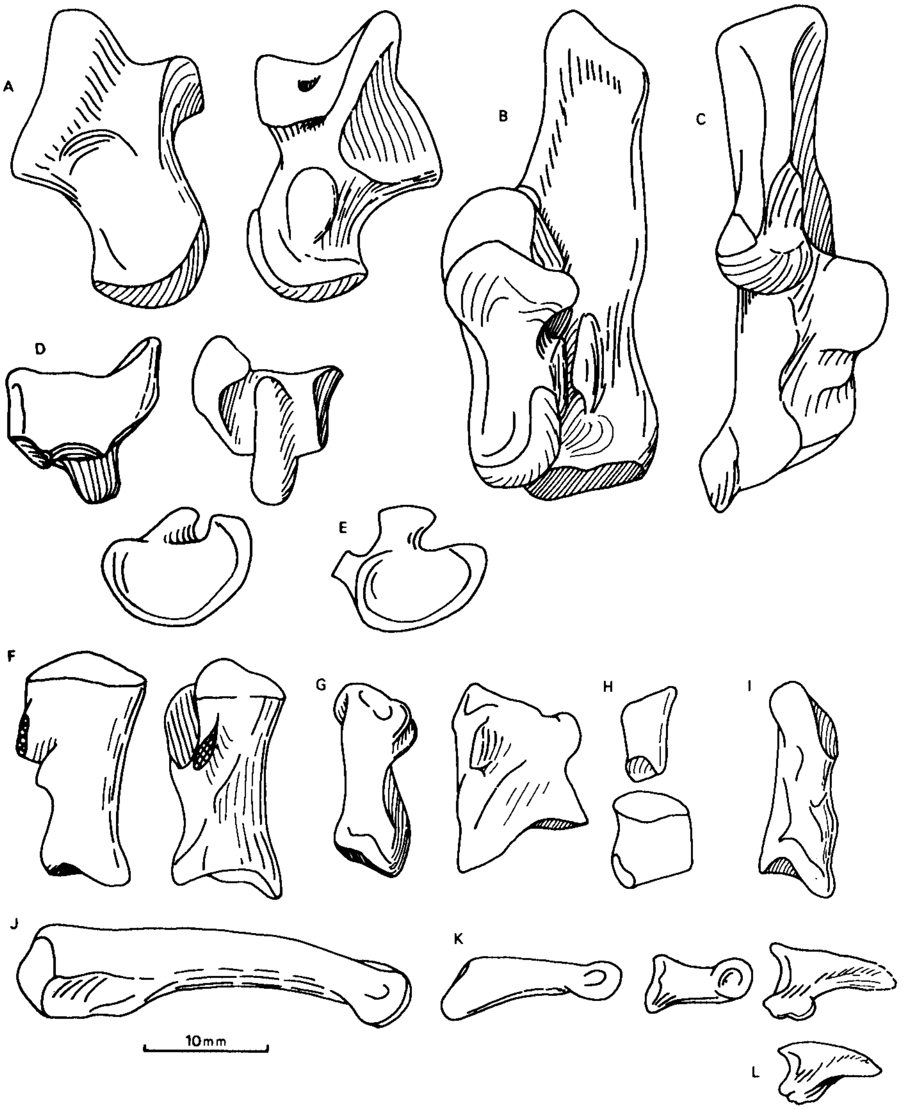


Fig. 14. Bones of right pes of *D. koenigswaldi;* A: astragalus, RGM 177 848 (holotype); B: astragalus, RGM 177 848, articulated with calcaneum, RGM 177 850 (holotype); C: calcaneum, RGM 177 850 (holotype), dorsal view; D: navicular, RGM 177 851 (holotype), dorsal, plantar and proximal views; E: navicular of *Echinosorex,* proximal view, for comparison; F: cuboid, RGM 177 899 (reversed), lateral and plantar views; G: ectocuneiform, RGM 177 890 (reversed), dorsal and medial views; H: mesocuneiform, RGM 177 854 (holotype), dorsal and lateral views; I: entocuneiform, RGM 177 888 (reversed), medial view; J: metatarsal II, RGM 177 895; K: phalanges of toe II, RGM 177 897, 901 and 904; L: ungual phalanx of toe IV, RGM 177 905.

The cuboid again resembles *Echinosorex,* differing only in the more extensive facet for the navicular on the proximal part of the medial side. Proximally on the plantar surface there is a deep concavity between a lateral and a medial crest. In *Erinaceus* the cuboid is relatively much shorter.

Metatarsals II to IV are shorter in proportion to their width than in *Echinosorex,* and more thickened in a dorsoplantar direction near their proximal ends. MT V is longer in proportion to the other metatarsals than in *Echinosorex,* being equal in length to MT II; its distal end is more nearly in line with MT III and IV. Of the three middle metatarsals, MT II is the longest and MT III the shortest, as in *Echinosorex.* In *Erinaceus* MT II - IV are of similar length and MT V is shorter. In the holotype skeleton MT II and MT III are similar in length to the corresponding metacarpals, but they are more slender towards their distal ends and have smaller distal joint surfaces. This is also true of *Erinaceus;* in *Echinosorex* the metatarsals are much longer than the metacarpals and the distal joint surfaces are of similar size on fore and hind feet.

MT I (RGM 177 892) is particularly short, with a length comparable with those of the basal phalanges of the other digits and only 26% of the length of MT II. Its dorsal surface bears prominent ridges for the insertion of ligaments.

Like the metatarsals, the basal phalanges of digits II - V are less elongated than in *Echinosorex* but less shortened than in *Erinaceus.* Those of digits II - IV are nearly equal in length, and that of V is somewhat shorter, as in the living erinaceids. The phalanges of the pes are similar in length to those of the manus, but more slender. In this they resemble *Erinaceus;* in *Echinosorex* phalanges of the manus and pes are almost indistinguishable. The basal phalanx of digit I (RGM 177 903) is much reduced in size. It resembles the middle phalanges of the other digits but is smaller, being only about half as long.

The middle phalanges of the pes are relatively shorter and broader than in *Echinosorex,* resembling *Erinaceus.* They are narrower than those of the manus. Two ungual phalanges are preserved from the articulated foot; one belongs to digit II, the other, which has a smaller claw, probably to digit V. In *Echinosorex* and *Erinaceus* the claw on digit V is smaller than those on digits II - IV. The claws are very similar to those of the manus, as in *Erinaceus;* in *Echinosorex* the claws of the pes are larger.

Five sesamoids were found in association with the articulated foot. Three are of a size and shape to have belonged to metatarsal-phalangeal joints. Two others were found on the plantar side of the ectocuneiform. In *Echinosorex* there is a small sesamoid associated with the joint between the entocuneiform and MT I, and a larger one near the base of MT V.

BODY PROPORTIONS

Measurements of the holotype skeleton were compared with corresponding measurements made on a complete skeleton of *Echinosorex gymnurus* (BMNH 67.1480), and expressed as a ratio *Deinogalerix/Echinosorex.* A reconstruction figured by Freudenthal (1972, pl. 6) shows an animal with a relatively large head and short trunk.

The ratio of skull lengths is 2.6. The greatest difference is in the length of the snout anterior to P^3 and the corresponding part of the mandible (ratio 3.9). The posterior part of the cranial base, posterior to the foramen ovale, is relatively less lengthened (ratio 2.1), and the width of the skull, measured across the palate or across the mastoid processes, is in a similar proportion (2.2). Least enlarged is the posterior part of the dentition: the total length of the lower molars has a ratio of only 1.6.

The widths across the atlas (2.1) and across the atlantoid surface of the axis (2.2) are in proportion with the posterior part of the skull, but the axis centrum is relatively short (1.8). The remaining cervical vertebrae are still shorter: when the cervical centra are put together their total length has a ratio of only 1.3. Thus the neck is only half as long, in comparison with the skull, as in *Echinosorex*. At the same time the cervical centra are relatively broad (ratio 2.8).

Shortening affects also the trunk vertebrae. The series of three thoracics, when compared with Th 3 - 5 of *Echinosorex*, have a ratio of 1.3. Farther back the ratios are somewhat larger: lengths of the series of eight, compared with Th 4 - 11 of *Echinosorex*, reach 1.6, and for the three lumbars, compared with L 1 - 3 of *Echinosorex*, the ratio is 1.5. Centrum widths remain at 2.8 throughout the series. Assuming that the vertebral formula of *Deinogalerix* was the same as in *Echinosorex*, the total length of the thoracolumbar vertebrae is estimated to be 20 cm.

The sacrum of the holotype has not been found, but RGM 179 294 appears to come from an individual of about the same size. In this specimen the length of the first two sacral vertebrae has a ratio of 1.5, and the length of the articulatory surface for the ilium has a ratio of 1.7. Width across the sacroiliac joints is estimated to have a ratio of 1.9. Anteroposterior measurements of the incompletely preserved pelvis give ratios of 1.9, but the ilium may have been shorter, in accordance with the sacrum. The distance between the skull and the acetabulum is estimated at 32 cm, in agreement with Freudenthal (1972). The total length of head and body, measured to the ischial tuberosity, was about 56 cm.

Lengths of caudal vertebrae, when compared with those of *Echinosorex* that they most resemble, have ratios of 1.5 - 1.7; their centra are proportionately wider (1.9 - 2.2). If the number of caudals was similar to that of *Echinosorex*, the tail length would be about 20 cm, but the vertebral number may have been less.

The ratio of clavicle length is 1.9. Of the scapula, only the region of the head is known in the holotype; its maximum diameter has a ratio of 2.3. The only complete scapula (RGM 179 285) is larger; if scaled down to the size of the holotype its length ratio, compared with *Echinosorex*, would be 2.2. The length of the humerus has a ratio of 2.0, but its distal end is relatively broader (ratio 2.6). The ulna (2.3) and radius (2.4) are longer in proportion to the humerus than in *Echinosorex*. The manus is broad like the humerus: the width of the basal row of carpals, and the combined width of the bases of metacarpals II - IV, gave ratios of 2.5 and 2.6 respectively. The digits are shorter: length of third metacarpal 1.8, length of the phalanges of the third digit 2.0.

In the hind limb the femur has the same length ratio as the humerus (2.0). The tibia is not lengthened as much as the bones of the forearm, but bears the same proportion to the femur as in *Echinosorex* (ratio 2.0). The tarsus is relatively longer, as is shown by ratios for calcaneum length (2.4) and astragalus length (2.5) in the holotype, and by the calculated length of the whole tarsus based on the articulated foot (2.3). The digits are relatively shorter than those of the manus (1.5 - 1.6). The pes is not broadened like the manus: ratios calculated from the articulated foot ranged from 1.9 to 2.2.

Most of the ratios fall in the range 1.9 - 2.2. Below this range are the lengths of the vertebrae, of the molar teeth and of the digits of the pes. Above

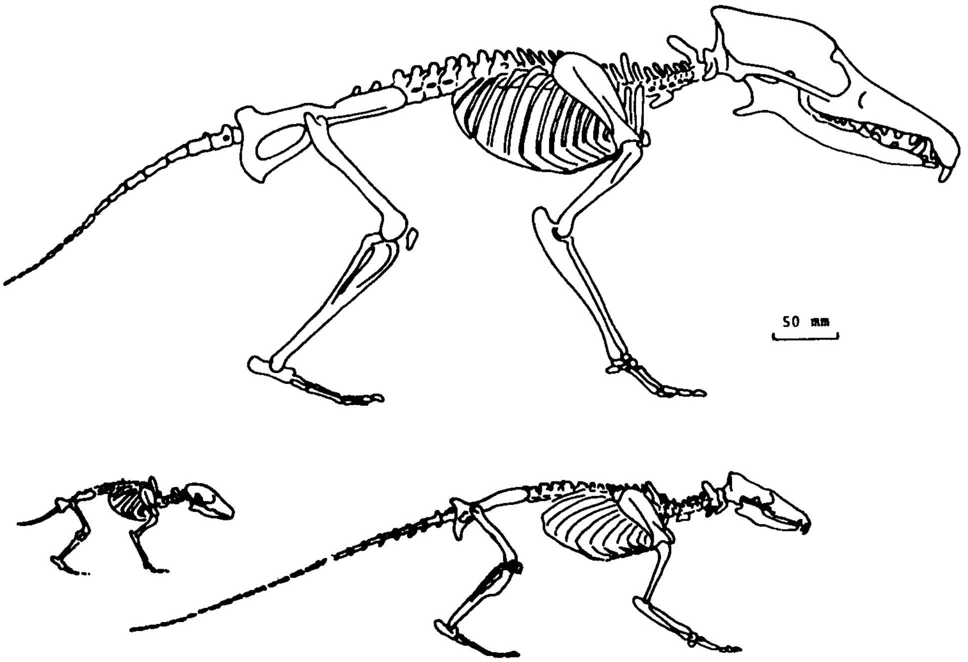


Fig. 15. Reconstruction of holotype skeleton, *D. koenigswaldi,* compared with *Hylomys suillus,* BMNH 1960.8.4.7, and *Echinosorex gymnurus,* BMNH 67.1480, drawn to the same scale.

it are the length of the snout, and the width of the vertebral centra, the manus and the distal end of the humerus. The humerus, femur and tibia, though long in proportion to body length, are median in relation to the ratios as a whole: the forearm however is longer.

The specimen of *Echinosorex* used in the comparison had a head and body length of 36 cm and weighed 867 g. Assuming that the head and body length of *Deinogalerix* was 56 cm, and that its transverse measurements were twice those of *Echinosorex,* the weight may be calculated as $867 \times \frac{56}{36} \times 2^2 =$ approximately 5.4 kg.

The holotype, on which this calculation is based, is regarded as a subadult female. Larger postcranial bones probably represent males, like the large skulls and mandibles. Most measurements of these large specimens fall into the range of 107 - 122% of those of the holotype, but the lengths of vertebral centra and of the ischium are greater, in the range 125 - 135%. It would appear that in large individuals the body was proportionately less shortened. The short body of the holotype may be partly due to immaturity, but not entirely so, for even in the large individuals the vertebrae are shorter, compared with the limbs and skull, than in *Echinosorex.* If it is supposed that in an adult male the body length was 30% greater and other measurements 15% greater than in the holotype, the body weight can be estimated to have been about 9 kg.

Speciation

The numerous fissures in which *Deinogalerix* has been found can be put into chronological order only on the basis of their fossil content. Ballman (1973) arranged the deposits according to the presence or absence of birds of prey; Freudenthal (1976) used the evolution of rodent teeth, especially of *Microtia,* to produce a more detailed sequence. *Deinogalerix* is of limited value in this respect, because of the small number of specimens obtained from most of the fissures, and the wide variation in size of specimens from the same fissure.

Only San Giovannino has yielded a large enough sample to allow conclusions on population variability. A minimum of 11 individuals is represented. Most material is referred to *D. koenigswaldi,* variation being ascribed mainly to sexual dimorphism and differences of individual age. There are however some specimens, including a skull, which indicate the presence of a smaller species with a shorter snout. San Giovannino Low, 5 m lower in the same fissure, has produced the remains of at least four individuals. Three of these fall into the range of *D. koenigswaldi,* but a femur and a fragment of mandible with the last two molars represent the smaller form.

San Giovannino is the youngest fissure deposit that contains *Deinogalerix.* There is evidence of the presence of two species, of different sizes, in some of the earlier deposits. From Gervasio and Fina H there are mandibles and postcranial bones that average only 75% of the size of the holotype of *D. koenigswaldi,* and are thus somewhat smaller than the small specimens from San Giovannino. Other specimens from the same and other fissures are larger, averaging about 93% of the holotype, and having a range of variation that overlaps with *D. koenigswaldi* from San Giovannino. Thus there appear to be two lineages. The larger species was present as far back as Fina D, evidenced by a femur within the range of *D. koenigswaldi,* and at a still earlier date this lineage is represented by a phalanx from Cantatore 3A and a caudal vertebra from Trefossi 1. However, at Rinascita 1 and Biancone 1, the oldest deposits, all the specimens are small.

Five species are distinguished: *D. freudenthali* is the small and probably ancestral form from Biancone 1; small specimens from later deposits (Fina H to Chiro 20) are called *D. minor,* and the larger specimens *D. intermedius;* most material from San Giovannino represents *D. koenigswaldi,* but the smaller specimens are called *D. brevirostris. D. intermedius* is clearly ancestral to *D. koenigswaldi.*

Owing to the fragmentary nature of the material, specific identification has to depend mainly on size. There appears to have been little if any increase of size in *D. minor* and *D. intermedius* in the time interval between Fina D and Chiro 20, but a rather rapid enlargement ensued between Chiro 20 and San Giovannino. As a result, *D. brevirostris* overlaps in size with *D. intermedius.* It is assumed that *D. brevirostris* was derived from *D. minor* and not from *D. intermedius* because (1) there is no indication of bimodality in *D. intermedius,* such as might be expected if it was giving rise to the two San Giovannino species, and (2) the spacing of its postcanine teeth, where known, is greater than in *D. brevirostris,* implying that *D. intermedius* was more advanced in the direction of *D. koenigswaldi. D. minor* may prove to be synonymous with *D. freudenthali,* with which it agrees in size, but it is known mainly from jaws and

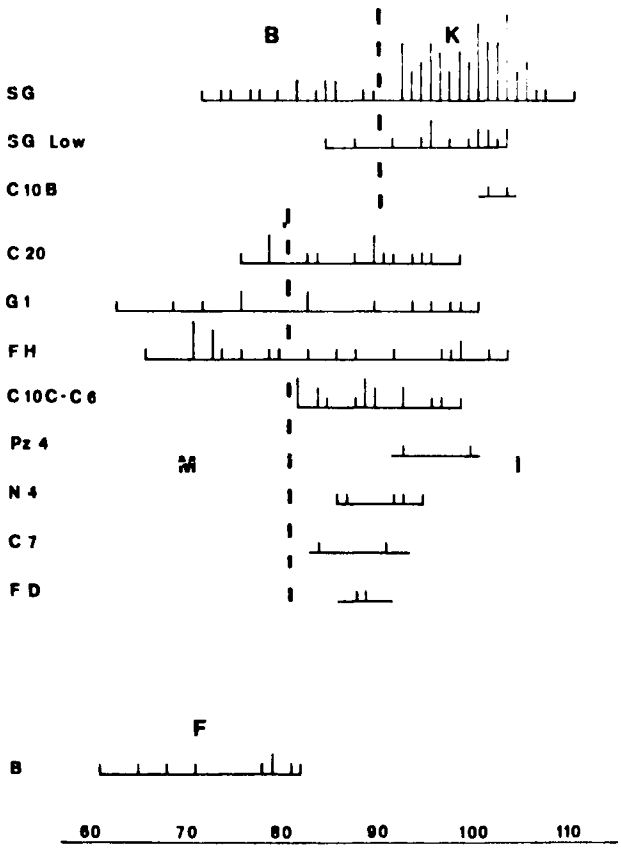


Fig. 16. Distribution of measurements of P^3_3 - M^3_3, expressed as percentages of the means of *D. koenigswaldi* from San Giovannino. Deposits arranged in time sequence according to Freudenthal (1976). C 10C - C 6 includes C 14A, C 9, C 29, C 5A, and Po 1B.
B = *D. brevirostris*, K = *D. koenigswaldi*, M = *D. minor*, I = *D. intermedius*, F = *D. freudenthali*.

lower teeth, whereas *D. freudenthali* is based on upper teeth, so that the two species cannot be directly compared.

TAXONOMY AND LIST OF SPECIMENS

Family ERINACEIDAE Fischer von Waldheim, 1817
Subfamily GALERICINAE Pomel, 1948

Genus *Deinogalerix* Freudenthal, 1972

Revised diagnosis — Galericinae which differ from *Echinosorex* as follows: (1) size greater (linear dimensions of adults about 1.5 times to more than twice those of *Echinosorex)*; (2) I^1 much larger than I^2 and I^3, I_3 absent; (3) upper canine premolariform, with two roots like P^1, P^2 and P_2; (4) C^1_1 — P^3_3 spaced in the larger species; (5) P^3_3, P^4_4 and the trigonid of M_1 enlarged, posterior molars reduced; (6) postglenoid part of skull shorter, face longer (especially in the

larger species); (7) mandible with small coronoid process, low condyle and a long angular process with a strong medial flange; (8) vertebral centra comparatively short and broad; (9) manus relatively broader, digits less unequal in length.
Type species — *Deinogalerix koenigswaldi* Freudenthal, 1972.

Deinogalerix freudenthali sp. nov.

Diagnosis — Much smaller than *D. koenigswaldi;* M^1 (holotype) measures 7.7 mm in buccal length and 9.8 mm in anterior width. It also differs from *D. koenigswaldi* as follows: hypocone of P^4 not divided; posterobuccal corner of P^4 less extended, so that the buccal edge of P^4 is shorter relatively to M^1; posterior cingulum of M^1 and M^2 interrupted in some specimens by the posterior crest of the metaconule; M^3 less reduced in size in comparison with M^1.
Holotype — RGM 178 100, unerupted right M^1, from Biancone 1, Gargano (prov. Foggia, Italy).
Paratypes — RGM 178 101, unerupted left P^4; RGM 178 098, lightly worn right M^2; RGM 178 104, unerupted left M^3. All are from Biancone 1, and probably belong to one individual.

Age — Biancone 1 is the oldest of the Late Miocene Gargano fissures (Freudenthal, 1976). Material referred to this species is also found in Rinascita 1, later than Biancone 1 but in the early part of the sequence.

Additional specimens

RGM 178 102	Biancone 1	Buccal part of an unerupted left M^2
RGM 178 106	,,	Unerupted right M^2; probably belongs to the same individual as the holotype
RGM 178 108	,,	A lightly worn left M^1 (in two pieces); is probably from a second individual, to which belong the M^2 and M^3 listed as paratypes
RGM 178 105	,,	Unerupted P^2
RGM 178 107	,,	A worn two-rooted upper tooth, possibly a milk canine
RGM 178 096	,,	Fragment of an unworn lower molar
RGM 178 103	,,	Trigonid of unerupted left P$_4$
RGM 179 109	,,	Tip of a developing lower canine
		(All these teeth probably belong to two juvenile individuals)
RGM 178 095	,,	Centrum of axis
RGM 178 116	,,	,, ,,
RGM 178 121	,,	,, ,,
RGM 178 128	,,	Centrum of a more posterior cervical vertebra
RGM 178 129	,,	Thoracic vertebra
RGM 178 113	,,	Caudal vertebra
RGM 178 123	,,	,, ,,
RGM 178 125	,,	,, ,,
RGM 178 127	,,	,, ,,
RGM 178 130	,,	,, ,,
RGM 178 134	,,	,, ,,
RGM 178 117	,,	Part of a rib
RGM 178 122	,,	Fragment of humerus
RGM 178 111	,,	Proximal part of radius
RGM 178 119	,,	Metacarpal II
RGM 178 118	,,	Metacarpal III
RGM 178 131	,,	Distal end of metacarpal ? IV
RGM 178 137	,,	Metacarpal V
RGM 178 112	,,	Calcaneum
RGM 178 124	,,	Cuboid
RGM 178 120	,,	Metatarsal II
RGM 178 133	,,	Basal phalanx of pes
RGM 178 135	,,	,, ,, ,,

RGM 178 136	Biancone 1	Basal phalanx of pes
RGM 178 138	,,	,, ,, ,,

Measurements of these bones are in the range 50 - 70% of the corresponding measurements of the holotype of *D. koenigswaldi,* with a median of 60%. This is less than the relative size of teeth from Biancone 1, which are in the range of 65% (P^4) to 91% (M^3). The disproportion may be ascribed to the juvenile condition of the individuals from which most of the bones have probably come.

RGM 178 160	Rinascita 1	Two-rooted tooth, P^1 or C^1
RGM 178 162	,,	,, ,, ,,
RGM 178 158	,,	Unerupted P_1
RGM 178 159	,,	Caudal vertebra
RGM 178 156	,,	Cuboid
RGM 178 155	,,	Metatarsal II
RGM 178 163	,,	Basal phalanx of pes
RGM 178 161	,,	Middle phalanx of pes
RGM 178 165	,,	,, ,, ,,

Deinogalerix minor sp. nov.

Diagnosis — Similar in size to *D. freudenthali;* total length of P_3 - M_3 39 mm in the holotype. Differing from *D. koenigswaldi* in the following characters of the mandible: symphysis relatively shorter; postcanine teeth little spaced; condyle more elevated; anterior edge of coronoid process steeper; angular process more slender, not widened at the tip and less out-turned.
Holotype — RGM 178 184, mandible broken off anteriorly to P_2, and lacking the top of the coronoid process and the tip of the angular process; it contains lightly worn P_2 - M_3. From Fina H.
Paratype — RGM 179 174, mandible, complete anteriorly but lacking the coronoid process and condyle; it contains heavily worn P_3 - M_3. P_2 had been lost during life. From Gervasio.

Age — According to Freudenthal (1976) Fina H is the youngest deposit of the Upper Miocene Gargano series in which Cricetidae have been found. Gervasio is a little younger. Referred specimens have been found in 11 deposits from Fina D to Chiro 24.

Additional specimens — These are referred to *D. minor* mainly because of their small size.

RGM 178 141	Fina D	Premaxilla
RGM 178 005	Chiro 20 E	C^1
RGM 178 014	,,	C^1
RGM 178 007	,,	P^1
RGM 178 016	,,	P^1
RGM 177 957	Chiro 7 A	C^1 or P^1
RGM 179 089	Nazario 4	C^1 or P^1
RGM 178 149	Fina D	DP^3
RGM 179 076	Chiro 14 A	M^2
RGM 179 175	Gervasio quarry	Mandible fragment with alveoli of C_1 - P_2
RGM 178 148	Fina D	P_2
RGM 178 199	Fina H	P_3
RGM 178 010	Chiro 20 E	M_2
RGM 179 296	Chiro 28 A	Atlas
RGM 179 072	Chiro 24	Lumbar vertebra
RGM 178 192	Fina H	Ulna
RGM 179 177	Gervasio quarry	Ulna
RGM 177 979	Chiro 20 A	Ulna
RGM 179 178	Gervasio quarry	Tibiofibula
RGM 179 184	,,	,,

RGM 179 292	Fina East Wall	Tibiofibula
RGM 177 972	Chiro 11 B	Astragalus
RGM 177 295	Chiro 28 A	Calcaneum

Deinogalerix brevirostris sp. nov.

Diagnosis — Smaller than *D. koenigswaldi* but a little larger than *D. freudenthali* and *D. minor;* P^3 - M^3 of holotype 39 mm, M^1 of holotype 8.5 × 11.5 mm, P_3 - M_3 of paratype 43 mm. Differs from *D. koenigswaldi* in that the face is much shorter, postcanine teeth much less spaced and sagittal crest is lower.
Holotype — RGM 179 134, skull lacking premaxilla, from San Giovannino, Gargano, prov. Foggia, Italy.
Paratypes — RGM 179 232, mandible, incomplete posteriorly, with P_3, P_4, talonid of M_1, M_2, teeth worn; RGM 179 237, premaxilla with I^1. Both are from San Giovannino.

Age — San Giovannino is the youngest of the Late Miocene deposits of Gargano. Two referred specimens come from San Giovannino Low, 5 m lower in the same fissure.

Additional specimens

RGM 179 245	San Giovannino	Maxillary fragment with P^4
RGM 179 256	,,	M^1
RGM 179 141	,,	Atlas
RGM 179 283	San Giovannino Low	Femur
RGM 179 217	,,	Mandible fragment with M_2 and M_3

Deinogalerix intermedius sp. nov.

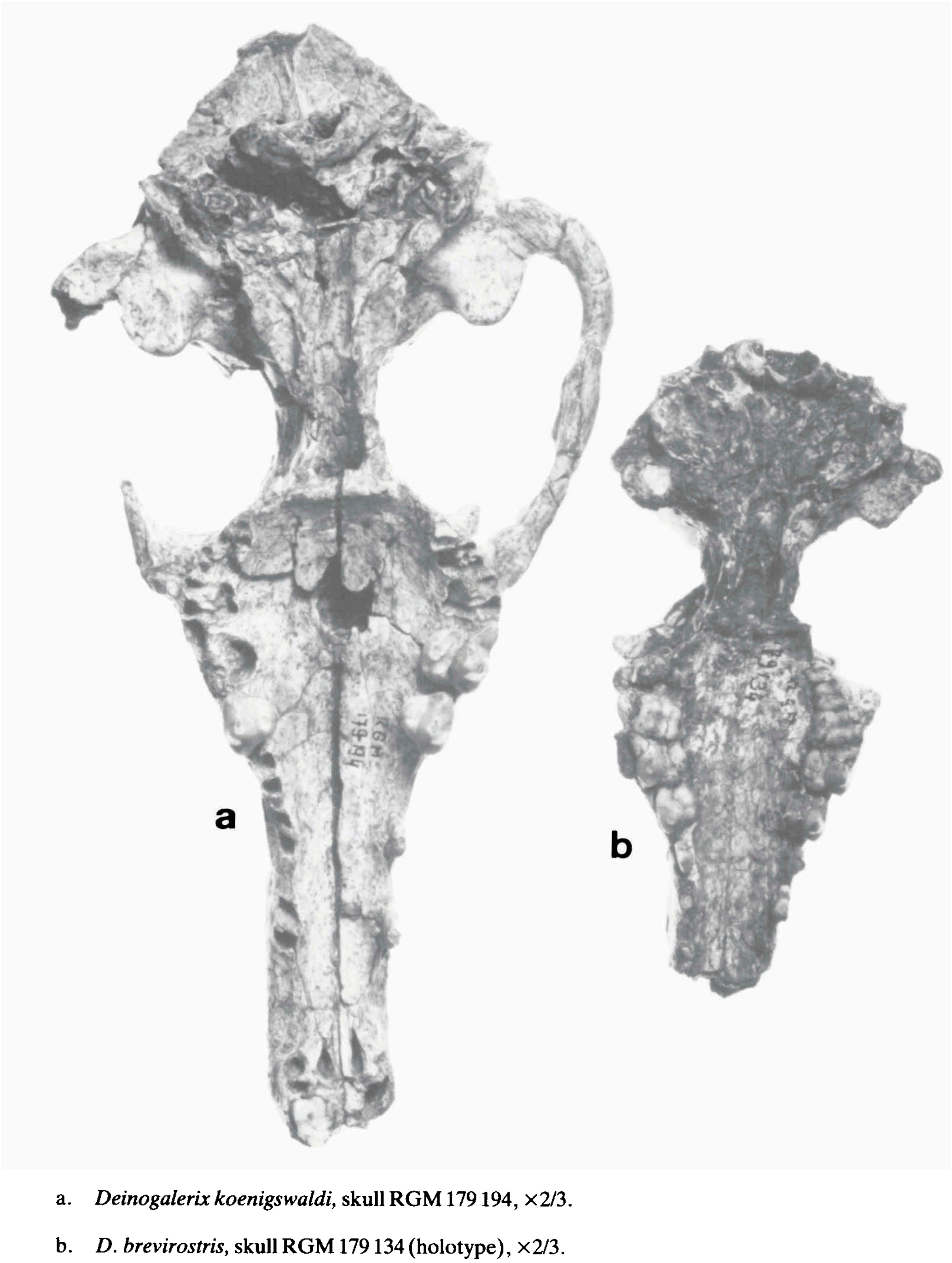
Diagnosis — Intermediate in size between *D. brevirostris* and *D. koenigswaldi;* M_3 - P_3 of holotype (measured on alveoli) 46 mm, M^1 of paratype 9.0 × 11.7 mm. Spacing of postcanine teeth greater than in *D. brevirostris* but less than in *D. koenigswaldi;* angular process less thickened distally and less out-turned than in *D. koenigswaldi.*
Holotype — RGM 179 063, mandible with P_3 - M_1, broken beyond the P_1 alveolus and lacking the coronoid process. From Nazario 4.
Paratype — RGM 177 982, maxilla with worn P^3 - M^2, from Chiro 20 C.

Age — Specimens placed in this species were found at 28 locations, of which the oldest is Trefossi 1 and the youngest is Chiro 24. The species was therefore contemporary with *D. minor.*

Additional specimens

RGM 177 981	Chiro 20 B	Premaxilla
RGM 177 997	Chiro 20 D	,,
RGM 178 091	M. Granata 1	I^1
RGM 178 144	Fina D	I^1, crown broken
RGM 178 089	M. Granata 1	Maxillary fragment with alveoli of P^1
RGM 178 208	Pepo 1 A	Maxillary fragment with roots of P^3 and P^4
RGM 177 975	Chiro 18	Maxillary fragment with P^4 - M^1
RGM 177 945	Chiro 5 A	Maxillary fragment with P^3 and P^4
RGM 177 989	Chiro 20 C	P^2
RGM 178 088	WG 348 279	P^2
RGM 177 956	Chiro 6	P^3
RGM 178 083	Pizzicoli 4	P^3
RGM 178 191	Fina H	P^3
RGM 178 004	Chiro 20 E	P^3

Plate 1



a. *Deinogalerix koenigswaldi,* skull RGM 179 194, ×2/3.

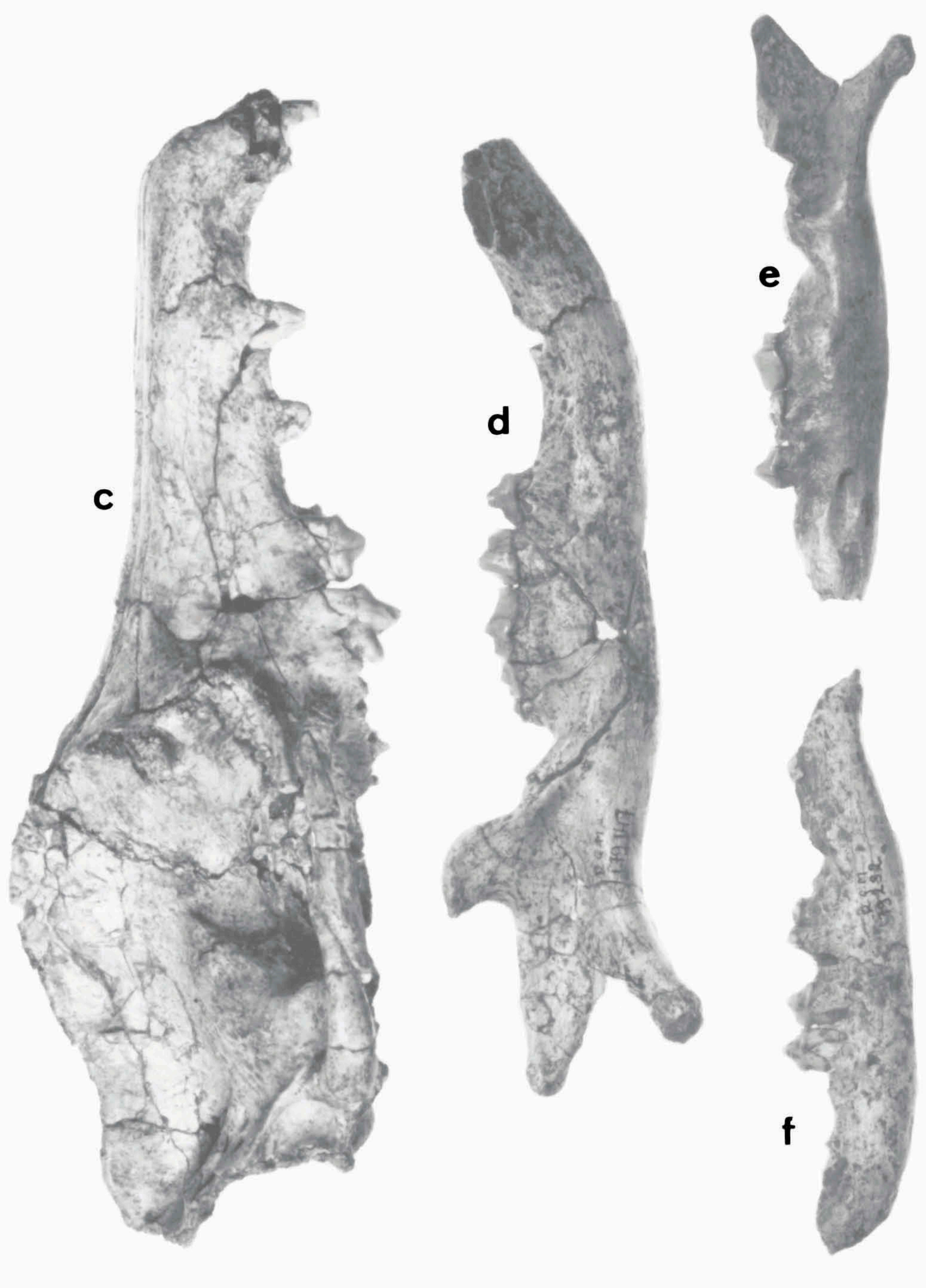
b. *D. brevirostris,* skull RGM 179 134 (holotype), ×2/3.

RGM 178 084	Posticchia 4	P^3
RGM 177 990	Chiro 20 C	M^1
RGM 177 970	Chiro 10 C	M^3
RGM 178 019	Chiro 20 E	Mandible fragment with P_2
RGM 178 205	Posticchia 1 B	Mandible fragment with alveoli of P_2 and P_1
RGM 177 947	Chiro 5 A	Broken C_1
RGM 178 023	Chiro 20 E	C_1
RGM 179 170	Gervasio quarry	Mandible with P_4 - M_3
RGM 178 204	Posticchia 1 B	Mandible with P_4 - M_3
RGM 179 093	Fina H	Mandible with P_4 - M_2
RGM 179 092	,,	Mandible with M_1 - M_3
RGM 179 079	Chiro 25	Mandible fragment with P_4
RGM 179 287	Chiro 29	Mandible fragment with M_1
RGM 178 087	Fina A/N	I_2
RGM 179 104	Fina H	P_3
RGM 178 009	Chiro 20 E	P_3
RGM 178 013	,,	P_3
RGM 177 967	Chiro 9	P_3
RGM 178 085	WG 354 294	P_3
RGM 177 968	Chiro 10 B	P_4
RGM 178 086	WG 354 294	P_4
RGM 177 959	Chiro 7 C	M_1
RGM 178 190	Fina H	M_1 fragment
RGM 177 974	Chiro 17	M_2
RGM 177 952	Chiro 5 A	M_2
RGM 178 150	Fina D	M_2
RGM 177 961	Chiro 11 A	Axis
RGM 177 976	Chiro 20 A	6th cervical vertebra
RGM 179 081	Trefossi 1	Centrum of cervical vertebra
RGM 179 064	Chiro 24	Lumbar vertebra
RGM 179 294	Chiro 28 A	Sacrum
RGM 179 082	Trefossi 1'	caudal vertebra
RGM 179 301	Chiro quarry	Humerus
RGM 178 195	Fina H	Humerus, distal end
RGM 178 188	Fina H	Ulna
RGM 179 176	Gervasio quarry	Ulna
RGM 178 018	Chiro 20 E	Pelvis
RGM 177 942	Chiro 3	Pelvis (ischium)
RGM 179 300	Nazario 4	Epiphysis of femur
RGM 177 941	Chiro 3	,,
RGM 177 953	Chiro 6	Femur
RGM 179 286	Fina D	,,
RGM 179 105	Pizzicoli 1	,,
RGM 178 198	Fina H	,,
RGM 178 203	,,	,,
RGM 178 200	,,	Head of femur
RGM 177 991	Chiro 20 C	,,
RGM 179 304	Nazario 4	Tibiofibula
RGM 179 182	Gervasio quarry	,,
RGM 179 183	,,	,,
RGM 177 994	Chiro 20 D	Calcaneum
RGM 179 065	Chiro 24	,,
RGM 179 090	Cantatore 3 A	Basal phalanx of pes

Deinogalerix koenigswaldi Freudenthal, 1972

Revised diagnosis — The largest species of the genus: in the holotype P^3 - M^3 = 45 mm, M^1 measures 10.0 × 12.7 mm, and P_3 - M_3 = 53 mm. Face anterior to P^3 and symphyseal part of mandible markedly lengthened; teeth between the canines and third premolars widely spaced; angular pro-

Plate 2



Deinogalerix koenigswaldi
c. Skull RGM 179 194, × 2/3.
d. Mandible RGM 179 147, × 2/3.

D. intermedius
e. Mandible RGM 179 063 (holotype), × 2/3.

D. brevirostris
f. Mandible RGM 179 232 (paratype), × 2/3.

cess enlarged at its distal end due to the deposition of bone on its ventral surface, and projecting laterally, markedly out of plane from the rest of the jaw.

Holotype — Specimens listed by Freudenthal (1972), nearly all representing a single individual. Exception however must be made of RGM 177 826 (a sternebra) which probably does not belong to this genus.

Age — This species is confined to San Giovannino and San Giovannino Low, the youngest of the Late Miocene deposits of Gargano in which *Deinogalerix* has been found. It was contemporary with *D. brevirostris.*

Additional specimens

RGM 177 918	San Giovannino	Skull
RGM 179 146	,,	,,
RGM 179 192	,,	,,
RGM 179 194	,,	,,
RGM 179 155	,,	Posterior part of skull
RGM 178 025	,,	Maxilla with broken P^3 and P^4
RGM 179 229	,,	I^1
RGM 179 230	,,	I^1
RGM 179 231	,,	I^1
RGM 179 311	,,	I^1
RGM 179 120	,,	I^2
RGM 179 121	,,	P^2
RGM 179 145	,,	Mandible
RGM 179 147	,,	,,
RGM 179 148	,,	,,
RGM 179 149	,,	,,
RGM 179 193	,,	,,
RGM 179 224	,,	,,
RGM 179 153	,,	Posterior part of mandible
RGM 179 154	,,	,, ,, ,,
RGM 179 242	,,	Fragment of mandible with unerupted premolars
RGM 179 238	,,	Fragment of mandible with unworn molars
RGM 179 228	,,	I_1
RGM 179 254	,,	I_1
RGM 179 159	,,	C_1
RGM 179 227	,,	C_1
RGM 179 313	,,	P_1

Plate 3

Deinogalerix minor

g. Mandible RGM 179 174 (paratype), × 2/3.
h. Mandible RGM 178 184 (holotype), × 2/3.

D. intermedius

i. Maxillary fragment RGM 177 982 (paratype), natural size.

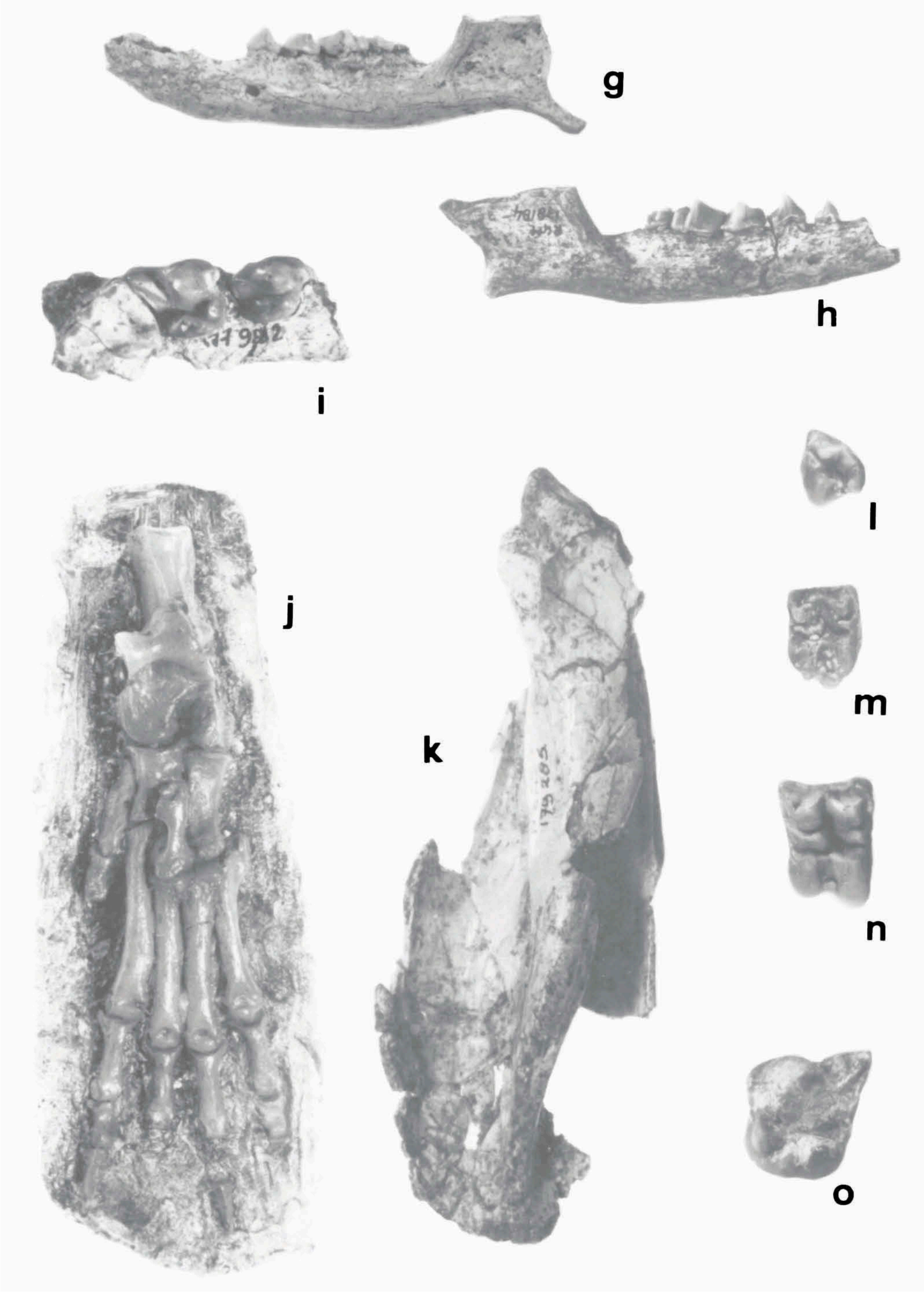
D. koenigswaldi

j. Cast of foot, natural size.
k. Scapula RGM 179 285, natural size.

D. freudenthali

l. M^3 RGM 178 104 (paratype), × 2.
m. M^2 RGM 178 098 (paratype), × 2.
n. M^1 RGM 178 100 (holotype), × 2.
o. P^4 RGM 178 101 (paratype), × 2.

Plate 3



RGM 179 106	San Giovannino	M_1	
RGM 179 302	,,	Axis	
RGM 179 140	,,	Cervical vertebra V	
RGM 179 138	,,	Cervical vertebra VI	
RGM 179 143	,,	Cervical vertebra VII	associated
RGM 179 142	,,	Thoracic vertebra I	
RGM 179 139	,,	Centrum of thoracic vertebra	
RGM 179 144	,,	,, ,, ,,	
RGM 179 135	,,	Posterior thoracic vertebra	
RGM 179 136	,,	,, ,, ,,	associated
RGM 179 137	,,	,, ,, ,,	
RGM 178 049	,,	Sacrum	
RGM 179 246	,,	Caudal vertebra	
RGM 179 247	,,	,, ,,	
RGM 179 248	,,	,, ,,	
RGM 179 285	,,	Scapula	
RGM 179 125	,,	Pelvis	
RGM 179 315	,,	,,	
RGM 177 919	,,	Femur	
RGM 179 316	,,	,,	
RGM 178 057	,,	Patella	
RGM 179 250	,,	,,	
RGM 178 056	,,	Tibiofibula	
RGM 179 236	,,	Epiphysis of tibiofibula	
RGM 177 885/907 RGM 178 073	,,	Bones of a pes, found in articulation	
RGM 179 195	,,	Middle phalanx of pes	
RGM 178 061	,,	Calcaneum	
RGM 178 062	,,	,,	
RGM 178 032	,,	,,	
RGM 179 107	,,	,,	
RGM 179 108	,,	,,	
RGM 179 221	San Giovannino Low	Facial part of skull	
RGM 179 199	,,	Premaxilla	
RGM 260 978	,,	Fragment of maxilla with C^1 and P^1	
RGM 179 268	,,	Fragment of squamosal	
RGM 179 275	,,	Fragment of occipital	
RGM 179 206	,,	Mandible	
RGM 179 260	,,	C_1	
RGM 179 264	,,	C_1	
RGM 179 267	,,	Posterior part of mandible	
RGM 179 220	,,	6th cervical vertebra	
RGM 179 211	,,	Humerus	
RGM 179 269	,,	Ulna	
RGM 179 215	,,	,,	
RGM 179 222	,,	Pelvis	
RGM 179 223	,,	,,	
RGM 179 258	,,	,,	
RGM 179 273	,,	,,	
RGM 179 205	,,	Tibiofibula	
RGM 179 266	,,	,,	
RGM 179 261	,,	Astragalus	

Comparisons and relationships

The subfamily Galericinae (= Echinosoricinae) appears first in the Oligocene of Europe and Asia, with the genera *Neurogymnurus, Tupaiodon* and *Tetracus*. Of these, *Neurogymnurus* was put into a separate subfamily, Neurogymnurinae, by Butler (1948) on account of the specialized structure of the mastoid region of the skull. A rather similar structure is present however in the erinaceine *Gymnurechinus* (Butler, 1956), as well as in the Brachyericinae (Rich & Rich, 1971), which do not show other evidence of relationship to *Neurogymnurus*. The skull of *Parasorex (= 'Galerix') socialis* has been only very superficially described (Fraas, 1870; Schlosser, 1887) and badly needs reexamination; otherwise, with the exception of *Deinogalerix,* the skulls of fossil Galericinae are too incompletely known for meaningful comparison. *Neurogymnurus* is here provisionally included in the Galericinae. The second Oligocene genus, *Tupaiodon,* is generally classified as an adapisoricid, but despite primitive characters its dentition shows so many resemblances to *Parasorex* that it can hardly be excluded from the Galericinae. Unfortunately, in the type species, *T. morrisi,* only the upper dentition, part of the face, and M_{2-3} are known. A second species, *T. minutus,* may not belong to this genus; it shows resemblances to *Ictopidium* (Sulimsky, 1969). *Tetracus* is clearly related to the Miocene galericines of Europe, especially to *Galerix (= 'Pseudogalerix'),* but it is known only from the lower jaw and part of the dentition (Lavocat, 1951; Crochet, 1974).

A confusing nomenclatorial situation has arisen over the genus *Galerix*. The type species is *Viverra exilis* Blainville, 1839 *(= Galerix viverroides* Pomel, 1848), based on a specimen from Sansan. Re-examination of this specimen by Baudelot (1972) showed that P_4 has a reduced metaconid and paraconid, and P_3 is equal in height to P_2. Except that P_3 is not so much reduced, this conforms with the definition of *Pseudogalerix stehlini* Gaillard, 1929, based on material from La Grive St. Alban; in the species commonly known as *Galerix exilis* the metaconid and paraconid of P_4 are higher and P_3 is larger than P_2. Moreover, Engesser (1972) showed that upper dentitions from Sansan resembled *Pseudogalerix* from La Grive in the weak development of the hypocone of P^3, and differed from *'Galerix exilis'* from La Grive in which the hypocone is equally developed on P^3 and P^4. *Pseudogalerix* thus becomes a synonym of *Galerix*. The oldest name for the species commonly called *Galerix exilis* is *Parasorex socialis* von Meyer, 1865, based on material from Steinheim (see Fraas, 1870). The generic name *Galerix* should therefore be restricted to *G. exilis* (type locality Sansan) and *G. stehlini* (type locality La Grive); the remaining species should be transferred to the genus *Parasorex*. In this sense, *Parasorex* appeared in the Burdigalian (Antunes & Mein, 1971) and survived in Austria and Greece till the end of the Miocene (Bachmeyer & Wilson, 1970; Rabeder, 1973; Rümke, 1976). In addition to the skull, Fraas (1870) briefly described some postcranial bones of *Parasorex,* and the pelvis was studied by Leche (1883). A species which may belong to this genus occurs at Gargano (Freudenthal, 1971).

Contemporary with *Parasorex* was the genus *Lanthanotherium,* which ranged in Europe from the Burdigalian *(L. piveteaui* Crusafont, Villalta &

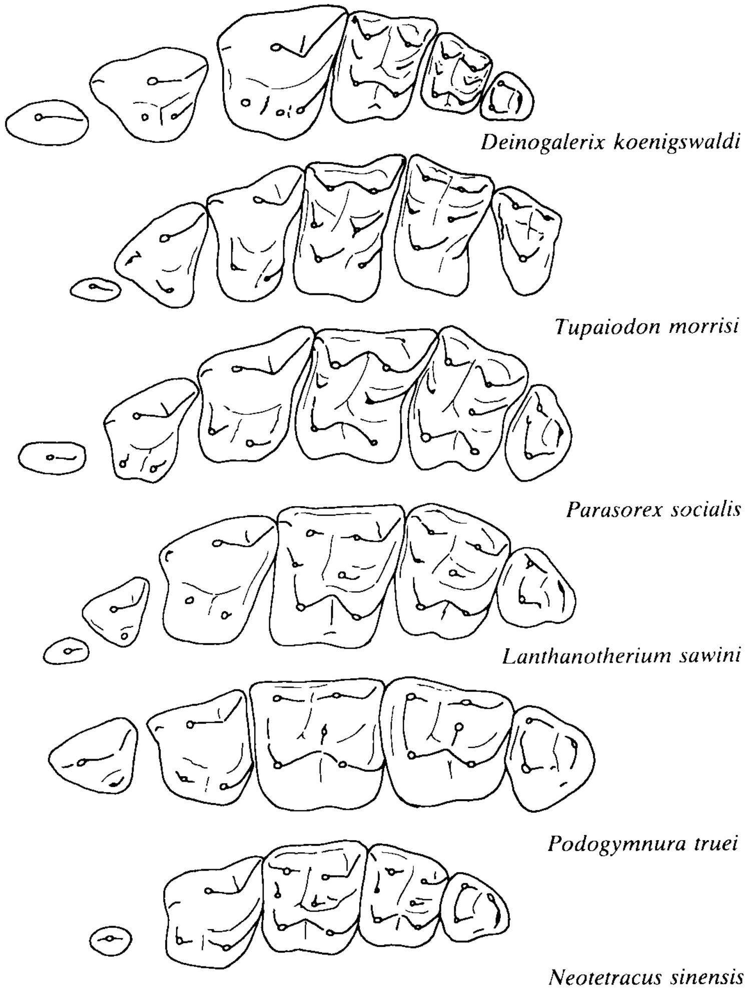


Fig. 17. Upper cheek teeth of some Galericinae. Not to scale.

Truyols, 1955; *L. lactorensis* Baudelot & Crouzel, 1976) to the Vallesian of Spain *(L. sanmigueli* Villalta & Crusafont, 1942) and the Turolian of Austria *(L.* cf. *sanmigueli,* Rabeder, 1973). Two species have been described from the Clarendonian of North America (James, 1963). *Lanthanotherium* has also been reported from the Miocene of East Africa, but undescribed new material shows that *Lanthanotherium* sp. of Butler (1969) is synonymous with *Galerix africanus* Butler, 1956, which is related to *G. stehlini.* The variety of species of *Lanthanotherium* implies that more than one line of evolution is involved (Engesser, 1979), but most species are poorly known. A crushed skull of *L. sansaniense* provides little information beyond the dentition, but something is known of the face and orbital wall in the American *L. sawini* (James, 1963). No postcranial bones have been identified.

Lanthanotherium seems to be near the ancestry of the living galericines. These belong to five genera, all confined to S.E. Asia. The small forms, *Hylomys, Neohylomys* and *Neotetracus* constitute a closely-knit group and may be only subgenerically distinct. *Echinosorex,* the largest living erinaceid, stands apart from these, but the related *Podogymnura,* which is much smaller, is in some ways more like *Hylomys.*

Analysis of the relationships of all these forms with *Deinogalerix* and with each other must inevitably depend largely upon the dentition. Evidence from the skull and postcranial skeleton, in the main available only from *Deinogalerix* and the living genera, merely supplements the evidence from the teeth.

A derived character of the dentition that *Lanthanotherium* shares with the living galericines is the specialization of the metacone of M^3 for shearing behind the transverse talonid crest of M_3. The shape of M^3 of *Parasorex* is primitive: it is triangular, with the anteroposterior length less than the breadth, and with the posterior apex in a median position, approximately equidistant from the buccal and lingual apices. However, M^3 is already advanced in that the metacone, a comparatively high cusp, usually has a lingual ridge running towards the protocone. In Recent galericines M^3 is longer, its posterior apex is displaced lingually, and the metacone ridge, which is strongly developed, differentiates to various degrees into a buccal and lingual cusp. The highest level of development is reached in *Echinosorex,* where in some specimens M^3 is much lengthened and possesses an additional posterior cusp (? hypocone). The metacone ridge is divided into two distinct cusps in *Lanthanotherium sansaniense* and *L. sanmigueli,* but in *L. sawini* the division is much less complete, as in *Podogymnura* and the *Hylomys* group (Engesser, 1979). *Deinogalerix* resembles these last forms.

A second derived feature of the living galericines is the division of the lingual root on P^4 - M^2. This also occurs in *Lanthanotherium sawini* (James, 1963), but it has not been reported in the European species of the genus. In *Deinogalerix* only the apical part of the root is divided.

Deinogalerix agrees with *Lanthanotherium* and the Recent genera in having an enlarged, vertical I^1, but this tooth is larger in comparison with I^2 in *Deinogalerix,* where it is probably secondarily specialized. The alveolar edge of the premaxilla lies at a more ventral level than that of the maxilla in *Deino*galerix, as in *Lanthanotherium* (James, 1963), *Echinosorex* and *Podogymnura,* but not in the *Hylomys* group. Division of the root of the upper canine is a primitive character, found in all Galericinae except *Neotetracus.* However, *Deinogalerix* is exceptional, and probably derived, in that its canine and P^1 are subequal in height. *Deinogalerix* resembles *Lanthanotherium* and the living genera in having an enlarged, procumbent I_1, but it differs from them in the bilobed crown of I_1 as well as in the absence of I_3. Moderate enlargement of the lower canine is a primitive character found in *Neurogymnurus, Tetracus, Galerix, Lanthanotherium,* and *Echinosorex,* but the comparatively large size of this tooth in *Deinogalerix* must be considered secondary.

P^1 is primitively two-rooted *(Tupaiodon, Neurogymnurus, Galerix, Parasorex, Deinogalerix).* A premolar has been lost in some species of *Lanthanotherium,* in *Podogymnura,* in *Neotetracus,* and (lower jaw only) in *Neohylomys* (Shaw & Wong, 1959). The missing lower tooth in *Podogymnura* is probably P_2, for the most anterior premolars shears against the posterior cutting edge of the upper canine. In *L. sawini* and in *Hylomys,* which have four premolars, P^1 has one root and P^2 two roots. The roots of P^2 have united in *Echinosorex.* P_1 always has one root, though this may be grooved in *Tetracus* and

Parasorex. P_2 primitively has two roots, which have united in *Echinosorex* and in *Parasorex zapfei* (Bachmeyer & Wilson, 1970).

A comparatively large P^3, with a length 75% or more of that of P^4, may be primitive for the Galericinae, for it occurs in *Neurogymnurus, Tupaiodon* and *Parasorex,* as well as in *Deinogalerix* and the living *Echinosorex* and *Podogymnura. Deinogalerix* agrees with *Tupaiodon* and *Parasorex* in having a well developed protocone on P^3, whereas in *Neurogymnurus* and the living genera the tooth is narrow and the protocone reduced. A hypocone is developed on P^3 only in *Deinogalerix* and *Parasorex. Galerix* also has a well developed protocone on P^3, but the tooth is reduced in relative size and the hypocone is weak. In *Lanthanotherium* and the *Hylomys* group P^3 is much reduced and simplified. P_3 varies in size correlatively with P^3; in *Galerix* it becomes smaller than P_2.

On P_4 of *Parasorex* the paraconid and metaconid are well developed, as in *Deinogalerix. Ictopidium* and *Tupaiodon minutus* show a similar condition, but in all other galericines the paraconid is reduced to a low anterior cusp and the metaconid is more or less merged into the posterolingual face of the elevated protoconid.

M^1 and M^2 of *Lanthanotherium* and the Recent genera are squarish teeth, approximately as long as wide; the metaconule is centrally placed and has lost its posterior crest. *Deinogalerix* resembles *Parasorex* and the Oligocene genera in having more transverse molars with metaconule crests. The oblique anterior edge of M^1, in which the protocone is situated more anteriorly than the paracone, is probably another primitive character, present in *Tupaiodon* and *Parasorex.* On the other hand, the strong development of the posterior crest of the hypocone may be an advanced character. It is shared with *Lanthanotherium* and the *Hylomys* group, but the crest is weak or absent in *Neurogymnurus, Tetracus, Galerix,* and *Parasorex,* as well as in *Echinosorex* and *Podogymnura.* In *Tupaiodon* the hypocone is small. The rudimentary mesostyle on M^1 and M^2 is a derived character that is paralleled in Pannonian species of *Parasorex* (Rabeder, 1973); it does not occur in *Lanthanotherium* or Recent forms. *Parasorex* resembles *Deinogalerix* in having a strongly transverse molar chewing action.

On M^1 and M^2 of *Deinogalerix* a groove forms a posterior outlet from the trigon basin, passing lingually to the metaconule and separating that cusp from the protocone and hypocone. This feature is well developed in *Lanthanotherium* and *Neotetracus;* in the other living genera the groove is variable and often shallow or absent. It occurs again in *Parasorex,* especially in the later species, but not in *Galerix* or the Oligocene genera.

The unique specialization of *Deinogalerix* is shown by many dental characters not found in other Galericinae: enlarged anterior upper incisors; large lower canines in combination with premolariform upper canines; third and fourth premolars with blunt cusps, adapted for crushing; exaggeration of the trigonid of M_1, which resembles *Exallerix* (McKenna & Holton, 1967); reduced size of the second and third molars. Most other characters are primitive, but a few derived characters are shared with *Lanthanotherium* or with *Parasorex.* Possibly significant resemblances to *Lanthanotherium* are the structure of M^3, incipient division of the lingual molar roots, and the posterior hypocone crest. However, derivation from *Lanthanotherium* seems to be excluded by the complexity of P^3 and P_4 and by the retention of the metaconule crest on $M^1$and M^2. Special resemblances to *Parasorex* concern mainly characters of the premolars, but they are partly shared with *Tupaiodon* and *Ictopidium*. Other resemblances to *Parasorex* seem to be either primitive characters or probable parallelisms such as incipient mesostyle development. Thus the dentition fails to provide firm evidence for the derivation of *Deinogalerix* from a known European galericine.

Turning to the skull, *Deinogalerix* again shares primitive characters with other galericines. Thus the face of *D. brevirostris* is similar in proportions to *Neurogymnurus, Parasorex* and *Lanthanotherium,* though the more elongated face of *D. koenigswaldi* is specialized. The zygoma is horizontal; the palate, which is not perforated, ends shortly behind the transverse crest; the postglenoid foramen opens on the posterior side of the postglenoid crest; there is no pit in the basisphenoid; the foramina of the orbital wall resemble *Neurogymnurus, Lanthanotherium* and *Hylomys;* and the structure of the tympanic chamber resembles *Neurogymnurus* and Recent galericines. The nasals, which reach beyond the level of the lachrymal foramina, are longer than in the Recent forms, but agree with *Neurogymnurus* and *Lanthanotherium.* There is a prelachrymal crest which hides the lachrymal foramen in lateral view, as in *Neurogymnurus, Parasorex* and *Hylomys.* (According to James (1963) this crest is not developed in *Lanthanotherium sawini,* but an undescribed specimen (UCMP 82731) possesses a well developed crest; in the holotype it seems to have been broken away.) The infraorbital foramen opens immediately anterior to P^4 as in all the genera except *Echinosorex* and *Podogymnura,* where it is more posterior.

The skull of *D. brevirostris* is four times as long as that of *Parasorex socialis* and three times as long as in *Neurogymnurus.* This size difference accounts for some differences of proportion: the relatively smaller braincase, the higher sagittal crest, and the narrower interorbital region. *Deinogalerix* is also specialized in the shortness of the posterior part of the skull base, resulting in a modification of the mastoid region, where the lambdoid area faces more posteriorly than in other erinaceids. An enlarged temporal muscle would account for the prominent postorbital processes, the high sagittal crest, and the overhang of the nuchal crest over the occipital surface of the skull. None of these derived characters is shared with other known galericines. However, if correctly interpreted, *Deinogalerix* agrees with *Echinosorex* in the reduced tympanic bone, which lacks the anterior process present in *Hylomys, Neotetracus* and *Neurogymnurus* (Butler, 1948).

In the mandible *Deinogalerix minor* is less specialized than *D. koenigswaldi* and approaches *Parasorex, Galerix* and *Neurogymnurus:* the condyle is more elevated than in *D. koenigswaldi,* the angular process is pointed, the symphysis is shorter and the anterior premolars are less spaced. *Lanthanotherium* and the living galericines differ from *Parasorex* in their more elevated condyle and broader angular process. *L. longirostris* (Thenius, 1949) is unusual in the elongation of the anterior part of the jaw, which has a long postcanine diastema; the symphysis is deeper than in *Deinogalerix,* probably due to the upright canine.

The postcranial skeletons of *Deinogalerix* and *Echinosorex* were compared in the descriptive part of this paper. A skeleton of *Hylomys suillus* (BMNH 1960.8.4.7) resembles *Echinosorex* and differs from *Deinogalerix* as follows: (1) The anterior cervical vertebrae possess hypapophyseal spines, associated with a highly developed ventral (longus colli) musculature. These are present also in the erinaceine *Gymnurechinus* (Butler, 1956), but not in *Deinogalerix* or living Erinaceinae. (2) The lumbar neural spines and transverse processes are more extended anteroposteriorly in Recent galericines than in *Deinogalerix*. In *Hylomys* the anterior edge of each neural spine fits into a groove in the spine in front, giving lateral rigidity to the lumbar region. (3) The long bones of the limbs are more slender in the living forms, and have less strongly marked muscle impressions. This is presumably due to the smaller body size. (4) In the manus, metacarpal V is short, metacarpal I is situated partly behind II, and the digits are longer and more slender. The ulna is not so long in comparison with the humerus (ratio 1.02 in *Echinosorex,* 1.09 in *Hylomys,* 1.17 in *Deinogalerix).* (It was not possible to disarticulate the carpus to see the distal surface of the lunate and cuneiform). (5) In the pelvis, the area for the origin of m. iliacus on the ventral surface of the ilium is narrower than in *Deinogalerix,* and the tuber ischii rises less abruptly from the dorsal edge of the ischium. (6) The anterior tibial crest is stronger and ends abruptly. The tibia is a little longer in proportion to the femur (ratio: 1.20 in *Echinosorex,* 1.26 in *Hylomys,* 1.15 in *Deinogalerix).* (7) The calcaneum reaches farther distally than the astragalus, so that the cuboid has only a small contact with the navicular. (8) The metatarsals are longer than the metacarpals, and metatarsal V is shorter than II.

Hylomys differs from *Echinosorex* in body proportions, having a shorter neck, trunk and trail as compared with the size of the head and the length of the limbs. It thus approaches *Deinogalerix.* It also resembles *Deinogalerix* in the sharpness of the lateral crest of the ilium, anterior to the acetabulum. In other respects it differs from both *Deinogalerix* and *Echinosorex:* the humerus has no supracondylar fenestra; the iliac blade of the pelvis approaches the acetabulum more closely; the neck of the femur is more flattened anteroposteriorly. Despite these differences, *Hylomys* stands nearer to *Echinosorex* than to *Deinogalerix.*

Little information is available on the postcranial skeleton of other fossil galericines. Fraas (1870) referred some bones to *Parasorex socialis.* A scapula, of which the spine is not preserved, is described as having the coracoid process strongly bent inwards, and the articulatory surface for the humerus is said to be flat. The first character would apply to both *Deinogalerix* and the Recent galericines, the second to neither. The humerus, of which there are many specimens, has an entepicondylar foramen and a supracondylar fenestra. Its measurements are given as length 18.5 mm, distal width 4.5 mm. It thus agrees in proportions with *Hylomys* but is narrower than in *Deinogalerix.* From the figure (op. cit., pl. 1, fig. 9) the entepicondyle is of a different shape from those of *Deinogalerix* and *Hylomys,* being more pointed medially, and the head of the humerus is wider in posterior view. Fraas also states that the 'upper crest' (presumably the deltoid crest) does not reach to half the length of the bone; this is not true of *Deinogalerix* or *Hylomys,* where the crest extends beyond the mid-length. The radius and ulna figured (pl. 1, fig. 10) are large in comparison with the humerus (ratio, ulna/humerus 1.30). The pelvis, which lacks the blade of the ilium, was described by Leche (1883). It differs from *Deinogalerix* in the shape of the tuber ischii, which rises to a posterodorsal point, but it agrees with *Deinogalerix, Hylomys* and *Echinosorex* in having a concave posterior border. As in *Deinogalerix,* the lateral crest of the ilium is sharp and it is dorsally placed, resulting in a broad surface for m. iliacus. The femur figured by Fraas (1870, pl. 1, fig. 7) differs from *Deinogalerix* and living galericines in that the greater trochanter does not project proximally beyond the head, and the lesser trochanter is less distal in relation to the greater trochanter. The specimen figured is slightly shorter than the humerus, but the distal epiphysis appears to be missing. The tibiofibula/ulna ratio is 1.21, intermediate between *Hylomys* and *Deinogalerix.* The shape of the tibial crest cannot be made out from the figure (op. cit., pl. 1, fig. 8), but the crest appears to be strongly developed. If these bones are correctly ascribed to *Parasorex* they do not support a close relationship with *Deinogalerix.*

Schlosser (1887) figured a humerus (pl. 3, fig. 38) as possibly belonging to *Neurogymnurus.* It appears to be erinaceid, but the proximal end is missing. A referred femur (op. cit, pl. 8, fig. 29) is also incomplete; it has a prominent gluteal crest as in erinaceids. A referred tibia (pl. 8, fig. 58) is not united with the fibula and therefore almost certainly not erinaceid.

The foregoing comparison of *Deinogalerix* with other Galericinae leads to the conclusion that the resemblances are for the most part shared-primitive characters that throw little light on phyletic relationships, and the differences are predominantly due to the peculiar specialization of *Deinogalerix.* A few dental characters suggest a distant relationship to *Lanthanotherium* and the living galericines, and it is possible that there are derived characters of the skeleton shared with this group but as yet unrecognized because of the lack of comparative material. It might be supposed that, isolated on an island, the ancestral *Deinogalerix* became so radically transformed that most evidence of its relationships has been lost. However, many primitive characters survived, and it is to be expected that some of the derived characters of the ancestral population would also be retained. It seems likely that when it first arrived on Gargano *Deinogalerix* had already differentiated from *Lanthanotherium* and *Parasorex.* Study of the small galericine from Gargano might throw further light on this matter.

There is reason to believe that the centre of galericine evolution was in Asia. The subfamily is known to have been present there in the Oligocene *(Tupaiodon, Ictopidium),* and it survives there today. *Tetracus* and *Neurogymnurus* in the Oligocene, and *Parasorex* and *Lanthanotherium* in the Burdigalian, appear in Europe as immigrants, and *Lanthanotherium* also invaded North America. Most likely *Deinogalerix* was another such immigrant, entering Gargano from the East, across the Adriatic. The Muridae may have followed the same route (Freudenthal, 1971).

Mode of life

The unbalanced composition of the fauna of Gargano (Freudenthal, 1971) suggests that colonization took place across the sea, by rafting or swimming. However, this would not explain the presence of Amphibia, which are killed by sea-water. It is possible that the impoverished relic of an older fauna has, like the Pliocene fauna of Sardinia (Pecorini, Rage & Thaler, 1974), been supplemented by later invasions.

Several species of rodent show a progressive increase of body size (Freudenthal, 1971, 1976): one of the two species of Gliridae, two of the three lineages of the murid *Microtia,* and the cricetid. The lagomorph *(Prolagus)* also reaches a large size. Release from selection due to predation by mammalian carnivores may have been a factor. The carnivore niche was by no means empty, however, for there were six species of owls and three species of diurnal birds of prey (Accipitridae) (Ballmann, 1973). These predaceous birds covered a wide range of size, the largest species being found in the younger deposits which contain the largest rodents. Gigantism of the mammals is therefore unlikely to be due to lack of predation; more probably it is an aspect of the adaptation of the fauna to a new environment (Sondaar, 1977). In the invasion of new niches, left vacant because of the restricted number of immigrant stocks, increased size might have a selective advantage. In the case of the rodents, gigantism might be a consequence, not of a lack of carnivores but of a paucity of ungulate herbivores. It must be remembered that not all lineages display gigantism: for example, in addition to *Deinogalerix* there was a small erinaceid, which presumably had the same habits as *Parasorex* on the mainland.

What niche did *Deinogalerix* occupy? Erinaceids in general feed on insects and other invertebrates such as earthworms and molluscs. *Erinaceus* also eats amphibians and snakes, and in captivity it can eat mice (Herter, 1938). *Echinosorex* feeds largely on aquatic animals such as fish and crabs, and it is usually trapped near streams. It is parasitized by a trematode whose intermediate host is fish, and it has been kept in captivity for seven years fed principally on fresh fish (Lim Boo Liat, 1967). Increased body size in Erinaceidae might be expected to be accompanied by a change of feeding habits, in which small invertebrates are increasingly replaced by vertebrates and the larger crustacea. It therefore seems more probable that *Deinogalerix* was a predator than that it was merely a scavenger as Freudenthal (1972) suggests. Freudenthal rejects the predator hypothesis because 'the construction of its legs seems to prove that *Deinogalerix* was not a fast-moving animal capable of catching a prey like a rat or a rabbit'. If *Erinaceus* can be taken as typical of the family, the method of hunting does not involve chasing fast-moving prey, as is usual in the Carnivora: rather it consists of searching among litter, vegetation etc. and snapping at the prey before it can escape. According to Herter (1938), hedgehogs in captivity will kill mice if they can corner them, but if the mouse escapes the hedgehog will not follow it. Probably the cerebral and visual equipment of insectivores is insufficient to allow true hunting in the carnivore sense. Cursorial adaptations of the limbs are therefore not required.

The elongated jaws of *D. koenigswaldi,* with spaced teeth that occluded only minimally, are clearly not adapted for picking up small objects by a forceps action such as we see in *Erinaceus.* They would be more efficient for gripping prey of the size of a frog or crayfish. As in *Echinosorex,* the enlarged lower canines pass up behind the upper incisors to produce a firm grasping mechanism for holding slippery prey. Harrison & Lim Boo Liat (1950) describe *Echinosorex* paddling about in water 6 cm deep and skilfully catching *Gambusia,* and it is not difficult to imagine *Deinogalerix* feeding on fish and other animals in shallow water in a similar way. The large posterior premolars and the trigonid of M_1 would be effective in breaking up the bones of vertebrates or the carapaces of crustaceans, and the food would then be ground by transverse action of the molars.

A number of modifications of the skull and mandible imply specialization of the temporal musculature. The strong postorbital process and frontal crest, together with the elevation of the anterior part of the sagittal crest, would be associated with a hyperdevelopment of the anterior part of the muscle, whose fibres run vertically to insert on the medial side of the base of the coronoid process. This part of the muscle would function in the crushing action of the posterior premolars and M_1 trigonid. Other modifications are associated with the posterior part of the muscle, where the fibres are more horizontal: the posterior inclination of the nuchal crest, the posterior displacement of the jaw articulation in the skull, the small coronoid process, the low condyle and the elongation of the posterior part of the mandible. These modifications imply a wide gape and long muscle fibres for closing the mouth, in other words an ability to close the mouth rapidly from a widely open position. Such a snapping action was probably used for catching prey. A low coronoid process is found also in sabre-toothed cats; it indicates a fleshy posterior temporal muscle that acted at a low mechanical advantage. Speed of closure, rather than force, would be required by *Deinogalerix* for prehension of prey. The laterally divergent angular processes would allow the jaw to be opened widely, as in the hippopotamus (Herring, 1975). *Deinogalerix* may well have used mouth-opening as a threat posture like *Echinosorex* (Lim Boo Liat, 1967). The strongly constructed angular process, with its medial flange, implies a strong internal pterygoid muscle, probably used in the transverse chewing action of the molars.

Freudenthal (1972) recognized that *Deinogalerix* was a slow-moving animal. It might be expected that increased size would be associated with loss of agility, and comparison of the skeleton with *Echinosorex* bears this out. The short, broad vertebral centra, the absence of hypapophyseal spines on the cervicals and the smaller lumbar processes imply a weaker vertebral musculature, and suggest that locomotion was ambulatory like that of *Erinaceus*. This interpretation is supported by the less developed tibial crest, indicative of a weaker m. biceps femoris, and by the short toes and the relatively larger lateral digits. The proportionately larger manus and longer forearm may indicate that the fore-limb was used for such actions as parting vegetation and turning stones during the search for food.

The coexistence of two lineages implies an ecological separation. Presumably the smaller species took smaller prey, and it is possible that there was a difference in environmental preference. Except in the oldest fissures, where only *D. freudenthali* occurs, larger and smaller species are found together, but the smaller species is always the less common. Perhaps the smaller species inhabited mainly drier ground while the larger species frequented stream margins. Equally problematic are the circumstances in which separation of the lineages occurred, whether it was sympatric or whether it involved isolation on adjacent islands (Freudenthal, 1976). *Deinogalerix* is very rare in the interval between Rinascita 1 and Fina D, but there is some indication that the larger form was present at Trefossi 1 and Cantatore 3A. The latter fissure is the oldest that contains two species of *Microtia;* it is slightly older than Fina D, where two species of *Tyto* first occur (Ballmann, 1973).

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Manuscript received 3 December 1980.

Tables of measurements

Table 1. Measurements (in mm) of upper teeth from San Giovannino and San Giovannino Low.

		D. koenigswaldi							*D. brevirostris*
		Holotype	Specimens from S. G.					S. G. Low	
			N	Range	m	s.d.	V		
I^1	length	8.5	5	8.2 - 9.4	8.82	0.49	5.6	8.7	6.6, 7.7
	height	17.0	1	17				13	13
I^2	length	3.7	2	3.7, 4.3					
I^3	length	5.3	1	5.3					4.5
C^1	length	8.3	5	8.0 - 10.3	9.22	1.04	11.3	8.8, 9.5	
P^1	length	8.0	5	8.0 - 8.6	8.22	0.30	3.7	8.0, 8.4	6.4*
P^2	length	8.5	5	8.2 - 9.7	8.66	0.62	7.1	9.0	7.6*
P^3	length	12.8	6	12.8 - 14.1	13.45	0.52	3.9	13.6	10.1*
	width	11.3	6	10.5 - 12.0	11.25	0.40	3.6	11.6	9.0*
P^4	buccal length	15.7	5	15.7 - 18.0	16.62	1.06	6.4	16.3	12.0*, 13.0
	width across paracone	14.0	4	13.8 - 15.5	14.57			14.9	10.8
M^1	buccal length	10.0	2	9.8, 10.0				10.0	8.3, 8.5*
	width	12.7	2	12.1, 12.7				12.8	11.0, 11.5*
M^2	length	7.0	2	7.0, 7.3				6.9	6.1*
	width	9.2	2	9.0, 9.2				9.5	8.3*
M^3	length	5.6	4	5.6 - 6.2	5.83				4.8*
	width	6.3	4	6.3 - 7.4	6.77				5.6*

* holotype

Table 2. Measurements (in mm) of lower teeth from San Giovannino and San Giovannino Low.

		D. koenigswaldi							*D. brevirostris*
		Holotype	Specimens from S. G.					S. G. Low	
			N	range	m	s.d.	V		
I_1	mesiodistal		3	8.0 - 8.7	8.3				
I_2	length	3.9							
C_1	length	8.7	6	8.7 - 9.0	8.88	0.12	1.3	8.8, 9.0	
	crown height	16.4	4	13.5 - 16.4	15.0			14.5, 15.8	
P_1	length	5.5	3	5.3 - 5.5	5.4				
P_2	length	6.7	3	6.7 - 7.3	7.0			7.0	
P_3	length	11.3	6	11.3 - 12.0	11.70	0.36	3.1	11.2	10.0
	width	6.5	6	5.9 - 6.7	6.32	0.10	1.6	5.8	4.9
P_4	length	12.2	7	11.5 - 13.0	12.34	0.56	4.5	11.7	10.1
	width	8.3	7	7.5 - 8.8	8.34	0.47	5.6	8.0	7.1
M_1	length	14.0	6	13.5 - 15.3	14.57	0.65	4.5	14.9	12.0^e
	width	9.5	6	9.0 - 9.8	9.45	0.32	3.4	9.4	
M_2	length	8.0	7	7.6 - 9.0	8.14	0.48	5.9		7.0, 7.2*
	width	7.2	6	6.7 - 7.3	7.08	0.21	3.0		6.0*
M_3	length	6.1	5	5.8 - 6.9	6.16	0.47	7.6		5.8*
	width	4.7	5	4.7 - 5.6	5.04	0.37	7.3		4.8*

* 179 217, S. G. Low, ^{e} estimated

Table 3. Measurements (in mm) of upper teeth from deposits other than San Giovannino.

	I^1		C^1	P^1	P^2	P^3		P^4		M^1		M^2		M^3	
	l	h	l	l	l	l	w	l	w	l	w	l	w	l	w
D. freudenthali															
Biancone 1, 178 100*, 102										7.7	9.8	5.7			
,, 178 101$^+$, 108, 098$^+$, 104$^+$								10.2	9.5	7.7		5.8	7.5	5.1	6.0
,, 178 105					6.5										
Rinascita 1, 178 162, 160			5.2	5.2											
D. minor															
Chiro 7 A, 177 957				4.8^a											
Chiro 14 A, 179 076												6.0	7.5		
Chiro 20 E, 178 005, 014, 016			6.4	5.7											
Fina D, 178 141	6.0														
Nazario 4, 179 089			5.7^a												
D. intermedius															
Chiro 5 A, 177 945						13.0	11.2	14.8							
Chiro 6, 177 956						11.4	9.5								
Chiro 10 C, 177 970														5.8	6.8
Chiro 18, 177 975								12.8	11.5	8.1	10.9				
Chiro 20 C, 177 989					7.8										
,, 177 982$^+$						11.3	9.3	13.2	11.6	9.1	11.8	6.3	8.2		
,, 177 990										8.9	12.2				
Chiro 20 E, 178 004						11.5	9.3								
Fina H, 178 191						12.3	10.7								
M. Granata 1, 178 091	6.8	13.2													
Pepo 1 A, 178 208						12.0									
Pizzicoli 4, 178 083						13.5	10.5								
Posticchia 4, 178 084						11.8	9.3								
WG 348 279, 178 088					7.7										

* holotype, $^+$ paratype, ^{a} either C^1 or P^1

Table 4. Measurements (in mm) of lower teeth from deposits other than San Giovannino

	I_2	C_1		P_1	P_2	P_3		P_4		M_1		M_2		M_3	
	l	l	h	l	l	l	w	l	w	l	w	l	w	l	w
D. freudenthali															
Biancone 1, 178 103								8.8^e	5.7						
Rinascita 1, 178 158				3.8											
D. minor															
Chiro 20 E, 178 010												6.4	5.4		
Fina D, 178 148					5.2										
Fina H, 178 184*					5.0	8.5	4.5	8.8	6.1	10.8	7.2	6.5	5.6		
,, 178 199						8.3	4.2								
Gervasio, 179 174$^+$						8.4	4.8	8.5		11.0	6.0	6.8	5.9	4.7	3.8
D. intermedius															
Chiro 7 C, 177 959										12.2	8.6				
Chiro 9, 177 967						10.4	5.2								
Chiro 10 B, 177 968								12.6	8.7						
Chiro 17, 177 974												7.1	6.3		
Chiro 20 E, 178 023		8.3	15.7												
,, 178 019					6.8										
,, 178 009						10.6	6.1								
,, 178 013						11.0	5.7								
Chiro 25, 179 079								12.4							
Chiro 29, 179 287										13.6	9.1				
Fina D, 178 150												7.2	6.3		
Fina H, 179 104						10.5									
,, 179 093								12.0	8.5	14.5	9.9	8.0	7.0		
,, 179 092										12.5	7.8	7.5	6.2	5.8	4.6
Fina A/N, 178 087	3.9														
Gervasio, 179 170								12.5	7.5	13.7	9.3	7.8	7.0	5.8	5.0
Nazario 4, 179 063*						10.0	6.0	10.7		13.4	8.8				
Posticchia 1 B, 178 204								11.0	7.3	12^e	8.5	7.6	6.4		
WG 354 294, 178 085, 086						8.9	5.0	9.7	6.7						

* holotype $^+$ paratype ^{e} estimated

Table 5. Measurements of skulls (in mm).

	D. koenigswaldi							*D. brevirostris*		*D. intermedius*						*D. minor*
	San Giovannino						S. G. Low	S. G.								Fina D
	177 777*	177 918	179 192	179 194	179 146	179 155	179 221	179 134*	179 237	Chiro 5 A 177 945	Chiro 20 B 177 981	Chiro 20 C 177 982$^+$	Chiro 20 D 177 997	Chiro 18 177 975	Pepo 1 A 178 208	178 141
Basal length (I^1-condyle)	199	197	226	219				155^e								
Length across incisor alveoli	19.5	19	20.5	19					14		16					11.5
Length premaxilla (alveolar border)	33.5	35.5	37.5	39	32^e				23				30^e			22.5
Anterior C - palatal crest	92	90	106	103	102		93^e	75								
Anterior C - anterior P^3 (alveoli)	39.5	41.5	50.5	46.5	48.5		41	29								
Total length P^3 - M^3	48.5	47	48	51	47.5		48.5	39								
Total length P^3 - P^4	28	31	31.5	34.5	32.5		31.5	25.5		29		25.5			25	
Total length P^4 - M^2	31	31	31	33	31.5		31	24.5				27		25		
Palatal crest - foramen ovale	36.5	39^e	44.5	46				30								
Palatal crest - condyle	73.5	70	87	79.5				61								
Width across canine alveoli	22.5	24.5^e	28.5	27	24.5			23.5								
Width across P^4	50.5		65	65	64		50.5	51								
Across mastoid processes	59.5		73.5	74		71		54								
Across condyles	27	29	31	30.5		32.5		23								

* holotype $^+$ paratype ^{e} estimated

Table 6. Measurements of mandibles (in mm).

	Length to angular process	Anterior to M_1	Between C_1 and P_3	Total length molars	Base of coronoid - condyle	Lingual depth below M_1	Top of coronoid - lower edge	Width condyle
D. koenigswaldi								
San Giovannino, 177 778, 779*	159	74^e	34	27.5	53	21.5	38	12.5
,, 179 224	165^e	72^e	35.5^e	27.5	68	23.5	44	19
,, 179 145, 147	190	92	46	31	69	27	42.5	18.5
,, 179 193	186^e	88^e	44.5	29	72	28.5	43	20
,, 179 149	180	90	48.5	29^e	64	26.5	44	
S. Giov. Low, 179 206		76^e	35	29.5		23	42	
D. brevirostris								
San Giovannino, 179 232$^+$		58	21.5	24		21		
D. intermedius								
Fina H, 179 092				25	52	20.5		12.5
Gervasio, 179 170				26		21	37	
Nazario 4, 179 063*			24^e	25.5	54	21.5		15
D. minor								
Fina H, 178 184*				23.2	36	16.5		10
Gervasio, 179 174$^+$		49^e	17	22.5		17		

* holotype $^+$ paratype ^{e} estimated

Table 7. Measurements of cervical vertebrae (in mm).

Atlas	Maximum length	Maximum width	Width across cranial articulation	Maximum height
D. koenigswaldi				
San Giovannino, 177 785*	21	48	33	25
D. brevirostris				
San Giovannino, 179 141			19[e]	
D. minor				
Chiro 28 A, 179 296	12			

Axis	Ventral length	Posterior width centrum	Width across atlantoid articulation	Posterior height centrum	Height spinal canal	Total height
D. koenigswaldi						
San Giovannino, 177 786*	23	14	25	8.5		
,, 179 302	22.5	15	26	9	11	52
D. intermedius						
Chiro 11 A, 177 961	20	12	21	8	10	
D. freudenthali						
Biancone 1, 178 095	11			4.2		
,, 178 116		10	17	4.1		
,, 178 121		8	15	3.0		

Other cervicals	Ventral length	Posterior width centrum	Length across zygapophyses	Posterior height centrum	Height spinal canal	Total height
D. koenigswaldi						
San Giovannino, 177 787* (C. 3)	8	14		9		
,, 177 788* (C. 4)	8	13.5		8.2		
,, 177 790* (C. 5)	7	13	12	8		
,, 177 791* (C. 6)	6.2	13		8		
,, 177 792* (C. 7)	6.2	14		7.5		
,, 179 140 (C. 5)	9.2	15	15	10		
,, 179 138 (C. 6)	9	14.5	15	9.5	8	25
,, 179 143 (C. 7)	8.7		13			
S. Giov. Low, 179 220 (C. 6)	8	16		8.5		
D. intermedius						
Chiro 20 A, 177 976 (C. 6)	6.5	12		7.5		
Trefossi 1, 179 081	5.2	10		5		
D. freudenthali						
Biancone 1, 178 128	3.6	8.0		4.0		

* holotype [e] estimated

Table 8. Measurements of thoracic and lumbar vertebrae (in mm).

Thoracics	Ventral length	Posterior width centrum	Width across mammillary processes	Posterior height centrum	Height spinal canal	Total height
D. koenigswaldi						
San Giovannino, 177 792*	7	13		8.3		
,, 177 793*	6.4	15		7		
,, 177 794*	6.5	14.5		7		
,, 177 795*	6.7	13.5		8.5		
,, 177 796*	7.3	14	28[e]	8.5	7.5	27
,, 177 797*	8.2	13	20.5	8.2	7.2	26
,, 177 798*	9	14.8	21	9	6.5	26
,, 177 799*	8	14.3	19	9	6.5	24
,, 177 800*	9	16	20.5	8	6.2	
,, 177 801*	9.7	16		9	6.2	
,, 179 142 (T 1)	9	18		11		35
,, 179 139	9.7	14		8.5		
,, 179 144	9.2	15		11		
,, 179 135 (T ?12)	10	20				
,, 179 136 (T ?13)	10.2	21.5		11		
,, 179 137 (T ?14)	12	20		12		
D. freudenthali						
Biancone 1, 178 129	5	8		3.6		

Lumbars	Ventral length	Posterior width centrum	Width across mammillary process	Posterior height centrum	Height spinal canal	Height to top mammillary process
D. koenigswaldi						
San Giovannino, 177 835*	10	18	21[e]	10	6	24
,, 177 836*	10.2	17.1	23.5[e]	11.3	5.8	24
,, 177 837*	11.1	17.5	19.5[e]	11	4.6	
,, 177 838*[a]	9.2	17.4	20.6[e]	9.5	6.5	
D. intermedius						
Chiro 24, 179 064	12.8	19	22.5	11.2	5.5	29
D. minor						
Chiro 24, 179 072	10	14		7.5	4.1	

* holotype [e] estimated [a] this specimen may belong to a different individual

Table 9. Measurements of ribs (in mm).

	Across head and tubercle	Greatest diameter at angle	Diameter mid-shaft	Length as preserved
D. koenigswaldi				
San Giovannino, 177 802 - 823*				
rib 2		6.8^e	5.6	42
„ 3		6.3	4.4	
„ 4	12.5	7.1	4.4	
„ 6	11.3	5.8	4.2	63
„ 7		6.0	4.2	65
„ 8	12.4	5.3	4.0	69
„ 9	11.8	5.3	4.0	
„ 10	11.1	5.1	4.0	71
„ 11		5.0	4.0	75
„ 12	9.3	5.2	4.1	76
„ 13	9.3	5.0	4.0	59
D. freudenthali				
Biancone 1, 178 117	6.0	3.2		

*holotype ^{e} estimated

Table 10. Measurements of sacrum and caudal vertebrae (in mm).

Sacrum	Length first 2 centra	Across iliac joints	Height from 1st mammillary process
D. koenigswaldi			
San Giovannino, 178 049	30^e	32.5	21^e
D. intermedius			
Chiro 28 A, 179 294	26	29	16.5

Caudals	Length centrum	Posterior width centrum	Width across transverse processes	Posterior height centrum	Maximum height
D. koenigswaldi					
San Giovannino, 177 876*	19.5^e	12.5	46	12	
,, 177 877*	17	12.5		12	
,, 177 878*	15	12	22	11	
,, 177 879*	18	12		10	
,, 177 880*	20.5	12	14	10	
,, 177 881*	20	10	12.5^e	9	
,, 177 882*	17.5	10	12.5	9	
,, 177 883*	19	9	10.5	7.5	
,, 179 248	17.5	14		13	
,, 179 247	19	14	23.5	12.5	
,, 179 246	18.5	12	16	10.5	
D. intermedius					
Trefossi 1, 179 082	16	8	9.5	6.2	
D. freudenthali					
Biancone 1, 178 130	11	6.0		6.0	10.5
,, 178 127	11.5	7.0	13	5.5	10
,, 178 125	10	6.1		6.1	10
,, 178 123	12	7.3	14	6.0	
,, 178 134	9.5	4.0	4.4	3.0	

* holotype ^{e} estimated

Table 11. Measurements of bones of shoulder girdle and fore limb (in mm).

Clavicle	Length	Greatest diameter mid-shaft
D. koenigswaldi		
San Giovannino, 177 824*	52	5.0

Scapula	Length along spine-acromion process	Maximum width blade	Greatest diameter head	Medio-lateral glenoid	Antero-posterio neck
D. koenigswaldi					
San Giovannino, 177 827, 828*			23	11.5	16
,, 179 285	113	41	24	12.7	18

Humerus	Length	Distal width	Anteroposterior, lower end of deltoid crest
D. koenigswaldi			
San Giovannino, 177 829*	102	31	16.7
San Giov. Low, 179 211		31	18
D. intermedius			
Chiro, 179 301		32	
Fina H, 178 195		31	

Ulna	Length	Proximal to coronoid process	Depth at anconeal process	Across sigmoid notch
D. koenigswaldi				
San Giovannino, 177 833*	121[a]	36[a]	18.5	13.5
San Giov. Low, 179 269		44	21.5	14.5
,, 179 215		38	17.5	13
D. intermedius				
Fina H, 178 188		36	16.5	12
Gervasio, 179 176		45	21	15
D. minor				
Fina H, 178 192		28.5	12	10.5
Gervasio, 179 177		30	13	11.5
Chiro 20 A, 177 979		30	12	10

Radius	Length	Greatest width head	Width neck
D. koenigswaldi			
San Giovannino, 177 831*	99[a]	13.2	6.1
D. freudenthali			
Biancone 1, 178 111		9.2	4.7

* holotype [a] without epiphyses

Table 12. Measurements of bones of manus (in mm).

D. koenigswaldi, San Giovannino (holotype)

Scaphoid	Mediolateral	Dorsopalmar
177 873	8.4.	10.1

Lunate	Mediolateral	Dorsopalmar	Proximodistal
177 874	5.5	6.8	8.5

Cuneiform	Mediolateral	Dorsopalmar
177 875	12.2	6.0

Metacarpals	Length	Dorsopalmar, proximal end
177 860 (I)	13.7	4.7
177 858 (II)	29.7	8.7
177 857 (III)	32.5	9.2
177 856 (IV)	31.3	8.4
177 859 (V)	26.0	9.0

Basal phalanges	Length	Proximal width
177 861 (I)	10.0	5.0
177 862 (II)	13.5	5.3
177 863 (III)	14.7	6.4
177 864 (IV)	13.9	7.1
177 865 (V)		6.1

Middle phalanges	Length	Proximal width
177 866	9.4	5.5
177 867	8.9	5.2
177 868	8.5	4.8

Ungual phalanges	Length	Proximal height
177 869	11.8	
177 870	11.5	6.3
177 871	9.4	5.6

D. freudenthali, Biancone 1

Metacarpals	Length	Dorsopalmar, proximal end
178 119 (II)	19	5.3
178 118 (III)	18	4.4
178 137 (V)	13.4	4.2

Table 13. Measurements of pelvis (in mm)

Pelvis	Diameter acetabulum	Posterior spine ilium - posterior acetabulum	Ischium posterior to acetabulum	Width ventral surface at ant. border acetabulum	Minimum width ischium	Width ventral branch ischium	Depth posterior border
D. koenigswaldi							
San Giovannino, 177 839, 840*	17.5	42	41	19	12.5	11.5	
,, 179 315	18^e		52	22	15.5		
,, 179 125	20		56.5	23	14.5	14	75
San Giov. Low, 179 273	18			21^e	14		
,, 179 223	17.5^e	45	51^e	22	12.5		
,, 179 258	18	42		21			
,, 179 222					13.5	11	
D. intermedius							
Chiro 3, 177 942					11		
Chiro 20 E, 178 018	17	39.5			12.5		

* holotype ^{e} estimated

Table 14. Measurements of femur (in mm)

Femur	Length	Length excluding distal epiphysis	Diameter head	Across head and greater trochanter	Width at 3rd trochanter	Width mid-shaft	Distal width
D. koenigswaldi							
San Giovannino, 177 841*	112	100	14.5	30	17	10.5	30^a
,, 177 842*							27
,, 179 316	125^e				23	12.5	30
,, 177 919	132^e	122^e	15.5	32	24	12.5	30
D. brevirostris							
San Giov. Low, 179 283	100		11.7	25.5	15	10.3	22^e
D. intermedius							
Chiro 3, 177 941							24
Chiro 6, 177 953		103^e	14	30^e	19	10.6	
Chiro 20 C, 177 991			14				
Fina H, 178 198			11.5	25			
,, 178 200			13.8				
,, 178 203			12	25	17.5	9.5	
Fina D, 179 286			12.5	28.5	21.5	10.5	
Nazario 4, 179 300							25
Pizzicoli 1, 179 105		101^e	12	27.5	19^e	10	

* holotype ^{e} estimated ^{a} distal epiphysis probably from a different individual

Table 15. Measurements of bones of hind limb (in mm).

Patella	Length	Width
D. koenigswaldi		
San Giovannino, 177 843, 844*	22.5	12.3
,, 179 250	24	14
,, 178 057	24.5	15

Tibiofibula	Total length	Length distal to union	Proximal width	Distal width	Thickness shaft
D. koenigswaldi					
San Giovannino, 177 845, 846*	135	75.5	32	23	10.9
,, 178 056	160	81.5	35	23	11.1
,, 179 236			36		
San Giov. Low, 179 266		77		22.5	11.2
,, 179 205		76.5		22.5	10.8
D. intermedius					
Gervasio, 179 182		67			8.8
,, 179 183		66[e]		19	8.8
Nazario 4, 179 304				20[e]	9.0
D. minor					
Fina East Wall, 179 292		58[e]		17	7.9
Gervasio, 179 178		57		16.7	7.8
,, 179 184		57		18	8.5

Calcaneum	Length	Maximum depth	Width at sustentaculum
D. koenigswaldi			
San Giovannino, 177 849, 850*	41	13	12.5
,, 177 885	37	13	12.7
,, 178 061	41.5	13.5	13
,, 178 062	40.3	14	12.6
,, 179 107	41	13.7	
,, 179 108	38	13	12.1
,, 178 032	37	12.9	13
D. intermedius			
Chiro 20 D, 177 994	37	12.4	11.6
Chiro 24, 179 065	37	12	11.8
D. minor			
Chiro 28 A, 179 295	32	10.5	8.8
D. freudenthali			
Biancone 1, 178 112	20.1	6.8	6.1

* holotype [e] estimated

Table 16. Measurements of bones of pes (in mm). (Continued on p. 72).

Astragalus	Greatest length	Greatest width
D. koenigswaldi		
San Giovannino, 177 847, 848*	24.5	18.5
,, 177 886	22.3	16.5
San Giov. Low, 179 261	24	18.5
D. minor		
Chiro 11 B, 177 972	16.5	12.2
Navicular	**Dorsal length**	**Greatest width**
D. koenigswaldi		
San Giovannino, 177 851*	7.2	12.7
,, 177 857	7.6	11.3
Cuboid	**Length**	**Proximal width**
D. koenigswaldi		
San Giovannino, 177 891	18.5	10.0
D. freudenthali		
Biancone 1, 178 124	10.3	6.1
Rinascita 1, 178 156	10.0	5.0
Cuneiforms	**Length**	**Greatest dorsoplantar**
D. koenigswaldi		
San Giovannino, 177 895 (Ecto-)	15.6	10.0
,, 177 854 (Meso-)*	7.7	6.6
,, 177 889 (Meso-)	7.4	6.9
,, 177 888 (Ento-)	17.4	6.1
Metatarsals	**Length**	**Proximal dorsoplantar**
D. koenigswaldi		
San Giovannino, 177 892 (I)	8.4	3.4
,, 177 893 (II)	31	8.4
,, 177 855 (II)*	33	8.4
,, 177 894 (III)	30	10.5
,, 177 853 (III)*	32	10.0
,, 177 895 (IV)	31	9.2
,, 177 896 (V)	29.5	7.4
,, 177 852 (V)*	30.5	6.7
D. freudenthali		
Rinascita 1, 178 155 (II)	21.5	4.8

Table 16. (Continued).

Basal phalanges	Length	Proximal width
D. koenigswaldi		
San Giovannino, 177 903 (I)	4.2	2.3
,, 177 897 (II)	14.7	6.1
,, 177 898 (III)	13	5.3
,, 177 899 (IV)	15	6.1
,, 177 900 (V)	13.2	6.3
D. intermedius		
Cantatore 3 A, 179 090	12.9	4.3
D. freudenthali		
Biancone 1, 178 133	9.7	4.2
,, 178 135	9.3	4.0
,, 178 136	9.8	4.4
,, 178 138	9.0	4.2
Middle phalanges	Length	Proximal width
D. koenigswaldi		
San Giovannino, 177 901	7.7	4.7
,, 179 195	8.2	4.2
,, 178 073	8.5	4.3
,, 177 902	7.3	4.4
,, 177 872*	8.1	4.0
D. freudenthali		
Rinascita 1, 178 161	5.5	2.7
,, 178 165	6.4	
Ungual phalanges	Length	Proximal width
D. koenigswaldi		
San Giovannino, 177 904	9[e]	6.0
,, 177 905	8.2	5.8

* holotype [e] estimated