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A new basal raoellid artiodactyl (Mammalia) from the middle Eocene Subathu Group of Rajouri District, Jammu and Kashmir, northwest Himalaya, India

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Abstract

A new artiodactyl of moderate size, *Rajouria gunnelli* nov. gen., nov. sp., is described on the basis of several dentaries, maxillae and isolated teeth from the middle Eocene Subathu Group of the Kalakot area, Rajouri District, Jammu and Kashmir, India. Despite its general resemblance with the family Dichobunidae by the retention of a paraconid on m1-2 and a simple P4 where endocristids do not form an anterior loph, this taxon shares with Raoellidae two unambiguous characters: the presence of a hypoconid on p4, and an asymmetrical P4. The phylogenetic position of the new taxon within the Cetacea–Raoellidae clade is strongly supported by seven non ambiguous synapomorphies, among which a cristid obliqua on lower molars anteriorly pointing towards the postectoprotocristid, and a P3 with only two roots. The presence of a new basal raoellid in the middle Eocene Subathu Group sheds new light on the phylogeny and paleobiogeography of raoellid artiodactyls.

Key words: Raoellidae; Artiodactyla; Subathu; India; Phylogenetic analysis ; Micro-CT scan

1. Introduction

Artiodactyls are the most common medium-sized mammals in the middle Eocene of the Indian subcontinent and Southeast Asia. The middle Eocene Subathu Group in northwest Himalaya is one of the most important geological units in India that is known for artiodactyls, especially Raoellidae. This family is important in the evolutionary history of cetartiodactyls because it is closely related to Cetacea (Thewissen et al., 2007). So far, raoellids have been described by several authors from localities such as Kalakot, Sindkhatuti, Chenpur, Tatapani, West Babbian Gala, East Babbian Gala, Moghala (or Moghla or Mougla), all in Rajouri (or Rajauri) District of Jammu and Kashmir and from the type area of Subathu in Himachal Pradesh (Ranga Rao, 1971; 1972; 1973; Sahni and Khare, 1971; Kumar and Sahni, 1985; Thewissen et al., 2007). They have been first related to different families of artiodactyls before they were given their own familial status by Sahni et al. (1981). Presently, raoellids are represented by four genera: *Indohyus*, *Khirtharia*, *Kunmunella*, and *Metkatius* (Kumar and Sahni, 1985). In this paper, we describe a new medium size raoellid artiodactyl on the basis of nearly complete upper and lower dentition, recovered from a new fossil locality located near the village of Aiji, Rajouri District, Jammu & Kashmir. The new locality, named East Aiji-2 (see Waqas and Rana, 2020), was discovered in 2017 by one of us (MW) ca. 2 km away from East Babbian Gala (Fig. 1). It yielded raoellid skulls, dentaries, maxillae, postcranial elements, and numerous isolated teeth. Raoellidae are mainly documented from the middle Eocene of India. However, they are also known from the Kuldana Fm. in Lammidhan and Ganda Kas (Punjab Province) and Chorlakkhi (Kohat District, North-West Frontier Province) in Pakistan (Dehm and Oettingen-Spielberg, 1958; West, 1980; Thewissen et al., 1987), and from Shanghuang fissure B, Jiangsu Province in China (Metais et al., 2008; Orliac and Ducrocq, 2012). The wellpreserved remains of the new raoellid from the Kalakot area provides new information on the morphological characters, phylogeny, and paleobiogeographic implications of the family.

2. Geological setting

The geology of the Subathu Group of the Kalakot area, northwest Himalaya has been described and discussed since nearly 150 years (e.g., Medlicott, 1876; Simpson, 1904; Wadia, 1928; Middlemiss, 1929; Pascoe, 1964; Karunakaran and Ranga Rao, 1979; Singh and Andotra, 2000). In the Kalakot area, the middle Eocene Subathu Group rocks are in the form of inliers, named Kalakot inlier, Metka inlier, and Moghala inlier, respectively (Fig. 1). The sequence of the Subathu Group rocks is rarely exposed but it always overlies the Precambrian Sirban limestone (Bhandari and Agarwal, 1966). In the Kalakot inlier there is an unconformity of 3–4 m sequence of chert breccia between the Eocene rocks and the Precambrian limestone. In the Metka and Moghala inliers the Subathu rocks are directly in contact with the underlying Precambrian Sirban limestone. At Kalakot and in the adjoining areas of Metka and Moghala, the typical Subathu sequence is composed of basal carbonaceous shale and intercalated sub-anthracitic coal seams (Lower Subathu), overlain by a succession of olive green shale alternating with thick foraminiferal limestones (Middle Subathu). The shale-limestone sequence underlies a rock unit comprised of purple shale, grey-red ossiferous siltstone, shelly limestone, and grey fossiliferous limestone (Upper Subathu). Above the fossiliferous horizon, marking the top of the Subathu series is a green quartzose sandstone bed, which is consistently present at the top of each section measured in the area (Murree Fm.). The locality of East Aiji-2 (33_290480' N, 74_290040' E) is located in the eastern part of Aiji village. In this locality, the Subathu Group is little exposed above and below the road. The Upper Subathu Group consists of red to grey maroon colour shale which yields most of the vertebrate fossils (Fig. 2). The middle Eocene age of the Subathu Group has been given by Sahni and Khare (1971, 1973) and confirmed by Mathur (1978) based on foraminifera, and then by later authors based on the mammalian fauna.

3. Material and methods

The specimens described in this paper were recovered from the middle Eocene Subathu Group by hand-picking in the red to grey maroon colour shale during the 2017 field season. Due to the hardness of the shale most of the specimens were extracted with hammer and chisel. They were all discovered from a bonebed representing a surface of about two square meters. Further laboratory preparation was done in the Department of Geology of the HNB Garhwal University, Srinagar with the help of a microscope and other equipments. Final preparation and photography have been done at the Royal Belgian Institute of Natural Sciences (RBINS), Brussels. Micro CT-scanning has also been done at RBINS using a RX-Solution Easy Tom with a voxel size of 29 μ m. The specimens are represented by well-preserved isolated upper and lower teeth as well as partial maxillae and dentaries. All specimens are stored in the paleontological laboratory of the HNB Garhwal University. The specimens were identified and compared with casts of published specimens and based on iconography from the literature. Dental terminology (Fig. 3) mostly follows Boisserie et al. (2010) and Orliac and Ducrocq (2012). The measurements were taken by using a Vernier calliper. The phylogenetic affinities of the new taxon were tested through a phylogenetic analysis widely based on Orliac and Ducrocq (2012). We kept the taxonomic sampling widely unchanged and coded the group of interest (i.e., Raoellidae) at the specific level. Two new characters, relevant at the raoellid scale, were included (characters 25 and 27). The matrix was treated under the assumption of the minimal model of unweighted parsimony, using PAUP* v. 4.0a (build 166; Swofford, 2003), with a Branch-and-Bound search. The data matrix and the character list are available in Appendix A.

Abbreviations: BMNH M: Museum of Natural History, Mammal Collection, London, UK; GSP-UM: Geological Survey of Pakistan-University of Michigan collection, Quetta, Pakistan;

GU/RJ: Rajouri collection, Department of Geology, H.N.B. Garhwal University, Srinagar, Uttarakhand, India; H-GSP: Howard University–Geological Survey of Pakistan, Quetta, Pakistan; IVPP: Institute of Vertebrate Paleontology and Palaeoanthropology, Beijing, China; LUVP: Lucknow University (Vertebrate paleontology), Lucknow, India; NMMP_KU: National Museum Myanmar, Paleontology, Kyoto University (stored in the National Museum, Yangon, Myanmar); ONG/K: Oil and Natural Gas Commission–Kalakot collection, Dehradun, India; UM: University of Michigan, Ann Arbor, Michigan, USA; UM2: Université Montpellier 2, Montpellier, France; USNM: Department of Paleobiology, United States National Museum of Natural History, Smithsonian Institution, Washington D.C.; VPL/K: Vertebrate Palaeontology Laboratory, Panjab University, Chandigarh, India; WIF/A: Wadia Institute of Himalayan Geology, Dehradun, Uttarakhand, India.

4. Systematic paleontology

Order Artiodactyla Owen, 1848

Family Raoellidae Sahni, Bhatia, Hartenberger, Jaeger, Kumar,
Sudre et Vianey-Liaud, 1981

Genus Rajouria nov. gen. Rana, Waqas, Orliac, Folie et Smith

Etymology: Named for the Rajouri District.

Included species: *Rajouria gunnelli* nov. gen., nov. sp. Rana, Waqas, Orliac, Folie et Smith (type and only species).

Diagnosis: Same as the type and only species, by monotypy.

Rajouria gunnelli nov. gen., nov. sp. Rana, Waqas, Orliac, Folie et
Smith

Figs. 4–8

Etymology: Named in honor of Dr. Gregg Gunnell (Duke Lemur Center, Durham, USA) who passed away unexpectedly in 2017.

Holotype: GU/RJ/362, left dentary with i3 erupting, dp3, m1-2, trigonid part of m3 and alveoli of i1-2, c, p1-2, and p4 (Figs. 4, 5(A–C)).

Referred material: GU/RJ/144, left dentary fragment with p2-4; GU/RJ/101, left dentary fragment with p4 and alveoli of p2-3; GU/RJ/341, left dentary fragment with dp4 (broken) and m1; GU/RJ/303, right dentary fragment with m1-2; GU/RJ/236, left dentary fragment with m1-m3; GU/RJ/289, right maxillary fragment with P2 erupting, DP3-4, M1, and broken M2; GU/RJ/290, left P3 (damaged) and P4; GU/RJ/314, right P4; GU/RJ/468, right P4; GU/RJ/345, right P4-M1; GU/RJ/233, right maxillary fragment with P4-M3; GU/RJ/145, right maxillary fragment with M1-3 and alveoli of P4; GU/RJ/117, right maxillary fragment with M1-3.

Horizon and type locality: Red to grey maroon color shale, upper Subathu Group exposed east of Aiji village on Metkha- Moghala Rajouri road, Rajouri District, Jammu and Kashmir.

Distribution: Subathu Group, middle Eocene, Kalakot, northwest Himalaya.

Measurements: see Tables 1 and 2.

Diagnosis: Medium sized Raoellidae that differs from all the species of the family by marked, individualized paraconid on m1- 2, reduced parastylid on p4, P4 with reduced lingual lobe and low, small protocone with reduced crest pattern; further differs from *Khirtharia* by lower dentition narrow bucco-lingually; and from *Indohyus* and *Kunmunella* by absence of mesio-distal elongation of the premolars.

Description:

Dentary and lower dentition. The holotype (GU/RJ/362) gives access to partial information regarding the anterior dentition of the new taxon (Figs. 4, 5(A–C)). This specimen represents a juvenile with partly erupted i3, dp3, and fully erupted m1-2. It underwent significant bucco-

lingual compression, but it is possible to say that it is rather narrow anteriorly and slightly broader posteriorly; the general outline of the tooth row is slightly bent upward from i3. The total length of this juvenile dentary cannot be determined as it is broken shortly after the root of the ascending ramus; the depth of the horizontal ramus is 1.7 cm at the level of the molars. The symphysis is long and extends to the anterior root of p2. There are small diastemata between c and p1 (2.8 mm), p1 and p2 (3.3 mm), and p2 and p3 (1.4 mm). There are two small mental foramina located just below p1 and p3 (Figs. 4(B), 5(B)).

The alveoli of i1 and i2 are visible. According to their shape, all deciduous premolars were double rooted, except dp1 which is single rooted. The alveolus of the deciduous canine is larger than that of the dp1. The dental formula of the lower dentition is 3.1.4.3. The eruptive i3 of the type specimen GU/RJ/362, partly in its crypt, represents the only documentation of the anterior dentition of *R. gunnelli* nov. gen., nov. sp. The virtual extraction of the tooth based on micro CT Scan data shows that it is still in formation (Fig. 4(D–H)). The crown has a pointed tip, strongly asymmetrical with a convex anterior protocristid and a longer, straight, postprotocristid. The labial surface is convex in its anterior part. There is no endocristid on the lingual surface, but the pre- and post- protocristid are lined by marked grooves. The posterior end of the postprotocristid bears a small styloid connected to what seems to be a lingual cingulid. The specimen GU/RJ/144 preserves unworn p2–4 in association (Fig. 5(G–I)). The size slightly increases from p2 to p4. The morphology of p2 and p3 is similar, with sharp, slightly crenulated pre- and postcristids, slightly bent lingually and joining the anterior and posterior cingulid respectively. There is neither parastyloid nor distostylid on p2–3. The crown is lined by a subtle but continuous cingulid, thicker anteriorly and posteriorly. On the lingual and labial aspects of the crown, the cingulid most probably will vanish with little wear. On the lingual surface, both the pre- and postprotocristids are lined by grooves, while on the labial aspect of the crown, only the postprotocristid is. The postprotocristid of p3 bears a very subtle lingual accessory cristid. The p4 is the longest tooth of the premolar row, slightly longer than p3 and wider than p2–3 (Fig. 5(G)). The protoconid length is only slightly shorter than the total length of the tooth and bears two thick, trenchant, distinct pre- and post- protocristids. There is no sign of a metaconid. The pre- and post- protocristids descend from the apex and connect the anterior and posterior cingulid, at a parastyloid and a hypoconid respectively. The postprotocristid of GU/RJ/144 is finely crenulated in its lowest part. The parastyloid occupies the antero-lingual corner of the crown, while the hypoco-nid is central to the posterior margin. The postprotocristid is bifid in its posterior part, its labial extremity connects the postero-labial cingulid and its short lingual end vanishes at the base of the protoconid. There is a small, moderately deep, talonid basin extending on the postero-labial and lingual sides of the tooth. The cingulid is finely crenulated, forming a shelf all along the tooth which is slightly faint at the medio-labial and lingual portions of the protoconid.

The enamel of the lower molars is finely wrinkled. Only one complete molar row is attributed to *R. gunnelli* nov. gen., nov. sp. (GU/RJ/236); the size of the molars greatly increases from m1 to m3, m1 being much smaller than m2 (Table 1). Generally speaking, the cuspids are bunodont but relatively high, the trigonid and talonid being separated by a deep transverse valley. Lower molars are double-rooted, each lobe of the crown being supported by a unique, massive, pillar. The m1 of the type specimen GU/RJ/362 is particularly well preserved and can be described in its finest details (Figs. 4(A–C), 5(A– C)). The m1 is more than two times longer than wide, anteriorly narrow, and posteriorly broad. The trigonid cusps are closely appressed, conical, and brachyodont. The trigonid basin is slightly higher and much smaller than the talonid basin. The metaconid is the highest cusp. The paraconid is a small cuspid, distinct from the anterior cingulum and lying antero-lingually to the metaconid. It bears its own cristid pattern with pre-, endo-, and postparacristids.

The preparamacristid joins the anterior cingulid on the anterolingual corner of the tooth, while the endoparamacristid connects the preprotocristid on the antero buccal corner. The premetacristid is subtle and joins a faint postparamacristid. The protoconid and the metaconid are closely apposed to each other, the protoconid being much smaller and lower than the metaconid. There are faint endocristids preserved on GU/RJ/303, the presence of postcristids on the anterior lophid is difficult to assess due to wear (Fig. 5(D–F)). There are subtle pre-, proto-, and metacristids (GU/RJ/303). The metaconid bears a sharp postectocristid lined by clear grooves. The buccal surface of the crown bears an elongated and deep hypoflexid. The talonid basin is sub-rectangular, moderately deep, longer and wider than trigonid. It is narrow anteriorly due to the lingually directed crista obliqua and broad posteriorly, closed by the endocristids of the entoconid and hypoconid. The cristidobliqua (prehypocristid) is thick and directed towards the junction of protoconid and metaconid, where it connects the central accessory cristid. The hypoconid is the most voluminous cusp of the crown, slightly higher than the entoconid but lower than the protoconid. The entoconid and the hypoconid are joint by faint endocristids. The ectoentocristid is well distinct and finely crenulated, it joins the postectometacristid at the lingual notch at the entoconid/metaconid junction. At the junction of the hypoconid and entoconid is a small posthypocristid that joins the posterior cingulid. The anterior and posterior cingulids are well distinct and finely crenulated; the buccal cingulum vanishes at the base of the protoconid and at the mid-distal part of the hypoconid, it is straight and sharp, and forms a crest at the base of the protoconid that could be assimilated to a postectoprotocristid. The lingual cingulum is absent on most specimens, excepted on the holotype where it is a faint structure, lining the postectometacristid.

The m2 is basically an enlarged version of the m1 (Figs. 5(A–C), 6(A–F)). Its general outline is slightly more regular; the protoconid and the metaconid are further apart and the talonid basin is somewhat larger. Contrary to m1, the trigonid portion of the tooth is wider than the talonid. The paraconid is present but smaller, pinched between the metaconid and the posterior margin of m1. The m3 is documented on GU/RJ/236 (Fig. 6(D–F)). This specimen shows a medium state of wear and most cristids are still visible. The m3 is larger than m2 and cusps are more bulbous than m1 and m2. The short paramacristid ends lingually at the anterior base of the metaconid to form what seems to be a vestigial paraconid. The metaconid is slightly more lingual than the entoconid and the protoconid slightly more labial than the hypoconid. The cristids are faintly developed and not as sharp as in m1 and m2 of the same specimen. The crista obliqua is broad and lined lingually by a groove. Like m2, and contrary to m1, the trigonid of m3 is wider than the talonid. The hypoflexid is broad and shallow. The hypoconulid is high and pointed, slightly lower than the hypoconid but higher than the entoconid. It is well separated from the entoconid and hypoconid by a deep transversal notch. The hypoconulid bears a clear prehypocristulid and a faint ectohypocristulid. The buccal cingulid is faintly developed anteriorly and posteriorly, interrupted at the hypoconid level. There seems to be no lingual cingulid.

Upper dentition. The upper dentition of *R. gunnelli* nov. gen., nov. sp. is documented from P2 to M3. Like lower premolars and molars, the enamel is finely crenulated (Figs. 7, 8).

The upper premolars of *Rajouria gunnelli* nov. gen., nov. sp. Are documented by a P2 still in the crypt (GU/RJ/289), a badly damaged P3 (GU/RJ/290), and a series of six P4 (GU/RJ/290, 203, 468, 345, 233, 314). The visible part of the erupting P2 (GU/RJ/289) allows to determine that it is a high and sharp tooth, narrow labiolingually (Fig. 7(A–C)). It is composed of only one cusp, the paracone, and two sharp cristae, the pre- and postparamacristae. The postparamacrista is sharp, finely crenulated and bears no accessory structures. There is no lingual basin, and thin anterior and posterior cingula are visible. What is preserved of the P3 (GU/RJ/290) indicates that the tooth was labio-lingually narrow and double rooted which is a shared character of

raoellid and cetaceans (Fig. 7(D–F)). It has no lingual basin and the crown is surrounded by a faint cingulum.

The general outline of P4 is subtriangular (Figs. 7(D–I), 8(A–I)). The tooth is three rooted and bears a high paracone and a small, sometime vestigial, protocone delineating a small lingual lobe. The paracone is labially convex with lingually recurved tip. The pre- and post-paracristae are thick and sharp. The preparacrista meets the anterior cingulum at the level of a small parastyle, and the postparacrista meets the posterior cingulum at a small distostyle. The base of the paracone bears a very small endocrista that meets – when present – a small endoprotocrista. The protocone is very small, positioned slightly anterior to the paracone and well separated from the latter by a deep longitudinal groove. It sometimes bears a preprotocrista joining the anterior cingulum and a very small endocrista (GU/RJ/203, 314, 468). The cingulum forms a continuous shelf all along the tooth which is slightly elevated at the parastyle, distostyle and protocone base. The surface of the crown is ornamented by fine longitudinal ridges and grooves just below the tip of the paracone. The buccal outline of the upper molar row is slightly convex; the buccal cusps bear antero-posterior crests that constitute altogether a continuous trenchant line (the ectoloph). The cristae of each molar delimit a deep, square, crushing basin, encased by crests. At the junction between molars, the postmetacrista of front molar joins the preparacristule and the preparacrista of the following molar, form a triple point receiving the tip of the protocone during occlusion. The M1 is much smaller than the M2, which is the biggest of the molar row. Upper molars are three-rooted, the lingual part of the crown being supported by a unique massive pillar. The M1 is subrectangular in shape, longer and wider than the P4 (Figs. 7(A–C, G–I), 8(G–K)). Its length nearly equals its width. The crown is slightly wider labially than lingually and has four main conical cusps and a small paraconule. The paracone is slightly higher than the metacone. The protocone is the largest and most voluminous cusp and extends slightly more lingually than the metaconule. The cingulum forms a continuous shelf all around the tooth, interrupted on the lingual side at the protocone and metaconule level for some specimens. The paracone bears two main cristae, the pre- and post- paracristae. The preparacrista is sharp, straight, and meets the anterior cingulum at a faint parastyle. The postparacrista is also sharp and straight, and meets the premetacrista forming a wide V-shaped valley in buccal view. The paraconule is distinct and bears a complex crest pattern. It lies closer to the protocone than to the paracone, well separated from the latter by shallow grooves. The preparacristule is sharp, longer than the postparacristule and joins the anterior cingulum at a small mesiostyle. The postparacristule is small and joins the base of paracone at the level of the endometacrista, which is variously present depending of the specimen. Judging from the almost unworn specimen GU/RJ/289, the protocone bears only two cristae, the pre- and post-protocrista (Fig. 7(A–C)). The preprotocrista is short and joins the tip of the paraconule. The postprotocrista joins the small premetacristule, forming a wide V-shaped valley in lingual view. The metacone bears three cristae. The premetacrista joins the postparacrista forming a buccal cutting edge; the endometacrista is a very discrete structure, low in the longitudinal valley. The postmetacrista is also sharp and joins the posterior cingulum at a tiny distostyle. The metaconule is the smallest cusp of the crown and bears three crests, a pre-, an endo-, and a postmetacristule, that join the postprotocrista, the endometacrista and the distal cingulum respectively.

The M2 is morphologically very close to M1 (Fig. 8(G–L)). Its size is much larger and the crown is proportionally wider buccolingually (Table 2). Compared to M1, cristae are less salient, especially on the lingual side, and the endometacrista is lacking. The cingulum, continuous on the anterior, buccal and posterior faces of the crown, is absent or faintly developed at the posterolingual base of the metaconule and at the antero-lingual base of the protocone. The M3 is similar in size to M2 but shows more irregular outline, especially, there is a small anterior swelling at the level of the paraconule (Fig. 8(G–L)). The metacone is placed more lingually and the posterior part of the tooth is much narrower than the anterior part at the

protocone/paracone level. The metaconule is closer to the protocone, reducing the length of the lingual aspect of the crown. The cristae pattern is similar to M2, but the lingual cristae are even more reduced. The endometacristule is particularly low and stocky, lined by clear grooves and looks like an incipient accessory conule. The protocone height and volume increase from M1 to M3. Deciduous dentition. The lower deciduous dentition of *R. gunnelli* nov. gen., nov. sp. is documented by a dp3 (holotype specimen GU/RJ/362), and by the posterior part of a dp4 (GU/RJ/341). The dp3 has a high sharp crown composed of the protoconid and pre- and postprotocristids (Fig. 5(A–C)). The anteriormost part of the tooth is broken; the postprotocristid joins a small distostylid on the postero-lingual corner of the crown.

The partial dp4 lacks the anterior portion of the crown (Fig. 6(A–C)). The crown is partly worn so that all the structures are not visible. The talonid is very similar to that of m1, only the crushing basin is smaller, being narrower in its anterior part. The entoconid is also particularly small, smaller than on m1. The protoconid and the metaconid both bear light precristids. The lingual cingulum is high and crenulated, extended onto the protoconid flank. The tooth does not show a median pillar under the protoconid/metaconid.

The upper deciduous dentition of *R. gunnelli* nov. gen., nov. sp. Is documented by the juvenile specimen GU/RJ/289 that preserves very fresh DP3 and DP4 (Fig. 7(A–C)). Crenulations of the enamel is particularly marked on these unworn specimens. The DP3 is three-rooted and bears three cusps, a massive paracone, a slightly smaller metacone and a posteriorly located protocone. The paracone tip is broken, but its crest pattern is clearly visible. It bears a sharp preparacrista joining the anterior cingulum at a parastyle (worn), an endoparacrista joining the preprotocrista lingually, and a postparacrista joining the prematacrista posteriorly. The metacone also shows sharp cristae, a long endometacrista connected to the endoprotocrista and a shorter postmetacrista joining the posterior cingulum at the postero-buccal corner of the tooth. The buccal cingulum extends from the base of the paracone to the level of the postmetacrista; there is no lingual cingulum. The DP4 is morphologically strikingly similar to M1, being basically just a smaller version of this tooth. Main differences lie in the fact that in buccal view, the crown of DP4 is lower than that of M1, and that the metaconule is smaller, lower, and placed more anteriorly on DP4.

Remarks:

Variability. Lower dentition. Three p4 of *Rajouria gunnelli* nov. gen., nov. sp. are documented (GU/RJ/144, 101, 116). The three specimens are unworn, they differ by the general outlines of their crown, GU/RJ/116 being more rectangular, and GU/RJ/101 (Fig. 6(G–I)) more bean-shaped. The three specimens present the same pattern of cristids, only the size and shape of the hypoconid varies slightly, from a clearly isolated small cuspid (GU/RJ/144; Fig. 5(G–I)), to a more cristid-like structure (GU/RJ/116). In addition to the type specimen, three other specimens referred to *R. gunnelli* nov. gen., nov. sp. preserve the m1 (GU/RJ/236, 303, 341). They all exhibit a large paraconid and the same pattern of cristids, wear being taken in consideration. Slight variations are observed in the proportion of the crown, the latter being more elongated relative to m2 in the type specimen (GU/RJ/362; Fig. 5(A–C)) than in the three others. Lingual cingulum is variously present depending of wear. The cristidlike buccal cingulum at the base of the protoconid is lacking in GU/RJ/341 (Fig. 6(A–C)). Similar range of variation is observed between the three m2 documented for the species. The crown of the m2 of the specimen GU/RJ/303 is particularly “fresh” and its metaconid and protoconid show both endo- and postcristids, these cristids are faint on other specimens, most probably due to wear (Fig. 5(D–F)).

Upper dentition. Six P4 are documented for *R. gunnelli* nov. gen., nov. sp. If the size of the specimens is rather homogeneous (Table 2), considerable variation is observed among this sample and concern the general proportions of the crown, and the size of the protocone. On

GU/RJ/203, 233, and 290, the protocone is very small and does not even have a cristae pattern for GU/RJ/233 and 290 (Figs. 7(D–F), 8(G–I)). It is slightly larger in GU/RJ/345 (Fig. 7 (G–I)), 314 (Fig. 8(D–F)), and 468 but it remains small and very low relative to the paracone compared to other raellid species (cf. below, Section 5). Size and proportions of the upper molars referred to as *R. gunnelli* nov. gen., nov. sp. are pretty conservative within our sample, only the M1 of GU/RJ/233 is slightly more elongated than in other specimens. The crest pattern is also homogeneous; most of the M2 specimens are lacking the endometacrista, it is however vestigial in GU/RJ/145 and 206.

Comparisons with other artiodactyls. By its bunodont morphology with a relatively simple dental pattern, *Rajouria gunnelli* nov. gen., nov. sp. roughly resembles early and middle Eocene artiodactyls. It differs from the most basal artiodactyl family, Diacodexidae, by having M1-2 that are more rectangular in shape, with larger, more lingual metaconule. It differs from most other dichobunoids by the absence of hypocone on upper molars (contra Homacodontidae, Helohyidae, and some Dichobunidae). Regarding Endemic European bunodont forms, *Rajouria gunnelli* nov. gen., nov. sp. differs from “choeropotamids” Choeropotamus and Haplobunodon by the lack of mesostyle on upper molars and the lack of mesoconulid on lower molars; and from cebochoerids by sharper crests and wider crushing basin on upper molars. The presence of wide crushing basins on upper and lower molars, the enamel crenulation, the reduced paraconules on upper molars, the increase in size from m1 to m3, the sharp and simple lower premolars, and the two-rooted P3 in *Rajouria gunnelli* nov. gen., nov. sp., fit with raellid affinities.

Comparisons with other raellid species. Lower dentition. The lower premolars of *Rajouria gunnelli* nov. gen., nov. sp. differ from those of *Kunmunella transversa* (H-GSP 97 187; Thewissen et al., 2001) and *Indohyus indirae* (ONG/K1; Ranga Rao, 1971) by several features. On the lower dentition, the lower premolars differ in their proportions, p2-4 are slenderer in *K. transversa* and *I. indirae* (Table 3); the protoconid, especially, is stockier in *R. gunnelli* nov. gen., nov. sp. and the portion anterior and posterior to the protoconid are shorter. The parastylid is smaller on p4 in *R. gunnelli* nov. gen., nov. sp., and the inflection of the crown basis on the lingual side is deeper in *K. transversa* and *I. indirae*. The lower premolars of *R. gunnelli* nov. gen., nov. sp. are intermediate in terms of proportion between *I. indirae* and *Khirtharia dayi* (V 65870; Thewissen et al., 1987: fig. 5E-F), and closer to the later in terms of parastylid development. The main difference on lower molars is the presence of a salient paraconid on m1, more relictual on m2. Specimens of *I. indirae* as illustrated by Ranga Rao (1971) and Kumar and Sahni (1985), *Metkatius kashmiriensis* (Kumar and Sahni, 1985: fig. 4A-C), *Khirtharia inflatus* (Kumar and Sahni, 1985: fig. 4F), *Khirtharia dayi* (Thewissen et al. 1987) do not show this salient paraconid on m1. The proportions and height of the crown of the lower molars are close to *I. indirae*, but markedly different from *Khirtharia* which are wider and much lower. Upper dentition. The P4 of *R. gunnelli* nov. gen., nov. sp. Differs from other raellid species by its simple crest and groove pattern and the reduction of the protocone size. There is no anterior loph formed by the endopara- and endoprotocrista. The upper molars of *R. gunnelli* nov. gen., nov. sp. are similar in size to *I. indirae* (Table 4); however, compared to the material illustrated by Kumar and Sahni(1985), the lingual profile of the crown is squarer due to a slightly superior size of the metaconule. The crest and groove pattern of *I. indirae* also seems to be more developed, notably at the level of the posterior cusps: in *R. gunnelli* nov. gen., nov. sp. there is no endohypocrista delimitating the posterior margin of the crushing basin, whereas this crest is present in *I. indirae* specimens. *R. gunnelli* nov. gen., nov. sp. differs from *Kunmunella* by the shape of the cusps, more pointed in *Kunmunella*, and by the relative size of the metacone on M2, where the latter is smaller than the paracone, which is not the case in *R.*

gunnelli nov. gen., nov. sp. Compared to *Khirtharia dayi* (BMNH M 15798) and *K. aurea* (H-GSP 97188, Thewissen et al. 2001), *R. gunnelli* nov. gen., nov. sp. is slightly larger and shows higher cusps with a less bunodont wear pattern.

5. Phylogenetic analysis

In order to determine the status of the new material, we tested the phylogenetic position of *Rajouria gunnelli* nov. gen., nov. sp. within Raoellidae by including this taxon to the phylogenetic analysis performed by Orliac and Ducrocq (2012). The taxonomic sampling of the latter was widely unchanged but we coded the group of interest (i.e., Raoellidae) at the specific level and included two new characters, relevant at the raoellid scale (Appendix A): Character 25- upper molars, metacone size on M2 (0) similar to paracone, (1) clearly smaller than the paracone; Character 27- upper molars, endometacrista (0) absent, (1) present. The cladistic analysis (Branch-and-Bound search under PAUP* v. 4.0a build 166; Swofford, 2003) retrieved eight most parsimonious trees (L = 71; CI = 0.54; RI = 0.80). The strict consensus tree (L = 72; CI = 0.54; RI = 0.79; Fig. 9) supports the monophyly of Raoellidae on the basis of two unambiguous characters (presence of a hypoconulid on p4, car. 191, RI = 0.8; metaconule of upper molars located on the distal side of the protocone, car. 291, RI = 0.66) and allows for discussing the relationships within the family. The new taxon *Rajouria* is placed as first offshoot as it retains primitive character states: presence of a paraconid on lower molars (car. 20, RI = 0.87) and a simple P4 where endocristidae do not form an anterior loph (car. 321, RI = 1.0). The two species of the genus *Kunmunella* form a clade supported by a reduction of the size of the metacone on M2 (car. 251, RI = 1.0). *Metkatius* is found as sister taxon to the *Khirtharia* clade based on the presence of low crown (car. 151, RI = 1.0). The genus *Khirtharia* is supported by an entoconid smaller than the hypoconid on lower molars (car. 30, RI = 0.71) and the loss of internal accessory cristids on lower molars (car. 90, RI = 1.0). As already found by Orliac and Ducrocq (2012), the alleged raoellid *Haqueina haichinensi*, preserving both upper and lower dentition (Vislobokova, 2004), is not part of the clade Raoellidae. It would have been more satisfactory to code *Haqueina* based on its type species *H. haquei*, which looks like raoellid a lot. However, many of the distinctive characters are on upper molars, which are unknown for *H. haquei* that has been described only on m2-3 (Delm and Oettingen-Spielberg, 1958: p.26, table 3). Family Raoellidae is the sister taxon to the archaeocete *Pakicetus* and shares with the latter seven unambiguous synapomorphies already retrieved at the Raoellidae-*Pakicetus* node by Orliac and Ducrocq (2012): presence of enamel crenulation (car 11, RI = 0.66), cristid obliqua of the lower molars anteriorly pointed toward the postectoprotocristid (car. 81, RI = 1.0), mesiostylid of p4 absent (car. 160, RI = 0.40), labial wall of the cusps of the upper molar about rounded (car. 261, RI = 0.87), paracone height on P4 higher than on the upper molars (car. 351, RI = 0.80), absence of protocone on P3 (car. 380, RI = 0.50), and double rooted P3 (car. 391, RI = 1.0).

6. Discussion

Despite its general resemblance with the family Dichobunidae due to the retention of two plesiomorphies, the presence of a paraconid on m1-2 and a simple P4 where endocristids do not form an anterior loph, the new taxon *Rajouria gunnelli* nov. gen., nov. sp. appears to be a member of the family Raoellidae. The nesting of *R. gunnelli* nov. gen., nov. sp. at the very base of the raoellid tree modifies the definition of the family. Indeed, according to Orliac and Ducrocq (2012) raoellids were unambiguously defined by the absence of a paraconid on lower molars (RI = 0.85), and P4 endocristae forming an anterior loph (RI = 0.50). Inclusion of the new species indicates that these character states were not observed in most primitive raoellids; according to the present results, Raoellidae are unambiguously supported by a combination of homoplastic characters. The phylogenetic position of *Rajouria* strongly relies on its nesting

within the Raoellidae-Pakicetus clade, strongly supported by seven non ambiguous synapomorphies. Among them, the presence of the paraconid (even if very vestigial in m3), which was previously not recorded in the family, is a new feature that tends to confirm the definition of the new taxon *Rajouria*, and sets it at the base of the clade. *Rajouria gunnelli* nov. gen., nov. sp. is therefore interesting and fills a gap in the evolution of early artiodactyls. While the order Artiodactyla is present since the earliest Eocene (56 Ma) with the diacodexids *Diacodexis ilicis* in North America and *D. gigasei* and *D. antunesi* in Northern and Southern Europe, respectively (Estravis and Russell, 1989; Gingerich, 1989; Smith et al., 1996; Boivin et al., 2018), the earliest artiodactyls of the Indian subcontinent are not recorded before 54.5 Ma with *D. indicus* and *D. parvus* from the Cambay Fm. in India (Bajpai et al., 2005; Kumar et al., 2010). The abundant *D. pakistanensis* from the Kuldana Fm. in Pakistan (Thewissen et al., 1983) appears much later around the Ypresian-Lutetian transition, and therefore has a maximum age estimation of 50 Ma (Gingerich, 2003).

The presence of the new, early diverging, raoellid *Rajouria gunnelli* nov. gen., nov. sp. in the middle Eocene of Kalakot increases the already known high diversity of raoellids in the Subathu Group. It also confirms that raoellids are almost restricted to Northern India-Pakistan with only one exception in China (Orliac and Ducrocq, 2012). Therefore, the paleobiogeographic origin of the raoellid family is very probably in this region, the Chinese taxon dispersing later after the India-Asia collision. Our results also show that the intraspecific variability is high in raoellid species for which a great amount of material is described. This leads to the difficulty to sort out a species within the material that is abundant, and sometimes deformed. Among the abundant raoellid dental material from East Aiji-2, we specifically selected young individuals of *R. gunnelli* nov. gen., nov. sp., to avoid worn teeth and deformed specimens that obviously alter the characterization of diagnostic features.

Interestingly, Kumar and Sahni (1985) noted that the vertebrate assemblage from Kalakot localities is different from that of Mettka-Moghala localities, the first one being dominated by artiodactyls and perissodactyls while the second was considered as dominated by rodents. The new rich locality East Aiji-2, although belonging to the Mettka-Moghala localities, is dominated by artiodactyls. This suggests that the three areas have similar faunas and that the difference in diversity previously observed rather results from local taphonomy and/or granulometry of these fluvial paleoenvironments (Sahni and Jolly, 1993; Srivastava and Kumar, 1996).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary information; Supplementary information (including the Nexus data file used for the phylogenetic analysis under PAUP* v. 4.0a) associated with this article can be found, in the online version, at: <https://doi.org/10.1016/j.geobios.2020.12.003>.

References

- Bajpai, S., Kapur, V.V., Das, D.P., Tiwari, B.N., Saravanan, N., Sharma, R., 2005. Early Eocene land mammals from Vastan Lignite Mine, District Surat (Gujarat), western India. *Journal of the Palaeontological Society of India* 50, 101–113.
- Bhandari, L.L., Agarwal, G.C., 1966. Eocene (Subathu series) of the Himalayan foothills, north India. *Publications of the Centre of Advanced Study in Geology, Punjab University* 3, 57–78.
- Boisserie, J.-R., Lihoreau, F., Orliac, M.J., Fisher, R., Weston, E., Ducrocq, S., 2010. Morphology and phylogenetic relationships of the earliest known hippopotamids (Cetartiodactyla, Hippopotamidae, Kenyapotaminae). *Zoological Journal of the Linnean Society* 158, 325–367.
- Boivin, M., Orliac, M.J., Telles Antunes, M., Godinot, M., Laurent, Y., Marandat, B., Vidalenc, D., Tabuce, R., 2018. New material of *Diacodexis* (Mammalia, Artiodactyla) from the Early Eocene of Southern Europe. *Geobios* 51 (4), 285–306.
- Dehm, R., Oettingen-Spielberg, T., 1958. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 2. Die mitteleocänen Säugetiere von Ganda Kas bei Basal in Nordwest-Pakistan. *Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen* 91, 1–54.
- Estravis, C., Russell, D.E., 1989. Découverte d'un nouveau *Diacodexis* dans l'Eocène inférieur de Silveirinha, Portugal. *Palaeovertebrata* 19, 29–44.
- Gingerich, P.D., 1989. New earliest Wasatchian mammalian fauna from Eocene of northwestern Wyoming: composition and diversity in a rarely sampled highfloodplain assemblage. *University of Michigan, Papers on Paleontology* 28, 1–97.
- Gingerich, P.D., 2003. Stratigraphic and micropaleontological constraints on the Middle Eocene age of the mammal-bearing Kuldana Formation of Pakistan. *Journal of Vertebrate Paleontology* 23, 643–651.
- Karunakaran, C., Ranga Rao, A., 1979. Status of exploration for hydrocarbons in the Himalayan region - contribution to Stratigraphy and structure. *Geological Survey of India Miscellaneous Publication* 41, 1–66.
- Kumar, K., Sahni, A., 1985. Eocene mammals from the Upper Subathu Group, Kashmir Himalaya, India. *Journal of Vertebrate Paleontology* 5 (2), 153–168.
- Kumar, K., Rose, K.D., Rana, R.S., Singh, L., Smith, T., Sahni, A., 2010. Early Eocene artiodactyls (Mammalia) from western India. *Journal of Vertebrate Paleontology* 30 (4), 1245–1274.
- Mathur, N.S., 1978. Biostratigraphical aspects of the Subathu Formation, Kamaun Himalaya. *Recent Researches in Geology* 5, 96–112.
- Medlicott, H.B., 1876. Notes on the Sub-Himalayan Series in the Jammu (Jammoo) Hills. *Records of the Geological Survey of India* 9, 49–57.
- Metais, G., Qi, T., Guo, J., Beard, K.C., 2008. Middle-Eocene artiodactyls from Shanghuang Jiangsu province, Coastal China and the diversity of basal dichobunoids in Asia. *Naturwissenschaften* 95 (12), 1121–1135.
- Middlemiss, C.S., 1929. Kalakot, Metka. Maghola and other coalfields of Jammu Province. *Mineralogical Survey Report, Jammu and Kashmir Government*, p.116.
- Orliac, M.J., Ducrocq, S., 2012. Eocene raoellids (Mammalia, Cetartiodactyla) outside the Indian Subcontinent: palaeogeographical implications. *Geological Magazine* 149 (1), 80–92.
- Pascoe, E.H., 1964. *A Manual of the Geology of India and Burma*. Geological Survey of India 3, 1345–2117.
- Ranga Rao, A., 1971. New mammals from the Murree (Kalakot zone) of the Himalayan foot hills near Kalakot, Jammu & Kashmir state, India. *Journal of the Geological Society of India* 12, 124–134.
- Ranga Rao, A., 1972. Further studies on the vertebrate fauna of Kalakot, India: new mammalian genera and species from the Kalakot Zone of Himalayan foot hills, Jammu & Kashmir State, India. *Special Paper - India, Oil and Natural Gas Commission, Directorate of Geology* 1, 1–22.
- Sahni, A., Bhatia, S.B., Hartenberger, J.-L., Jaeger, J.-J., Kumar, K., Sudre, J., Vianey-Liaud, M., 1981. Vertebrates from the Subathu formation and comments on the biogeography of Indian subcontinent during the Early Paleogene. *Bulletin de la Société géologique de France* 23, 689–695.
- Sahni, A., Jolly, A., 1993. Eocene mammals from Kalakot, Kashmir Himalaya: community structure, taphonomy and paleobiogeographical implications. *Kaupia* 3, 209–222.
- Sahni, A., Khare, S.K., 1971. Three new Eocene mammals from Rajouri District, Jammu and Kashmir. *Journal of the Palaeontological Society of India* 14, 41–53.
- Sahni, A., Khare, S.K., 1973. Additional Eocene mammals from the Subathu Formation of Jammu and Kashmir. *Journal of the Palaeontological Society of India* 17, 31–49.
- Simpson, R.R., 1904. Report on the Jammu coalfields. *Memoirs of the Geological Survey of India* 32, 189–225.
- Singh, B.P., Andotra, D.S., 2000. Barrier lagoon and tidal cycles in Paleocene to Middle Eocene Subathu Formation, NW Himalaya, India. *Tertiary Research* 20, 65–78.
- Smith, R., Smith, T., Sudre, J., 1996. *Diacodexis gigasei* n. sp., le plus ancien Artiodactyle (Mammalia) belge, proche de la limite Paléocène-Eocène. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 66, 177–186.

- Srivastava, R., Kumar, K., 1996. Taphonomy and palaeoenvironment of the Middle Eocene rodent localities of northwestern Himalaya, India. *Palaeogeography, Palaeoclimatology, Palaeoecology* 122 (1-4), 185–211.
- Swofford, D.L., 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, MA, USA.
- Thewissen, J.G.M., Cooper, L.N., Clementz, M.T., Bajpai, S., Tiwari, B.N., 2007. Whales originated from artiodactyls in the Eocene epoch of India. *Nature* 450, 1190–1194.
- Thewissen, J.G.M., Gingerich, P.D., Russell, D.E., 1987. Artiodactyla and perissodactyla (Mammalia) from the Early-Middle Eocene Kuldana formation of Kohat (Pakistan). *Contributions from the Museum of Paleontology, The University of Michigan* 27, 247–274.
- Thewissen, J.G.M., Russell, D.E., Gingerich, P.D., Hussain, S.T., 1983. A new dichobunid artiodactyl (Mammalia) from the Eocene of north-west Pakistan. *Dentition and classification. Proceedings of the Koninklijke Nederlandse Academie van Wetenschappen B* 86, 153–180.
- Thewissen, J.G.M., Williams, E.M., Hussain, S.T., 2001. Eocene mammal faunas from northern Indo-Pakistan. *Journal of Vertebrate Paleontology* 21 (2), 347–366.
- Vislobokova, I.A., 2004. A new representative of the family Raellidae (Suiformes) from the Middle Eocene of Khaichin-Ula 2, Mongolia. *Paleontological Journal* 38, 220–226.
- Wadia, D.N., 1928. The Geology of Poonch State (Kashmir) and adjacent portions of the Punjab. *Memoirs of the Geological Survey of India* 51, 185–362.
- Waqas, M., Rana, R.S., 2020. New Raellidae (Artiodactyla) from the Subathu Group (Middle Eocene), Rajouri District, Jammu and Kashmir, India and their significance. *Himalayan Geology* 41, 171–182.
- West, R.M., 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas Region, Pakistan. *Journal of Paleontology* 54, 508–533.

Figures and tables

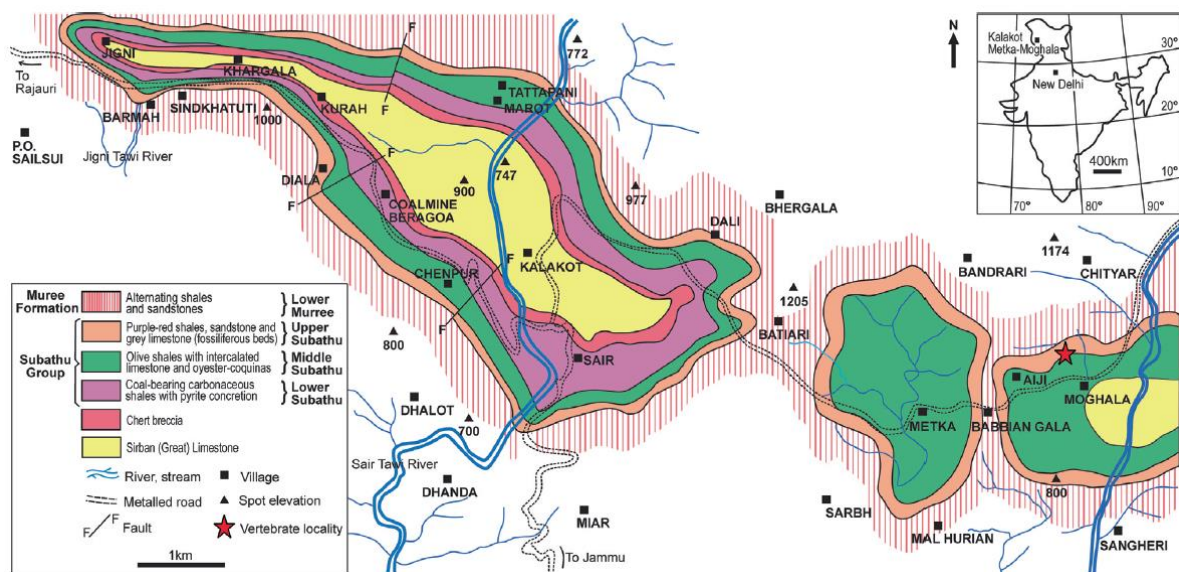


Fig. 1. Location of the new fossil locality East Aiji-2 in the eastern part of Aiji village, Rajouri District, Jammu and Kashmir, North India (Modified after Kumar and Sahni, 1985).

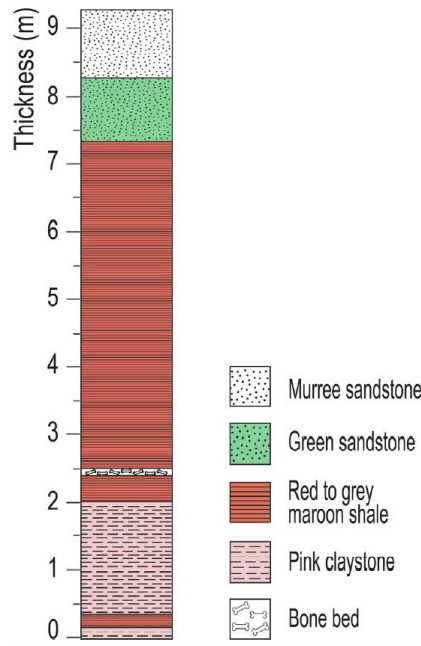


Fig. 2. Stratigraphic log of the Subathu Group in the locality of East Aiji-2. The fossil vertebrate layer is located in the lower part of the red to grey maroon shale.

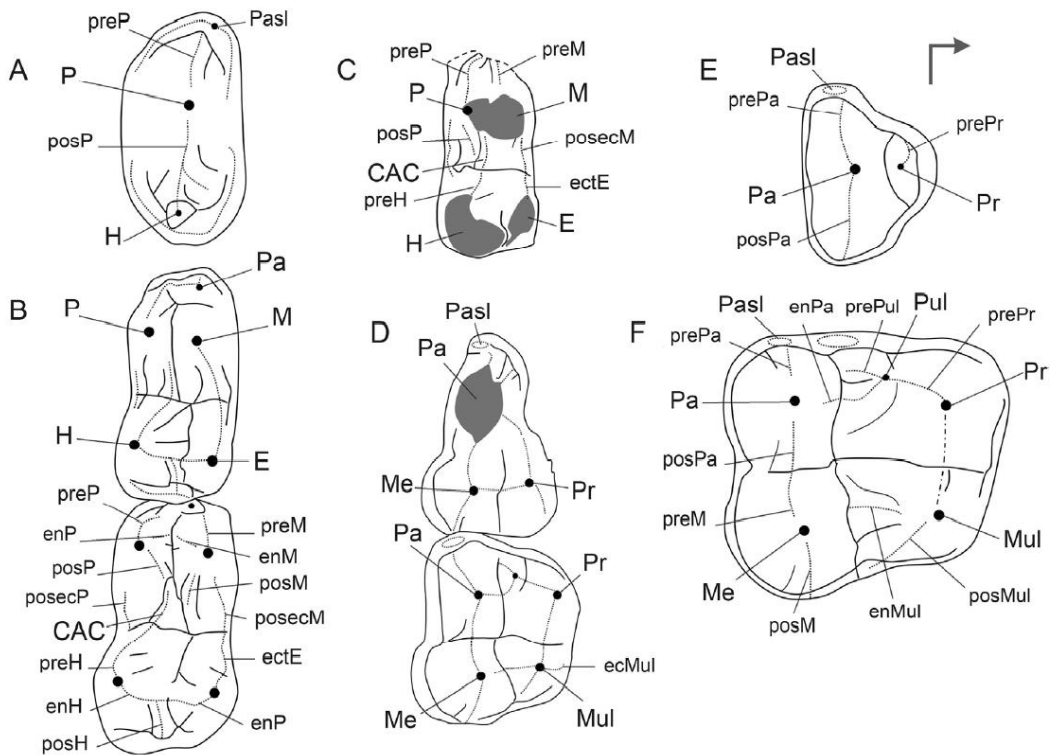


Fig. 3. Illustration of the structure of the lower (A-C) and upper (D-F) dentition of *Rajouria gunnelli* nov. gen. nov. sp. A: p4; B: m1-2; C: dp4; D: DP4-M1; E: P4; F: M1. Abbreviations for A-C: CAC, central accessory cristid; ectE, ectoentocristid; enH, endohypocristid; enP, endoprotocristid; enM, endometacristid; H, hypoconid; M, metaconid; P, protoconid; Pa, paraconid; Pasl, parastyle; posH, posthypocristid; posecM, postectometacristid; posecP, postectoprotocristid; posM, postmetacristid; posP, postprotocristid; preH, prehypocristid; preM, premetacristid. Grey areas indicate the surfaces corresponding to broken surfaces. Abbreviations for D-F: ecMul, ectometacristule; enM, endometacrista; enMul, endometacristule; enPa, endoparacrista; Me, metacone; Mul, metaconule; Pa, paracone; Pasl, parastylid; prePa, preparacrista; posM, postmetacrista; posMul, postmetacristule; posPa, postparacrista; PrePul, preparacristule; posPr, postprotocrista; Pr, protocone; preM, premetacrista; preMul, premetacristule; prePr, preprotocrista; Pul, paraconule.

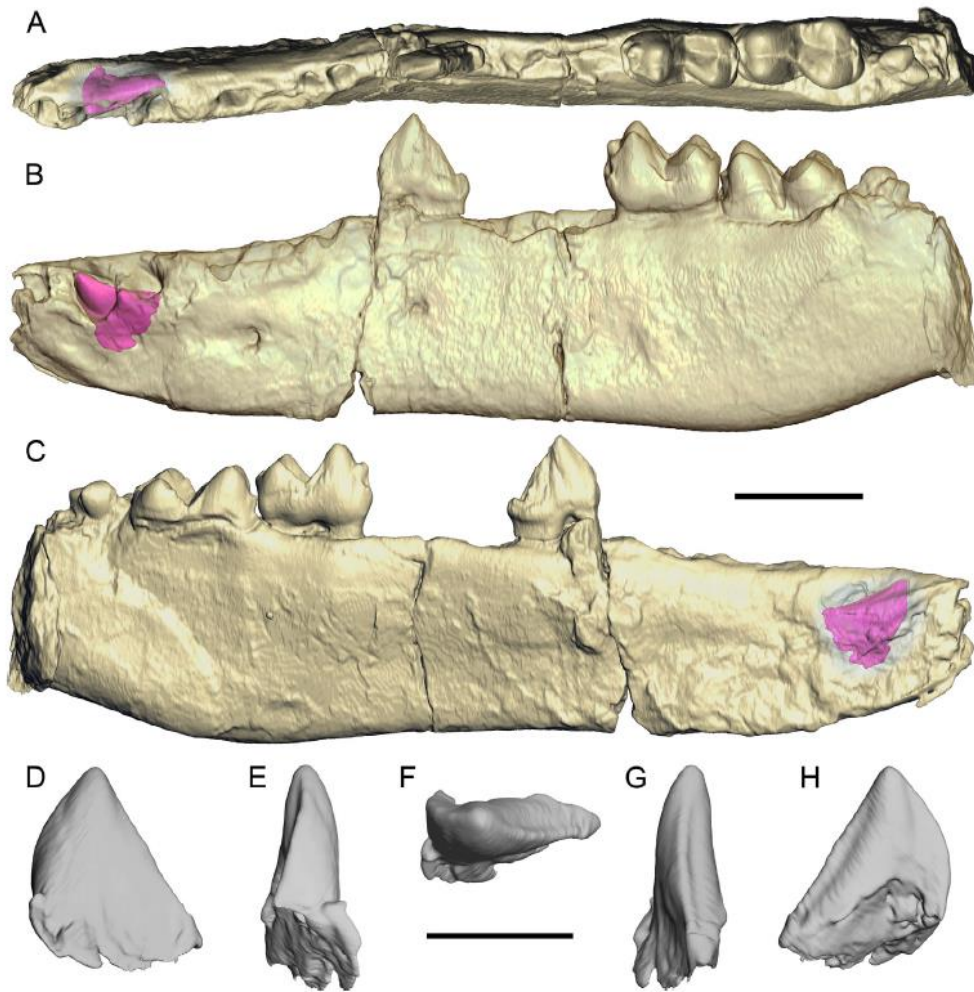


Fig. 4. A-C. Volume rendering of GU/RJ/362, holotype, left dentary of *Rajouria gunnelli* nov. gen., nov. sp., with i3 erupting (colored), dp3, m1-2, trigonid part of m3 and alveoli of i1-2, c, p1-2, and p4 in occlusal (A), labial (B), and lingual (C) views. D-H. i3 virtually extracted in labial (D), anterior (E), occlusal (F), posterior (G), and lingual (H) views. Scale bars: 10 mm (A-C), 5 mm (D-H).

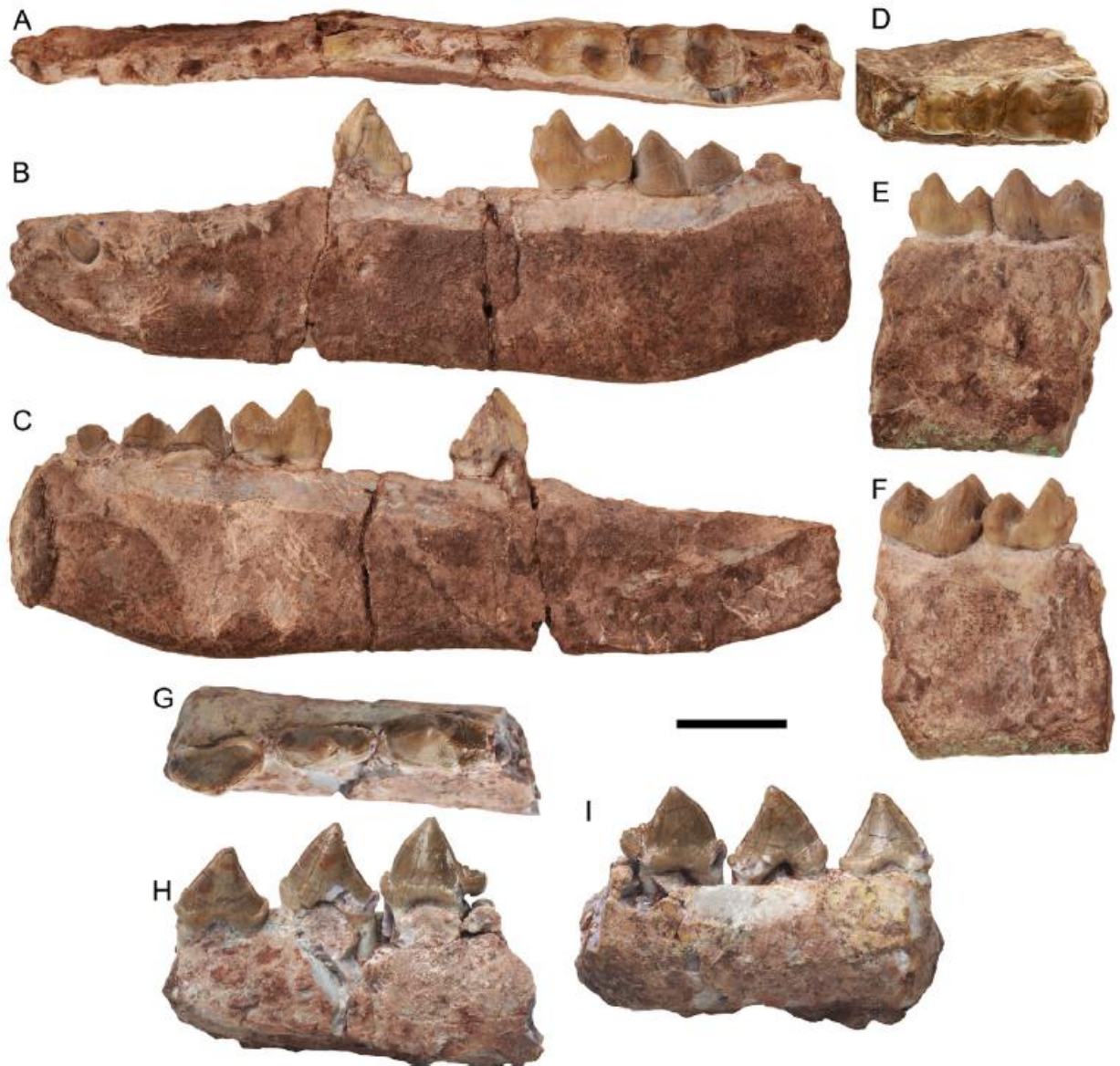


Fig. 5. Lower dentition of *Rajouria gunnelli* nov. gen., nov. sp. A-C. GU/RJ/362, holotype, left dentary with i3 erupting, dp3, m1-2, trigonid part of m3 and alveoli of i1-2, c, p1-2, and p4 in occlusal (A), labial (B), and lingual (C) views. D-F. GU/RJ/303, right dentary fragment with m1-2 in occlusal (D), labial (E), and lingual (F) views. G-I. GU/RJ/144, left dentary fragment with p2-4 in occlusal (G), labial (H), and lingual (I) views. Scale bar: 10 mm.



Fig. 6. Lower dentition of *Rajouria gunnelli* nov. gen., nov. sp. A-C. GU/RJ/341, left dentary fragment with dp4 (broken) and m1 in occlusal (A), labial (B), and lingual (C) views. D-F. GU/RJ/236, left dentary fragment with m1-m3 in occlusal (D), labial (E), and lingual (F) views. G-I. GU/RJ/101, left dentary fragment with p4 and alveoli of p2-3 in occlusal (G), labial (H), and lingual (I) views. Scale bar: 10 mm.

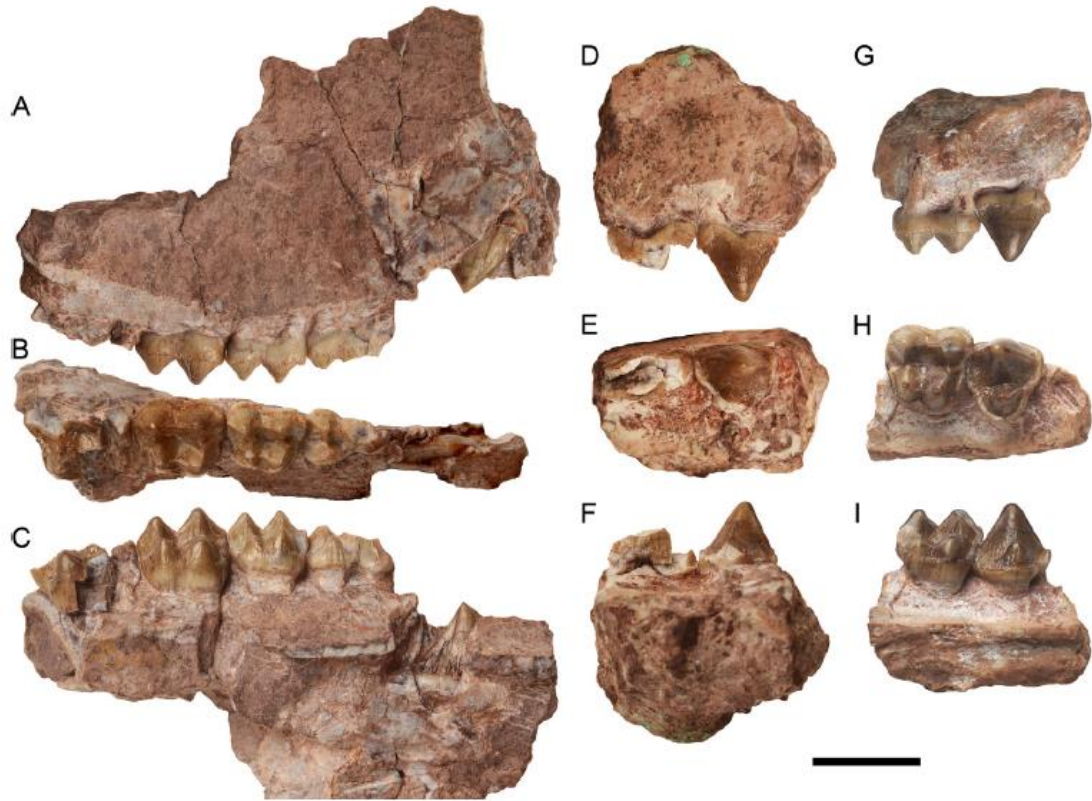


Fig. 7. Upper dentition of *Rajouria gunnelli* nov. gen., nov. sp. A-C. GU/RJ/289, right maxillary fragment with P2 erupting, DP3-4, M1, and broken M2 in labial (A), occlusal (B), and lingual (C) views. D-F. GU/RJ/290, left P3 (damaged) and P4 in labial (D), occlusal (E), and lingual (F) views. G-H. GU/RJ/345, right P4-M1 in labial (G), occlusal (H), and lingual (I) views. Scale bar: 10 mm.

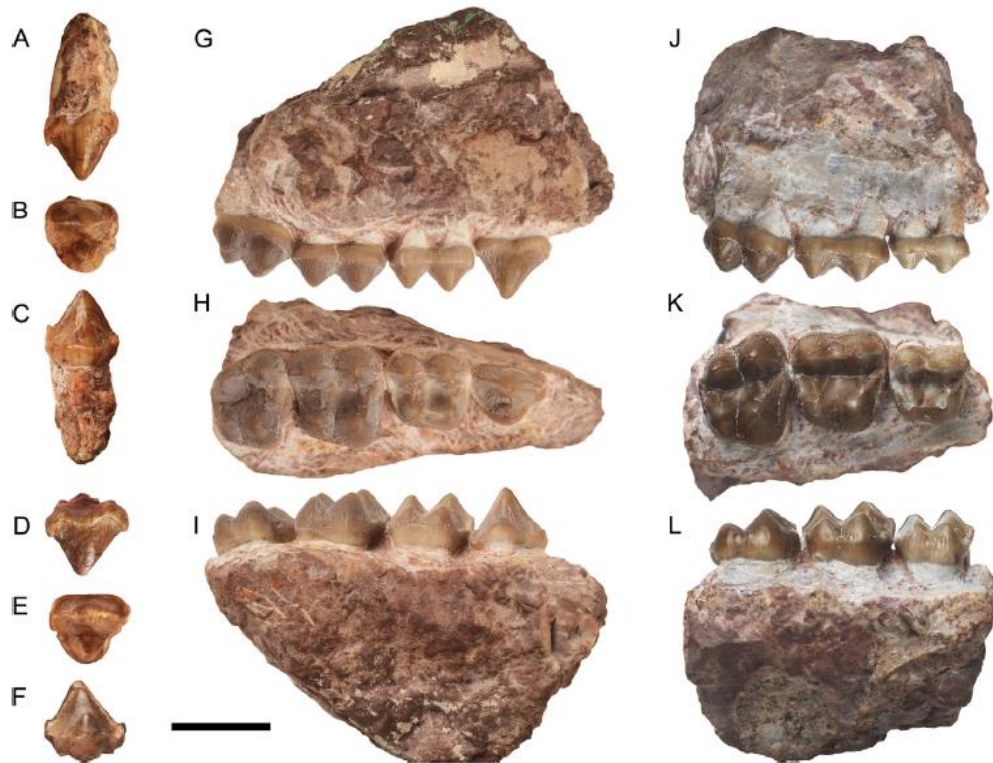


Fig. 8. Upper dentition of *Rajouria gunnelli* nov. gen., nov. sp. A-C. GU/RJ/468, right P4 in labial (A), occlusal (B), and lingual (C) views. D-F. GU/RJ/314, right P4 in labial (D), occlusal (E), and lingual (F) views. G-I. GU/RJ/233, right maxillary fragment with P4-M3 in labial (G), occlusal (H), and lingual (I) views. J-L. GU/RJ/117, right maxillary fragment with M1-3 in labial (J), occlusal (K), and lingual (L) views. Scale bar: 10 mm.

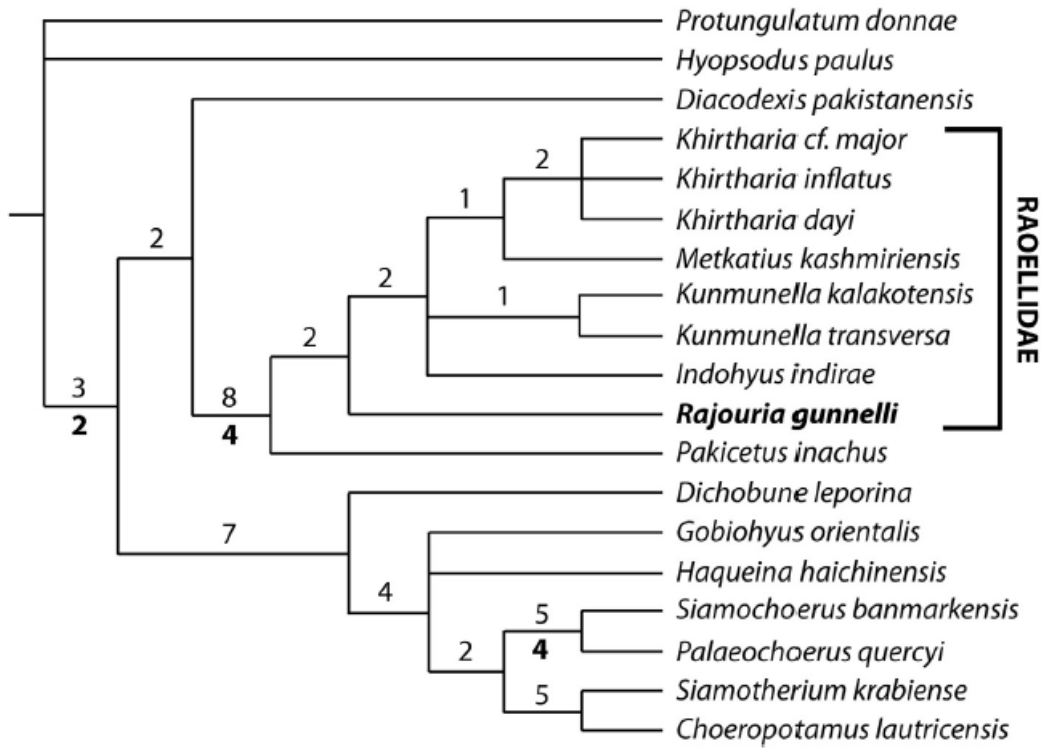


Fig. 9. Strict consensus (L = 72; CI = 0.54; RI = 0.79) of the eight most parsimonious trees (L = 71; CI = 0.54; RI = 0.80) retrieved by the cladistic analyses. Bremer indices below nodes, number of non-ambiguous synapomorphies above.

Tab. 1. Measurements (in mm) of the lower teeth of *Rajouria gunnelli* nov. gen., nov. sp. L: length; W: width; Wtri: width of the trigonid; Wtal: width of the talonid; *: estimation of the measure (broken tooth).

GU/RJ/	p2		p3		p4		m1			m2			m3		
	L	W	L	W	L	W	L	Wtri	Wtal	L	Wtri	Wtal	L	Wtri	Wtal
101					9.2	4.91									
144	8.72	4.08	9.32	3.96	9.93	5.24									
236							8.01	5.03	5.53	9.12	6.01	6.51	12.77	7.29	6.42
303							8.64	4.61	5.02	10.63	6.28	6.11			
341							8.21	3.65	3.97	8.88	4.69	5.03			
362			9.22*	2.71			9.20	4.60	4.65	10.34	5.14	5.78			

Tab. 2. Measurements (in mm) of the upper teeth of *Rajouria gunnelli* nov. gen., nov. sp. L: length; W: width; Want: width of the anterior part; Wpost: width of the posterior part; *: estimation of the measure (broken tooth).

GU/RJ/	P3		P4		M1		M2			M3			
	L	W	L	W	L	Want	Wpost	L	Want	Wpost	L	Want	Wpost
117					8.49	8.21	7.82	9.88	10.66	9.76	9.67	11.93	9.54
289	9.94	2.34	8.06	5.33	7.71	6.63	6.83	8.58	7.79	7.84	10.32*		
290	9.45	4.05	7.71	6.52									
314			8.83	7.43									
345			7.7	7.62	8.46	8.53	7.99						
468			7.96	8.29									

Tab. 3. Summary measurements (in mm) for lower teeth of different raellids. L: length; W: width; tri: trigonid; tal: talonid. Between parentheses are the number of specimens (n) followed by the standard deviation.

Taxon name	Specimen number	p2		p3		p4		m1			m2			m3			Reference
		L	W	L	W	L	W	L	Wtri	Wtal	L	Wtri	Wtal	L	Wtri	Wtal	
<i>Indohyus indirae</i> Ranga Rao, 1971	ONG/K/1 (holotype), 2 to 5; VPL/K 516; GSP-UM 696	9.0	4.5	13.0	5.0	10.0	4.7	8.5 (n = 2; 0)	5.45 (n = 2; 0.35)	9.57 (n = 3; 0.09)	6.2 (n = 3; 0.39)	13.56 (n = 4; 0.66)	7.03 (n = 4; 0.19)				Ranga Rao, 1971; Kumar and Sahni, 1985; Thewissen et al., 1987
	GSP-UM 102							8.9 (m1 or m2)	5.8 (m1 or m2)								Thewissen et al., 1987
<i>Indohyus major</i> Thewissen et al., 1987	GSP-UM 1435 (holotype)										10.0						Thewissen et al., 1987
<i>Khirtharia dayi</i> Pilgrim, 1940	LUVK 15014; GSP-UM 68, 74, 87, 1467, 1514, 1536, 1538, 1644, 1708, 1711, 1730; M 15796, 15797; H-GSP 96,360					7.0		7.2	5.6	7.65 (n = 2; 0.65)	6.45 (n = 2; 0.45)	10.38 (n = 13; 0.71)	6.85 (n = 12; 0.48)				Sahni and Khare, 1973; Thewissen et al., 1987; Thewissen et al., 2001; Orlac and Ducrocq, 2011
	GSP-UM 115, 1466, 1470, 1482, 1520, 1558, 1559, 1733							7.93 (m1 or m2) (n = 8; 0.73)	6.3 (m1 or m2) (n = 7; 0.57)								Thewissen et al., 1987
<i>Khirtharia cf. dayi</i>	GU/RJ/218											12.9	7.8	6.3			Waqas and Rana, 2020
<i>Khirtharia inflatus</i> (Ranga Rao, 1972)	VPL/K 545					7.3	3.6	7.0	5.5	8.2	6.5	11.6	7.3				Kumar and Sahni, 1985
<i>Khirtharia aurea</i> Thewissen et al., 2001	H-GSP 97,191													7.0			Thewissen et al., 2001
<i>Kunmunella kalakotensis</i> (Ranga Rao, 1971)	ONG/K/7 (holotype)							7.5	5.1	5.5	9.2	6.3	6.5	11.8	7.3	6.2	Ranga Rao, 1971
	VPL/K 572											12.5	6.3				Kumar and Sahni, 1985
<i>Kunmunella transversa</i> Kumar and Sahni, 1985	H-GSP 97,187	9.1	3.9	9.7	4.3	11.1	5.1	7.9	4.8	5.6	9.4	6.2	6.2	14.9	8.4	6.7	Thewissen et al., 2001
<i>Metkattus kashmiriensis</i> Kumar and Sahni, 1985	VPL/K 562					7.5	2.5			6.5	3.5	9.0	4.5				Kumar and Sahni, 1985
<i>Metkattus babbiangulensis</i> Waqas and Rana, 2020	GU/RJ/194 (holotype), 229, 212, 339							6.73 (n = 4; 0.82)	4.05 (n = 4; 0.52)	4.65 (n = 4; 0.61)	7.85 (n = 2; 0.55)	5.4 (n = 2; 0.30)	5.9 (n = 2; 0.90)	10.5 (n = 2; 0.55)	6.35 (n = 2; 0.55)	6.1	Waqas and Rana, 2020
<i>Rajouria gunnellinov. gen., nov. sp.</i>	GU/RJ 101, 144, 236, 303, 341, 362	8.72	4.08	9.27 (n = 2; 0.05)	3.34 (n = 2; 0.63)	9.57 (n = 2; 0.37)	5.08 (n = 2; 0.17)	8.52 (n = 4; 0.46)	4.47 (n = 4; 0.51)	4.79 (n = 4; 0.57)	9.74 (n = 4; 0.75)	5.53 (n = 4; 0.64)	5.86 (n = 4; 0.54)	12.77	7.29	6.42	This paper

Tab 4. Summary measurements (in mm) for upper teeth of different raellids. L: length; W: width; tri: trigonid; tal: talonid. Between parentheses are the number of specimens (n) followed by the standard deviation.

Taxon name	Specimen number	P3 L	W	P4 L	W	M1 L	Want	Wpost	M2 L	Want	Wpost	M3 L	Want	Wpost	Reference	
<i>Indolybus indirae</i> Ranga Rao, 1971	ONG/K 1 (holotype), 3, 4; VPL/K 511, 512	10.53 (n = 3; 0.88)	4.15 (n = 2; 0.15)	9.65	6.75	7.8	7.0		9.5	10.5		9.0	11.5		Ranga Rao, 1971; Kumar and Sahni, 1985	
<i>Khirtharia aurea</i> Thewissen et al., 2001	H-GSP 97,192 (holotype), 97,188						9.6					10.5	14.0		Thewissen et al., 2001	
<i>Khirtharia dayi</i> Pilgrim, 1940	LUVPI 15015; GSP-UM114, 133, 694, 1414, 1418, 1475, 1477, 1513, 1548, 1554; H-GSP96350, 1979	5.2	4.4	5.8	5.9	7.2	8.3		7.8 (n = 2; 0.70)	9.15 (n = 2; 1.75)		7.63 (n = 13; 0.69)	9.12 (n = 10; 0.78)		Sahni and Khare, 1973; Thewissen et al., 1987; Waqas and Rana, 2020	
<i>Khirtharia dayi</i> Pilgrim, 1940	GSP-UM70, 89, 141, 283, 1421, 1463, 1485, 1501, 1507, 1706					7.3 (M1 or M2) (n = 9; 0.43)	9.06 (M1 or M2) (n = 9; 0.77)									Thewissen et al., 1987
<i>Khirtharia cf. dayi</i>	GU/RJ/265					7.5	8.4		8.6	9.8					Waqas and Rana, 2020	
<i>Khirtharia inflatus</i> (Ranga Rao, 1972)	VPL/K 546								8.2	10.0					Kumar and Sahni, 1985	
<i>Kummunella kalakotensis</i> (Ranga Rao, 1971)	VPL/K 525	9.5	5.8	7.8	8.5	7.9	9.0		8.6	10.5		10.0	11.3		Kumar and Sahni, 1985	
<i>Kummunella rajouriensis</i> Sahni and Khare, 1971	LUVPI 15,004											10.5	14.0		Sahni and Khare, 1971	
<i>Kummunella transversa</i> Kumar and Sahni, 1985	VPL/K 526 (holotype)	8.6	6.2	6.5	9.6	7.5	9.5		7.0	11.5		9.2	12.5		Kumar and Sahni, 1985	
<i>Metkatius kashmiriensis</i> Kumar and Sahni, 1985	VPL/K 562 (holotype)			5.5	5.5										Kumar and Sahni, 1985	
<i>Metkatius babbiangalensis</i> Waqas and Rana, 2020	GU/RJ/118					7.0	7.1		8.4	9.0					Waqas and Rana, 2020	
<i>Rajouria gummellin</i> nov. gen., nov. sp.	GU/RJ/117, 289, 290, 314, 345, 468	9.70 (n = 2; 0.25)	3.20 (n = 2; 0.86)	8.05 (n = 5; 0.41)	7.04 (n = 5; 1.02)	8.22 (n = 3; 0.36)	7.79 (n = 3; 0.83)	7.55 (n = 3; 0.51)	9.23 (n = 2; 0.65)	9.23 (n = 2; 1.44)	8.8 (n = 2; 0.96)	9.96 (n = 2; 0.33)	11.93	9.54	This paper	