

DEMOCRICETODON FEJFARI SP. NOV. AND REPLACEMENT OF CRICETIDAE BY MURIDAE IN SIWALIK DEPOSITS OF PAKISTAN

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Lindsay, E. (2017): *Democricetodon fejfari* sp. nov. and replacement of Cricetidae by Muridae in Siwalik deposits of Pakistan. – Fossil Imprint, 73(3-4): 445–453, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: *Democricetodon* is a core genus within the family Cricetidae; it is recorded in many regions of Asia and Europe, and has left many descendants. One of the early radiations of *Democricetodon* was in southern Asia, where it radiated for about 10 my, from about 18 Ma to about 8 Ma, during the Miocene epoch. *Democricetodon* was replaced in southern Asia by one of its cousins, *Antemus*, in the family Muridae, the Muridae later became one of the most diverse and abundant family of mammals. Cricetidae and Muridae persisted together in Siwalik deposits for a period of about four million years (18 Ma to 14 Ma).

Key words: Cricetidae, Muridae, Miocene, Siwalik, Pakistan

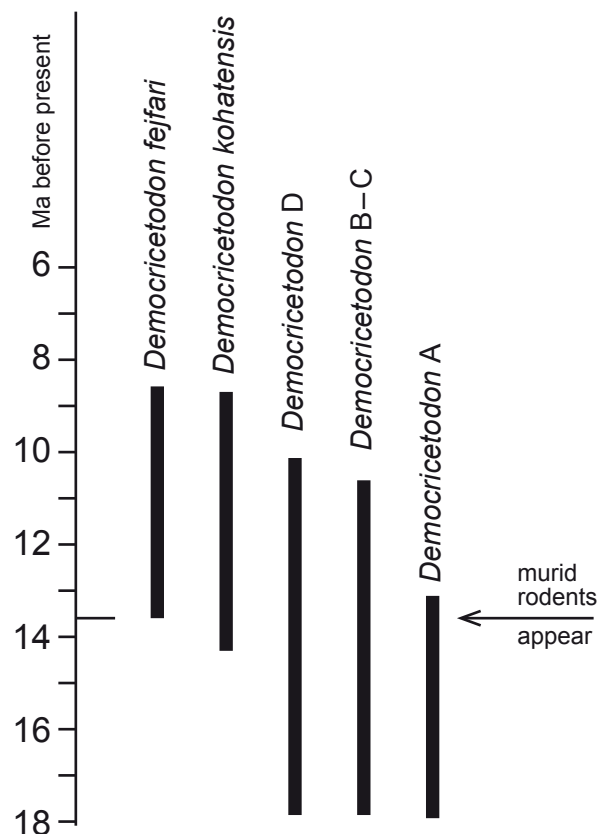
Received: July 8, 2017 | Accepted: December 18, 2017 | Issued: December 31, 2017

Introduction

The Siwalik sequence of sediments in southeastern Asia have produced an excellent record of mammals during the late Cenozoic Era, in sediments resulting from uplift of the Himalayan and Hindu Kush mountains, along with erosion and subsequent deposition of sediments on the flanks and lower slopes of those mountains. Features of these deposits were initially described by Medlicott (1864), Wynne (1875), and by Medlicott and Blanford (1879) but the potential record of former life and environments of the Siwalik deposits were not realized until publications by Pilgrim (1913) and Colbert (1935) both of whom recognized a significant radiation of mammal evolution recorded in Siwalik deposits.

Evolution of Plate Tectonics in recent decades, and the potential to better understand human and biological evolution renewed interest in Siwalik sediments in the latter half of the 20th century, including inspiration for the Fifth North American Paleontological Convention in 1992 (Badgley and Behrensmeyer 1995), and specialized monograph (Barry et al. 2002). Cricetid rodents share an important position in the Siwalik fossil record, including (1) origin of the family Muridae, the most abundant and widespread group of rodents, and (2) replacement of the family Cricetidae by the family Muridae in Siwalik deposits, spanning about four million years (14–8 Ma), partially illustrated in Text-fig. 1.

Barry et al. (2002) updated the stratigraphic and chronologic record of Siwalik deposits, with emphasis on the large mammals. This contribution is based on the data similar to that described by Barry et al. (2002), adding



Text-fig. 1. Stratigraphic/Chronologic ranges of *Democricetodon* in Siwalik deposits of Pakistan.

new information of the rodent taxon *Democricetodon*, an important genus in the family Cricetidae, recorded in the Miocene from Asia and Europe as the subgenus *Democricetodon* (*Democricetodon*) and in North America as the subgenus *Democricetodon* (*Copemys*). As noted by Jacobs (1977) and by Flynn et al. (1985) the rodent family Muridae was derived from the genus *Potwarmus*, a member of the Cricetidae, with appearance of the genus *Antemus chinjiensis* in the Chinji Formation of Pakistan. The Siwalik record also demonstrates the replacement of cricetid rodents by murid rodents during the Tertiary Epoch (see Text-fig. 1). Five species of *Democricetodon* are recorded from Siwalik deposits in Pakistan; these include *Democricetodon kohatensis*, described by Wessels et al. (1982), with 228 specimens recorded from central Pakistan, *Democricetodon fejfari* sp. nov., with 155 specimens recorded from central Pakistan in this contribution, and three smaller and unnamed species (*Democricetodon* sp. D, *Democricetodon* sp. B-C, and *Democricetodon* sp. A) whose stratigraphic ranges are shown in Text-fig. 1. The longer range of species in this group are *Democricetodon* sp. D with 432 specimens, and *Democricetodon* sp. B-C with 348 specimens; the three smaller species (*Democricetodon* sp. A. (recorded from 84 specimens), *Democricetodon* sp. B-C, and *Democricetodon* sp. D) are all represented in the oldest known Siwalik deposits, dated about 18 Ma, suggesting that they (or at least *Democricetodon* sp. A) may have lived prior to the deposition of the Siwalik deposits in Pakistan. The rodent *Democricetodon fejfari* sp. nov. was last recorded later (about 8.7 Ma) than any other cricetid rodent in Siwalik deposits of Pakistan. The appearance of *D. fejfari* sp. nov. was also about the same time as appearance of murid rodents, about 13.6 Ma. As mentioned above, Murid rodents eventually replaced cricetid rodents in Siwalik deposits and are now distributed worldwide.

Material and methods

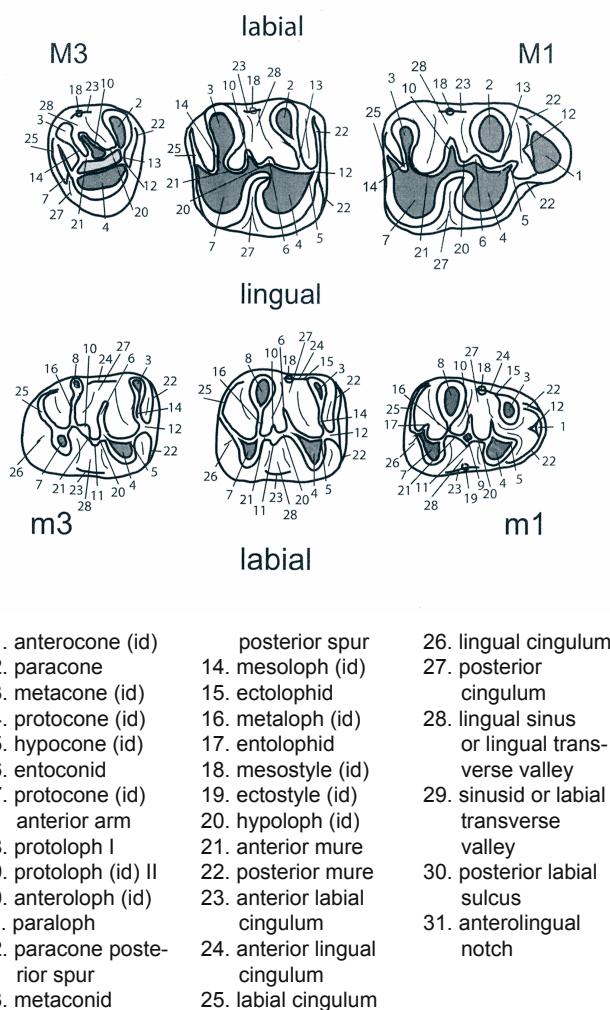
Fossils described in this contribution were recovered from Siwalik sediments in Pakistan by the process known as **screen washing**, wherein large quantities of sediment are collected with hand inspection of fine-grained sediments that contain scraps of fossilized bone. We make the assumption that most of the small mammal fossils were preserved as owl pellets that accumulate below a roosting location (such as a large tree, or a high rocky ledge) over a relatively short interval of time, and these owl pellets were later scattered and transported, along with the sediments, by rains or streams, to become embedded with the fine-grained sediment, as Siwalik deposits. Presence of small bone fragments in these deposits are our clues that they should contain the remains of owl pellets. After the collection process these fine grained sediments are spread out on large sheets of plastic or cloth and dried in the sun for several days, which aids in reducing the size of collected blocks of sediment. The fine grained sediments are then placed in screen boxes (open rectangular boxes with bottom and parts of two sides covered by wire screens), which are then placed in water, either a gently flowing stream or a large tub of water. We use two screen boxes, a smaller box that fits inside the larger box, with

coarser-sized screen (openings of about 2 mm) inside of a slightly larger screen box with finer-sized screen (openings of about 0.5 mm). That way we collect two samples of sediment (and we hope, of fossils), sorted by size. Most of the finer grained sediments flow through both screen boxes, leaving two samples of slightly different sized sediments (and we hope fossils) in the screen boxes. This process is repeated several times, each time reducing the quantity of sediment in our collected samples, and thereby reducing the quantity of sediment but keeping (we hope) the fossil remains. Throughout this process the site from which the sample was collected is identified with the resulting sediment concentrates. Usually, the larger-sized sample from each site is “picked” (that is, fossil remnants are removed) while in the field area, and the remaining sediment of that size is discarded; all of the smaller-sized sample is bagged up and brought back to the United States where it is concentrated further by floating the lighter fossils by using heavy liquids (liquids that are more heavy than the sediments and fossils) to remove most of the remaining sediment. The final concentrate is then “picked” under a microscope to recover the identifiable fossil fragments.

This repeated processing of sediment in water will cause some loss of fossils by breakage, and usually will destroy any association of fossils (such as separate teeth from the same individual) but this process is extremely good at recovering available fossils; thus, we end up with thousands of isolated teeth but few associated dentitions. The associated dentitions are extremely valuable, and highly prized for fossil identification. Consequently, we rely primarily on the size and “cusp” morphology of isolated teeth for identification of similar genera and species of the rodent taxa.

I describe the process of screen washing in more detail than usual, primarily because Oldřich Fejfar was a pioneer in development of the process of screen washing for small mammals, and we all learned from the methods that Oldřich, and others, helped to develop.

The name given to dental features is always subject to errors and confusion. A preferred terminology for dental features is illustrated in Text-fig. 2 in hope of avoiding some of the confusion. Dental terms should reflect the point of origin on the tooth and should follow a general “plan” of how these features were developed. Keep in mind that the teeth of all mammals are formed, over time, in a tooth bud located below the tooth row, by the growth of dentine and enamel within the tooth bud. The number of teeth, number of cusps, and union of cusps and ridges in each tooth are all determined genetically, prior to eruption (and wear) of the each tooth from the tooth bud. Also, the rodents in this study have only a single set of teeth that will “wear out” if subjected to excessive use; we humans have two sets of teeth, plus dentists who can rebuild or replace any teeth that we may lose during our lifetime. If a female cricetid rodent is fortunate enough to live for 12 months, she will probably die of starvation because her teeth will be worn down to smooth nubbins that cannot crush and prepare her food for digestion. To a cricetid rodent the durability of their teeth is as important as their ability to avoid predators; we measure the longevity of these rodents in months rather than years. My point is that for a rodent the function and durability of their teeth are extremely important, and any change in tooth



Text-fig. 2. Dental terminology for cricetid rodents.

development or wear can have a great effect on the durability of their teeth and their life.

One of the most variable features in the dentition of these rodents is development of the mesoloph, a thin ridge (we call it a loph) that forms between two of the major cusps in their teeth. Palaeontologists have argued for many years over how important, or unimportant, is development of the mesoloph. Moreover, we have wondered if a mesoloph might have developed in these rodents more than once, or by different means; in other words, are all mesolophs the same? In modern rodents the mesoloph develops as a ridge of enamel from a central ridge, called a mure, that divides the tooth lengthwise, more or less, into a right and left half. In the late Oligocene cricetid rodents a ridge called a **mesoloph** may develop between two major cusps (the paracone and metacone in upper teeth or the metaconid and entoconid in lower teeth) from the posterior arm of a major cusp (the protocone posterior arm in upper teeth and the protoconid posterior arm in lower teeth) rather than from the mure which is where a mesoloph usually develops in cricetid rodents. Rarely two thin ridges (lophs) may develop between these cusps in this area of the tooth of cricetid rodents, one ridge developed from the protoconid arm and one ridge developed from the mure. In this study, we try to identify whether the

thin ridge called a mesoloph develops from the posterior protocone (or protoconid) arm, which we call the protocone posterior spur, or from the mure, which we call a mesoloph. Ideally, dental features with a similar function but a different origin can (and should) be given different names as long as their source location is sufficiently distinct. Because of this, the structure that resembles a mesoloph in the teeth of these Siwalik cricetid rodents, but is derived from the arm of the protocone (or protoconid), is called the protocone posterior spur (upper teeth) or the protoconid posterior spur (lower teeth), see Text-fig. 2. Later, in the Miocene, the loph derived from the protocone (and protoconid) arm was lost as the rodents evolved, so the name and derivation of a mesoloph in late Miocene and younger rodents isn't as interesting.

Measurements of specimens were obtained by using an optical micrometer with resolution to the nearest 0.01 mm and estimating smaller divisions when overlap occurred. Cusp height is a very important feature of rodent teeth, primarily because a common trend in rodents (as in many other mammals) was to develop ever-growing cheek teeth; also, cusp height in these rodent teeth is highly variable between different teeth in the same individual. Therefore, cusp height was measured, as a standard on M2, from the base of enamel to the labial inflection in the middle of the tooth. Dental formulae follow standard usage and nomenclature for cricetid rodents following Wood and Wilson (1936) with modifications by Lindsay (1972) and Mou (2011). Terminology for dental features is illustrated in Text-fig. 2. Upper teeth are designated by letters in upper case (M) and lower teeth are designated by letters in lower case (m). All specimens are currently located at the University of Arizona in Tucson; they are the property of either the GSP or the PMNH.

Abbreviations

CV, coefficient of variation; GPTS, Geomagnetic Polarity Time Scale; h, crown height; H, index of crown height (h/w); L, left; l, greatest antero-posterior length; M, mean; Ma, megannum (one million years of the radiometric time scale); N, number of specimens; Max, maximum; Min, minimum; my, million of years, as an interval of time; NALMA, North American Land Mammal Age; R, right; OR, observed range; SD, standard deviation; w, greatest transverse width.

Institutional abbreviations

AMNH – American Museum of Natural History, New York, USA; GSP – Geological Survey of Pakistan, Pakistan; PMNH – Pakistan Museum of Natural History, Pakistan.

Systematic palaeontology

Order Rodentia BOWDICH, 1821

Family Cricetidae FISCHER [DE WALDHEIM], 1817

The Cricetidae are a very successful and widespread clade of mammals, with a good fossil record, and they are widely recognized as the rodents that evolved into the clade Muridae in the Miocene Epoch and the clade Arvicolidae in the Pliocene Epoch. Much of the terminology and

knowledge of fossil cricetids was described by the German palaeontologist Samuel Schaub (1925), who called these rodents “Cricetodontidae”. A later German palaeontologist, Volker Fahlbusch (1964) collected much more abundant material from southern Germany, and assigned much of Schaub’s “Cricetodontidae” into two large subgroups he called the genera *Democricetodon* and *Megacricetodon*. Fahlbusch’s subgroups can be easily recognized dentally by *Democricetodon* having a single cusped anterocone on M1 and *Megacricetodon* having a bicusped anterocone on M1. Actually, Fahlbusch had identified a third group among the cricetids from Germany that he called *Cotimus*, a genus described from North America. Fahlbusch later decided that *Megacricetodon* and *Cotimus* are the same genus, so we now recognize two major groups among the Miocene Cricetidae, *Democricetodon* and *Megacricetodon*. Another feature of *Democricetodon* is that it sometimes has what can be called two mesolophs, thin ridges of enamel that are directed labially between the two main labial cusps (paracone and metacone) in upper teeth, or two mesolophids, similar thin ridges that are directed lingually in the middle of lower teeth. *Democricetodon* from Pakistan may have two mesolophs (upper teeth) or mesolophids (lower teeth) in its dentition in which case the anterior loph is derived from the protocone (id) posterior spur and the posterior loph is derived from the mure. This (along with other features) is how we recognize *Democricetodon* in Miocene deposits of Pakistan.

Genus *Democricetodon* FAHLBUSCH, 1969

Democricetodon fejfari new species

Text-fig. 3a–f

Holotype. Left dentary with m1–3 (YGSP 19321) (Text-fig. 3c); type specimen will be deposited in collection of the Geological Survey of Pakistan.

Etymology. *fejfari*, named for Oldřich Fejfar a distinguished vertebrate palaeontologist and long-time friend who is well known for his numerous contributions and insight on the history and evolution of small mammals.

Type locality. YGSP locality 388, Pakistan.

Distribution. Middle Miocene, about 13.8 to 8.7 Ma (YGSP locality 491 to YGSP locality 387).

Diagnosis. *Democricetodon fejfari* sp. nov. is a large cricetid rodent (see Tab. 1), larger than any currently known species of *Democricetodon* in Pakistan, comparable in size to *Democricetodon lindsayi* in Asia, to *Democricetodon affinis* and *Democricetodon gaillardi* in Europe, and to *D. (Copemys) longidens* and *D. (Copemys) barstowensis* in North America. *Democricetodon fejfari* sp. nov. has a small single cusped anterocone on M1 that is slightly asymmetrical, elongated transversely with a short labial and longer, thinner lingual side; the anteroconid on m1 is also small and single cusped, with near equal (slightly longer labial) side lophs. Principal cusps in upper molars are nearly opposite to the opposing cusps, with only slight anterior shift in position of lingual cusps relative to labial cusps; principal cusps of lower molars are more offset, with lingual cusps located opposite to the anterior side of labial cusps. In upper molars the distal end of the anterior arm of the protocone is often flexed labially, forming a short protocone anterior loph (that resembles a mesoloph) directed toward the paracone; and in lower molars the distal arm of the protoconid posterior arm is flexed lingually (to resemble the mesolophid), directed toward the lingual margin. A thin mesoloph, and mesolophid, are usually short, if present.

Differential diagnosis. *Democricetodon fejfari* sp. nov. differs from *Democricetodon lindsayi* in having a single cusped anterocone on M1, which is slightly bilobed in *D. lindsayi*; *D. fejfari* sp. nov. differs from *D. affinis* that has the paraloph descend posteriorly from the paracone apex, to join the posterior arm of the protoconid whereas the paraloph on M1 of *D. fejfari* sp. nov. is always directed anteriorly to join the anterior arm of the protoconid; *D. fejfari* sp. nov. differs from *D. gaillardi* that usually has two lophs from the paracone that join both the anterior and posterior arms of the protoconid, while the paraloph in *D. fejfari* sp. nov. is always directed anteriorly, never joining

Table 1. Calculations of *Democricetodon fejfari*. Measurements in mm.

	M1 length	M1 width	M2 length	M2 width	M3 length	M3 width
N	27	30	33	33	3	3
M	2.401	1.491	1.644	1.464	1.55	1.427
SD	0.185	0.097	0.104	0.110	0.416	0.038
Min	2.17	1.32	1.50	1.23	1.30	1.40
Max	2.98	1.66	1.96	1.63	2.03	1.47
CV	7.71	6.036	6.30	6.56	26.82	2.65
	m1 length	m1 width	m2 length	m2 width	m3 length	m3 width
N	18	18	33	34	14	14
M	1.898	1.323	1.652	1.419	1.623	1.322
SD	0.269	0.150	0.160	0.155	0.257	0.161
Min	1.03	0.96	1.14	0.98	1.26	1.01
Max	2.13	1.56	1.88	1.72	2.40	1.56
CV	14.15	11.30	9.68	10.91	15.816	12.22

the posterior arm of the protoconid. *D. fejfari* sp. nov. differs from *Democricetodon kohatensis* and all of the other species of *Democricetodon* recorded from the Siwalik sequence in being larger in size.

Description. Details of the dentition are described by tooth, in the following format.

M1. Occlusal outline is lozenge shape, longer than wide, and narrow anteriorly. Largest cusp is the anterocone, followed by the hypocone that is slightly smaller, and about equal to size of the metacone, both are slightly larger than the protocone that is slightly larger than the paracone. Lingual cusps are positioned slightly anterior to labial cusps with minimal transverse offset of opposing cusps. The anterocone is large, single cusped, elongated transversely with the cusp apex located slightly labial to the midline. Protocone anterior arm is medium length, directed toward the lingual side of the anterocone where it usually joins the anteroloph lingual to the midline and joins the paraloph near the midline; protocone posterior arm is medium length, directed toward the metacone where it usually joins the posterior mure and/or the paraloph near the midline. As noted in the methods section, the protocone posterior spur is identified by a pronounced change in orientation of the protocone posterior arm, that resembles a mesoloph. Hypocone anterior arm is prominent and medium length, it is usually directed toward the paracone and usually joins the posterior mure near the midline; hypocone posterior arm is short, directed toward the posterior midline where it merges with the posterior cingulum. The paracone lacks a posterior spur. The anteroloph is short and low, directed posteriorly from the lingual side of the anterocone to usually join the protocone arm or the paraloph lingual to the midline; an anterior paraloph is usually absent (present in 3 of 22) directed antero-lingually from the paracone to join either the protocone anterior arm or the anteroloph (or both) lingual to the midline; a posterior paraloph, descends lingually from the paracone apex and is flexed posteriorly to join the anterior mure near the midline. Protoloph I is usually minute or absent. A mesoloph is usually minute or indistinct (12/20) or long (8/20), directed posterolabially from the mure near the midline. A mesostyle, ectoloph, ectostyle and anterior metaloph are all absent. A posterior metaloph is medium length and low, it descends posterolingually from the metacone apex toward the posterior cingulum to (usually) join the posterior cingulum near the midline. The central mure is short and low, it weakly joins the protocone posterior arm and the hypocone anterior arm. A lingual anterior cingulum is short, descending lingually from the anterocone apex, then curving posteriorly to terminate anterior to the base of the protocone; a labial anterior cingulum is short, of moderate height, directed labially from the anterocone apex to terminate near (or join) the anterolabial base of the paracone. Transverse shelves are low and synclinal (lower in middle), usually aligned (more or less) opposite to one another, and closed medially by the mure. The lingual sinus is elongated transversely and narrow, it is slightly closed by the low lingual cingulum. The lingual cingulum is short and low; a labial cingulum is minute or indistinct; the posterior cingulum is long and straight, rarely with a slight expansion in mid-length (possibly an incipient hypoconulid II), and

either terminates posterior to the metacone or rarely curves anteriorly to ascend the posterior metacone. There are three roots, a large, transversely elongated medial root plus a large round anterior root and smaller round posterolabial root.

M2. Occlusal outline is a rounded rectangle with a short posterolingual corner, longer than wide and slightly wider anteriorly. Largest cusp is usually the hypocone (22/31) or the protocone which is almost as large, followed in size by the paracone, and the smaller metacone. Lingual cusps are usually (26/34) located opposite to the center of labial cusps, or labial cusps are located opposite to the anterior side of lingual cusps (7/34), with a slight transverse offset of cusps. Protocone anterior arm is short, it is directed anterolabially to join the anteroloph near (19/29) or slightly lingual to (10/29) the midline. Protocone posterior arm is short and narrow, directed toward the metacone to join the protocone posterior spur (33/35) and the anterior mure near the midline; the protocone posterior spur is directed toward the paracone and is usually shorter than the mesoloph and terminates freely. Hypocone anterior arm is prominent and long, directed toward the paracone to join the entoloph and posterior mure near the midline; hypocone posterior arm has features like M1, except that several (8/35) M2 show an incipient hypolophid II. A paracone posterior spur is usually absent or indistinct.

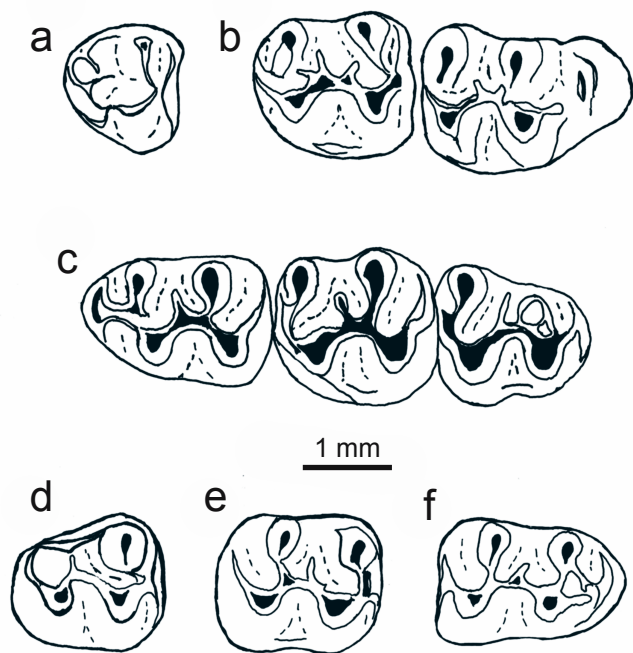
The anteroloph is short or minute, it is located near or slightly lingual to the midline. A paraloph is medium length, it descends lingually or anterolingually from the paracone apex to usually join both the anteroloph and the protocone arm (24/30), or only the protocone arm (6/30), near the midline. Protoloph I is minute and usually joins the paraloph. Protoloph II is interpreted the "Protocone posterior spur". A mesoloph is low, directed labially from the posterior mure, it is usually (25/32) low and medium length, or short (7/32), and terminates freely. A mesostyle, ectoloph and ectostyle are all absent. The metaloph is medium length, it descends lingually from the metacone apex to usually (32/34) join the hypocone anterior arm or the hypocone posterior arm (1/34) or both (1/34) near the midline. The central mure is short and low; it usually joins the protocone posterior arm and the hypocone anterior arm. A lingual anterior cingulum is medium length, it descends lingually from the anterocone and curves posteriorly to terminate near the lingual base of the protocone; the labial anterior cingulum remains relatively high and straight, until it approaches the tooth margin then curves posteriorly and descends to terminate near the anterior base of the paracone. The transverse shelves are narrow and synclinal (lower in middle), placed more or less opposite to one another, and are closed medially by the mure. The lingual sinus has features like that seen on M1. A lingual cingulum is short to medium length; a labial cingulum is short and low (or indistinct); the posterior cingulum is long, gently curving anteriorly and descending to terminate at the base of the metacone, or rarely to ascend the metacone. A short hypolophid II may be developed (8/35) on the posterior cingulum near the midline. There are three roots, as on M1.

M3. Occlusal outline is a rounded and inflated triangle, with a more straight anterior margin. Largest cusp is the protocone that is slightly larger than the paracone; the hypocone is small and the metacone is usually minute (2/4) or indistinct (2/4). Protocone anterior arm is medium length, directed anteriorly to join the anterior cingulum lingual to

the midline. Protocone posterior arm is medium length, it is directed posterolabially and is continuous with the hypocone and posterior cingulum. A protocone posterior spur is usually absent (3/4) or short (1/4), it is directed toward the paracone from the distal protocone arm to join the small hypocone and the posterior cingulum. The hypocone anterior arm is short, it bifurcates distally to join the posterior mure and the metaloph near the midline. Hypocone posterior arm is high and robust, it is confluent with the posterior cingulum. The anteroloph is high and short, it is located near the midline to join the paraloph and, distally, the mure. The paraloph descends lingually from the paracone apex to join the anteroloph (3/4) or the anterior cingulum (1/4) near the midline. Protoloph I is absent; protoloph II is interpreted the protocone posterior spur. A thin mesoloph is directed labially (2/3) from the central mure, or is absent (1/3). A mesostyle, ectoloph and ectostyle are all absent. A metaloph descends lingually from the indistinct metacone to join the mure near the midline; metaloph II is absent. The central mure is medium length and relatively high, oriented anteroposteriorly, and joining the paraloph and metaloph near the midline. Lingual anterior cingulum is high, it descends lingually from the high anterior cingulum lingual to the midline and curves posteriorly to terminate near the lingual base of the protocone; labial anterior cingulum is high and relatively long, it curves posteriorly near the tooth margin to merge with the anterior base of the paracone slightly short of the labial tooth margin. Transverse shelves are indistinct. A lingual sinus is indistinct between the protocone and hypocone, marked only by a slight but distinctive inflection of the lingual margin. A labial cingulum is low and continuous; a lingual cingulum is absent or indistinct; the posterior cingulum is moderately

high and thin, directed labially from the hypocone and gently curving labial to the minute metacone near the posterolingual margin. Roots are unknown.

m1. Occlusal outline is lozenge shape, longer than wide, and wider posteriorly. Largest cusp is usually the entoconid or the hypoconid, both are slightly larger than the metaconid and the protoconid, which are much larger than the anteroconid. Lingual cusps are placed opposite to the anterior side of labial cusps with noticeable but slight transverse offset of opposite cusps. The anteroconid is small, centrally located on the anterior cingulum and may be symmetrical (8/18), or shorter lingually (6/18), or longer lingually (4/18). Protoconid anterior arm is medium length, it is directed anterolingually to weakly join the paralophid and anterolophid (9/18), or only the paralophid (2/18), or the anterior cingulum (2/18), or only the anterolophid (1/18), or terminate (4/18) near the midline. Protoconid posterior arm is usually medium length, it is directed toward the entoconid to join the protoconid posterior spur (15/19), or to join the anterior mure (3/19) near the midline, or it is indistinct (1/19). The protoconid posterior spur (like the protocone posterior spur of M1) is interpreted the distal end of the protoconid posterior arm that is marked by an angular change in orientation; it is variable in length, directed lingually and terminates freely. The hypoconid anterior arm is short or medium length, directed anterolingually toward the metaconid to join the entolophid and posterior mure near or slightly labial to the midline. The hypoconid posterior arm is short, directed toward the posterior midline to merge with the inflated posterior cingulum. The anterolophid is usually short and low, or indistinct, located slightly labial to the midline. A protolophid is usually minute (15/20) or absent (5/15); it is directed lingually from the protoconid toward the metaconid. The metalophid is highly variable, it descends labially or anterolabially from the metacone apex and either curves anteriorly (8/18) to joins the anterolophid, or bifurcates (7/18) to join both the protoconid and the anterolophid, or it continues labially to weakly join (3/18) the protoconid. There is neither a metalophid II nor a mesolophid. Note that either a protoconid posterior spur or a mesolophid is developed in these teeth, but that both lophes, (which resemble one another) usually never occur in the same tooth. A mesostylid, hypolophid I, hypolophid II, and an ectostylid are also absent. An ectolophid is usually (18/21) absent, or rarely low and medium length (3/21) but terminating freely. The entolophid descends labially from the entoconid apex to join the hypoconid anterior arm slightly labial to the midline. The central mure is short, usually straight (or slightly curved), located slightly labial to the midline. A lingual anterior cingulum is usually medium length (15/19) or short, it descends lingual to the anteroconid and curves posteriorly to either terminate (18/19) or ascend (1/19) the anterolingual base of the metaconid. A labial anterior cingulum is long, it descends labial to the anteroconid, curves posteriorly and terminates near the labial base of the protoconid. Transverse shelves are slightly offset with lingual side slightly anterior to the labial side that is slightly lower and more synclinal than the lingual shelf; transverse shelves are closed medially by the mure. A labial sinusid is deep and wide, with a gently rounded (9/18) or straight (9/18) inner margin. A lingual cingulum is indistinct or low and short; a labial cingulum



Text-fig. 3. Selected specimens of *Democricetodon fejfari* sp. nov. a: right M3, YGSP 19262; b: right maxilla with M1 and M2, YGSP 19285; c: left dentary with m1, m2, and m3 (holotype), YGSP 19321; d: left right m3, YGSP 19330; e: right m2 (reversed), YGSP 19324; f: right m1, YGSP 19279.

is medium length and low; posterior cingulum is long, high and slightly inflated, gently curving anteriorly to terminate at the posterolingual base of the entoconid and partially close a shallow posterolingual basin. Posterior labial sulcus is shallow. There are two roots, a round anterior root and a transversely elongated posterior root.

m2. Occlusal outline is a rounded rectangle, longer than wide, slightly wider posteriorly. The four main cusps are very uniform in size although usually (18/31) the labial cusps appear slightly larger than the lingual cusps. Lingual cusps are placed opposite to the anterior side of labial cusps, with a slight transverse offset of opposing cusps. Protoconid anterior arm is medium length, directed toward the anterior midline to join either the minute anteroloph (16/31) or the anterior cingulum (15/31) slightly labial to the midline. Protoconid posterior arm is usually short or medium length, it is directed toward the entoconid to join the protoconid posterior spur and the anterior mure slightly labial to the midline. A protoconid posterior spur is usually short or medium length, it is directed labially from the junction with the protoconid arm and usually (31/35) terminates freely, or weakly joins (4/35) the posterior mure. A metaconid posterior spur is absent. Hypoconid anterior arm is usually short or medium length, it is directed toward the metaconid to join the posterior mure slightly labial to the midline; the hypoconid posterior arm has similar features to those seen on m1. Anterolophid is minute or indistinct, it is located slightly labial to the midline. Metalophid I is usually short (26/32), or absent (6/32); it descends anterolabially from the metacone apex to usually join the anterior cingulum lingual (26/32) to the midline, or (6/32) the protoconid anterior arm near the anterolophid. Metalophid II is absent. Mesolophid and mesostylid are absent or indistinct. An ectolophid is usually absent, it is weakly developed and long on a single specimen (inv. no. 44137). Ectostylid is absent. Entolophid I is medium length, it descends labially from the entoconid apex and is flexed anteriorly to join the posterior mure near the midline. Hypolophid I is minute; hypolophid II is absent. The central mure is short, it is rarely (4/35) oriented slightly oblique (anterior end more lingual) to the tooth, located near the midline and joins the protoconid posterior arm with the hypoconid anterior arm. Labial anterior cingulum is high near the midline, it descends labially and curves posteriorly to terminate near the labial base of the protoconid; lingual anterior cingulum is high, it merges with the metaconid short of the lingual tooth margin. Transverse shelves are synclinal; the labial shelf is slightly lower and wider than the lingual shelf; shelves are closed medially by the central mure. A labial sinusid has features like that seen on m1. A lingual cingulum is short or indistinct; a labial cingulum is medium length and low; the posterior cingulum has features like those seen on m1. Roots have features similar to those of m1.

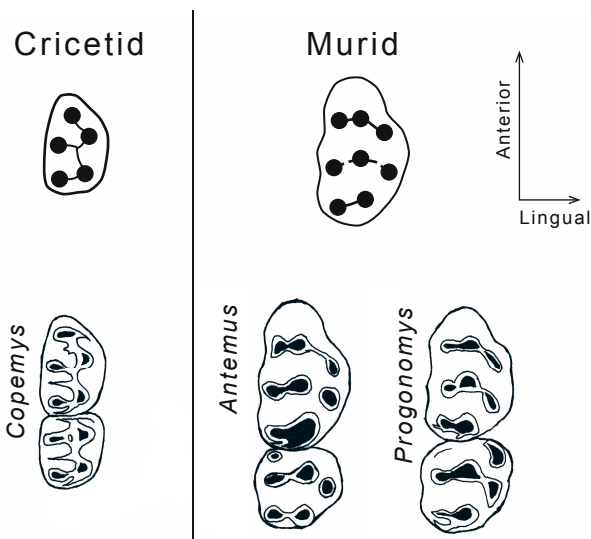
m3. Occlusal outline is lozenge shape, longer than wide, and much more narrow posteriorly. Largest cusp is the protoconid which is slightly larger than the hypoconid, and both are larger than the metaconid; the entoconid is absent or indistinct. The metaconid is located opposite to the anterior side of the protoconid, and the hypoconid is placed posterior to the protoconid. Protoconid anterior arm is short, it is directed toward the anterior midline to join either the anterior cingulum (7/8) or anterolophid (1/8) near the midline. Protoconid posterior arm is medium length, it is directed

toward the lingual margin where an entoconid should be located, and joins both the protoconid posterior spur (if present) and the anterior mure near the midline. Protoconid posterior spur is short and narrow, it is directed lingually and terminates short of the lingual margin. Metaconid posterior spur is absent. Hypoconid anterior arm is short, it is directed toward the lingual margin to join the remnant lophid of the entoconid near the midline. Hypoconid posterior arm is short, it merges with the posterior cingulum near the midline. Anterolophid is indistinct or absent; metalophid I is short, it descends anterolabially from the metaconid apex and gently curves anteriorly to join the anterior cingulum (or rarely the anterolophid) lingual to the midline. Metalophid II, mesolophid, mesostylid, ectolophid, and ectostylid are all absent. An entolophid remnant is represented by its distal loph (the entoconid is absent) that joins the posterior mure near the midline and is posterior to the protoconid posterior spur; the entolophid remnant terminates short of the lingual margin. Hypolophid II is absent. The central mure is short, located near the midline; it is slightly flexed near the middle and joins the protoconid arm and the hypoconid arm near the midline, with two thin lophs (protoconid posterior arm and the entolophid remnant) directed lingually. Labial anterior cingulum may be indistinct or, if distinct, descends from the high anterior cingulum near the midline, and gently curves posteriorly to terminate near the labial base of the protoconid; lingual anterior cingulum is medium length, high and straight, it is directed lingually from the midline to terminate short of the lingual margin anterior to the metaconid. Transverse shelves and lingual sinusid have features similar to those in m2. Lingual cingulum is moderately high and continuous between the metaconid and posterior cingulum; labial cingulum is short and low; posterior cingulum is high and slightly inflated on the gently curving posterolingual tooth margin, weakly joining the labial cingulum. Labial sulcus is deep and relatively wide, as in m2. Roots have features similar to those on m2.

Democricetodon feffari sp. nov. was a relatively large cricetid rodent, the last species of cricetid rodent to inhabit Pakistan, replaced by advanced rodents of the family Muridae. Muroid rodents in Siwalik deposits of Pakistan represent three closely related taxonomic groups, the Cricetinae, Myocricetinae, and Murinae. As pointed out by Barry et al. (2002) the fossil record of later Miocene deposits (Chinji and Dhok Pathan Formations) in Pakistan is rich and highly informative; the earlier fossil record in Pakistan (Kamlial Formation) is not so rich but is also very informative, especially as we search for climatic information in the fossil record. The success or failure of diverse and widespread taxa, such as Cricetinae, Myocricetinae, and Murinae in Siwalik deposits remains poorly understood. The climatic significance of Murinae replacing Cricetinae warrants more scrutiny in hope of learning the role of climate change with regard to faunal replacement.

Faunal replacement of Cricetidae by Muridae in Pakistan

What causes faunal replacement? And, what can we learn about evolution by searching for causes of faunal



Text-fig. 4. Comparison of cusp positions and connections in cricetid and murid rodents (figures not to scale).

replacement? Faunal replacement of one family by another close family must be relatively common feature in evolution; however, the cause of faunal replacement is poorly understood. Perhaps the replacement of Cricetidae by Muridae in Siwalik deposits of Pakistan is one of the best examples that we can find for a replacement mechanism. Possible factors that might cause faunal replacement include (a) climate, (b) a physical change in structure, (c) change in reproductive capacity, (d) change in aggressive behavior, or (e) genetic change (e.g., mutation). Let's evaluate these possible causes.

Climate. If climate were an important factor in the replacement of Cricetidae by Muridae we should see a significant difference in the distribution of cricetids, relative to murids, in the successive global distribution of these families. This has not been observed, although no detailed study of distribution of cricetids and murids subsequent to the Miocene has ever been made, to my knowledge, so it doesn't look like climate is a likely cause of this faunal replacement.

Structural change. There is a significant change in the position of cusps of teeth between cricetid and murid rodents. Cricetid dentitions tend to have alternating cusps, whereas murid dentitions tend to have cusps aligned in chevrons (see examples in Text-fig. 4). Prior to 1977 when Louis Jacobs named and described *Antemus chinjiensis* the identification of cusps in murid teeth were poorly known. Cusps of murid teeth were often assigned letters (like cusp t1, cusp t2, etc.) to identify separate cusps of individual teeth. Jacobs (1977) was able to identify the terminology long-established for cusps of rodents (protocone, hypocone, paracone, metacone, and entocone) in murid dentitions enabling identification of individual tooth cusps in murid teeth. Homology of murid tooth cusps is no longer a problem, following the interpretations proposed by Jacobs. As proposed by Jacobs (1977), early murids had changed the position (and union) of several cusps inherited from cricetids, along with adding one or two additional cusps on the lingual side of upper teeth and the labial side of lower teeth. Text-fig. 4 illustrates the first

and second upper molar of the cricetid of subg. *Copemys*, and two early murid genera, *Antemus* and *Progonomys*. Opposing cusps of cricetid teeth tend to be placed and joined by alternation of cusps (as in *Copemys* in Text-fig. 4); cusps of murid teeth tend to be placed and joined in transverse rows consisting of three cusps arranged like a chevron, with the middle cusp slightly anterior to the lateral cusps (as in *Antemus* and *Progonomys* in Text-fig. 4).

Reproductive capacity. Biology of modern cricetids (as well as murids) is well established, based on decades of mammalian biology, summarized in a multiauthored volume, edited by J. A. King (1968). Based primarily on that information, we see that there appears to be little difference in the reproductive biology of cricetids and murids, both well-studied and described for many years, concluding that little difference occurs between the number of embryos (mean of 3.4, with differences from 2 to 5). It appears that the availability of food is probably the most important factor, with seasonality the main determinant reflecting differences in reproductive capacity. In both families gestation and litter size are comparable, with embryo development similar. I see no significant difference that would cause replacement of cricetids by murids.

Aggressive behavior. Both cricetid rodents and murid rodents are small mammals. Aggressive behavior is never a smart attitude for any small mammals. It is unlikely that this faunal replacement was caused by aggressive behavior.

Genes. Genetics of both cricetid rodents and murid rodents is relatively well established, primarily because of role these mammals have played in medical science; however, none of this genetic information has been directed toward the possible cause of faunal replacement. Perhaps future study of genetic variation in cricetid and murid rodents might shed light on possible genetic change between these two very diverse groups but to my knowledge genetic none of the genetic differences between these two families supports faunal replacement.

We have not exhausted all of the possible causes for faunal replacement; however, among the more obvious and reasonable causes we have evaluated, the only cause that currently bears merit is a structural change in the position of cusps in cricetid and murid rodent teeth, changing from alternation of opposing cusps in cricetids to union of three cusps in rows, in murids, with alignment of these cusps as a chevron, with the middle cusp anterior to the adjacent cusps. This structural change is well established, and thereby serves as a possible hypothesis for cause of this faunal replacement. Further study of this hypothesis is warranted.

Acknowledgements

This contribution is dedicated to my friend and colleague, Oldřich Fejfar whom I have known for many years, and with whom I have shared many pleasant times. I have always admired Oldřich's work, and I am delighted to contribute to this publication, honoring an esteemed colleague. I also wish to acknowledge the help and support of all those colleagues (and institutions) who contributed to the collection of fossils from Siwalik deposits in Pakistan. The Siwalik fossil record is truly outstanding, and having shared in the collection

and assembly of that record I have numerous cherished memories, too many to count. Colleagues like Oldřich are priceless. Many thanks for all the memories we share Oldřich. It has been very memorable, and deeply cherished.

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