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First mammal of Gondwanan lineage in the early Eocene of India

Premiers mammifères de la lignée gondwanienne dans l'Éocène inférieur de l'Inde

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ABSTRACT

Based on well-preserved lower dentition, a new adapisoriculid from the Cambay Shale Formation (basal Eocene, ~54.5 Ma) in the open cast lignite mine of Vastan, Gujarat State, western India, is described. *Indolestes kalamensis* gen. et sp. nov adds significantly to the diversity of basal eutherians from Vastan as it represents a family hitherto not known from the Eocene of the Indian Subcontinent. Phylogenetic analysis suggests that *Indolestes* is derived relative to *Deccanolestes* and *Afrodon*, but primitive relative to the European adapisoriculids *Bustylus* and *Adapisoriculus*. The new data from the early Eocene provide evidence for continued survival of a Gondwanan mammal lineage following the Deccan volcanic activity (Cretaceous–Paleogene transition) in the Indian Subcontinent.

RÉSUMÉ

Basée sur une dentition inférieure, la description d'un nouvel adapisoriculidé de la formation Cambay Shale (Éocène basal, environ 54,5 Ma) dans la mine à ciel ouvert de Vastan, État de Gujarat, Inde occidentale, est ici présentée. *Indolestes kalamensis* gen. et sp. nov. ajoute de manière significative à la diversité des euthériens de base de Vastan, en ce qu'il représente une famille jusqu'à présent inconnue dans l'Éocène du sous-continent Indien. Une analyse phylogénétique suggère que *Indolestes* serait dérivé de *Deccanolestes* et *Afrodon*, mais primitivement des adapisoriculidés européens *Bustylus* et *Adapisoriculus*. Les nouvelles données sur l'Éocène inférieur fournissent l'évidence d'une survie continue d'une lignée mammalienne gondwanienne suivant l'activité volcanique du Deccan à la transition Crétacé–Paléogène dans le sous-continent Indien.

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1. Introduction

Small mammals belonging to the family Adapisoriculidae have perplexed paleontologists for over a century and have been variously assigned to different groups including didelphids, nyctitherids, leptidectids, mixodectids and palaeoryctids owing to the presence of several plesiomorphic dental characters (e.g., De Bast et al., 2012). These characters include transverse elongation of teeth, prominent parastyle and stylocone, variable stylar cusps, long prepara- and postmeta-cristae on a wide stylar shelf, rectilinear or dilambdodont centrocrista, separation of paracone and metacone down to their bases, reduced height difference between trigonid and talonid compared to cimolestids, and cristid obliqua extending high on to the posterior wall of the trigonid. Currently, adapisoriculids are represented by seven genera (*Deccanolestes, Afrodon*, *Bustylus*, *Adapisoriculus*, *Garatherium*, *Remiculus* and *Proremiculus*) with the oldest record (*Deccanolestes*) known from the Late Cretaceous (Maastrichtian) Deccan intertrappean deposits of peninsular India (Prasad et al., 2010). Adapisoriculids are also known from the Paleocene and Eocene of Europe and Africa (De Bast et al., 2013; Gheerbrant, 1995; Gheerbrant and Russell, 1991). Taxa restricted to Africa include *Garatherium*, while those known only from Europe include *Bustylus*, *Proremiculus* and *Remiculus*. Still others, such as *Adapisoriculus* and *Afrodon* are common to Africa and Europe (De Bast et al., 2012, 2013; Gheerbrant, 1988, 1991, 1995; Gheerbrant and Russell, 1989, 1991; Gheerbrant et al., 1998; also refer Table 1, Figs. 1 and 2, present study).

Though possible euarchonton affinities have been suggested for adapisoriculids based on tarsal bone morphology (Boyer et al., 2010; Prasad and Godinot, 1994; Smith et al., 2010), phylogenetic analysis of combined dental and tarsal characters demonstrated that adapisoriculids are basal eutherians and that *Deccanolestes*, the oldest known adapisoriculid, is a sister taxon of the Early Paleogene *Afrodon* from Africa (Goswami et al., 2011). Here we describe a new adapisoriculid from the same geographic region (peninsular India) that is known to yield the oldest record of this group (i.e., *Deccanolestes*). The new find reported here is approximately 10 million years younger in age than *Deccanolestes*.

2. Locality and age

The material described in this paper comes from the North Pit of the Vastan Lignite Mine (21°25′47″N; 73°07′30″E) situated about 65 km northeast of the city of Surat and close (about 3 km) to a small village Nani Naroli in District Surat, Gujarat, western India (Fig. 3). Details of lithofacies and depositional environments are discussed in Prasad et al. (2013). Data on dinoflagellates, δ^{13}C and

Table 1
List of known adapisoriculids.
Tableau 1
Liste des adapisoriculidés.

Taxon	Locality	Geographic area	Age	Author(s)
Deccanolestes hislopi	Naskal, India	Indian Subcontinent	Late Cretaceous (Maastrichtian)	Prasad and Sahni, 1988
Deccanolestes robustus	Naskal, India	Indian Subcontinent	Late Cretaceous (Maastrichtian)	Prasad et al., 1994
Deccanolestes cf. *hislopi*	Naskal, India	Indian Subcontinent	Late Cretaceous (Maastrichtian)	Prasad et al., 1994
Deccanolestes narmadensis	Kisalpuri, India	Indian Subcontinent	Late Cretaceous (Maastrichtian)	Prasad et al., 2010
Afrodon chleuhi	AdrarMgorn 1, Morocco	Africa	Late Paleocene	Gheerbrant, 1988
Afrodon tagourtensis	N'Tagourt 2, Morocco	Africa	Early Eocene	Gheerbrant, 1993
Afrodon ivani	Pyrenees, Spain	Europe	Late Paleocene	López-Martínez and Peláez-Campomanes, 1999
Afrodon gheerbranti	Hainin, Belgium	Europe	Early Paleocene (MP1-5)	De Bast et al., 2012
Bustylus cernaysi	Cernay, France	Europe	Late Paleocene	Gheerbrant and Russell, 1991
Bustylus marandati	Hainin, Belgium	Europe	Early Paleocene (MP1-5)	Gheerbrant, 1991
Bustylus folieae	Hainin, Belgium	Europe	Early Paleocene (MP1-5)	De Bast et al., 2012
Bustylus marandati	Hainin, Belgium	Europe	Early Paleocene (MP1-5)	De Bast et al., 2012
Bustylus germanicus	Walbeck, Germany	Europe	Late Paleocene	De Bast et al., 2013; Gheerbrant and Russell, 1989
Garatherium mahboubii	El-Kohol, Algeria	Africa	Early Eocene	Crochet, 1984
Proremiculus lagnauxi	Hainin, Belgium	Europe	Early Paleocene (MP1-5)	De Bast et al., 2012
Remiculus deutschi	Walbeck, Germany	Europe	Late Paleocene	Russell, 1964
Remiculus delsatei	Dormaal, Belgium	Europe	Early Eocene	Smith, 1997
Adapisoriculus minimus	Cernay, France	Europe	Late Paleocene	Lemoine, 1885
Indolestes kalamensis gen. et sp. nov.	Vastan, India	Indian Subcontinent	Early Eocene	Present study

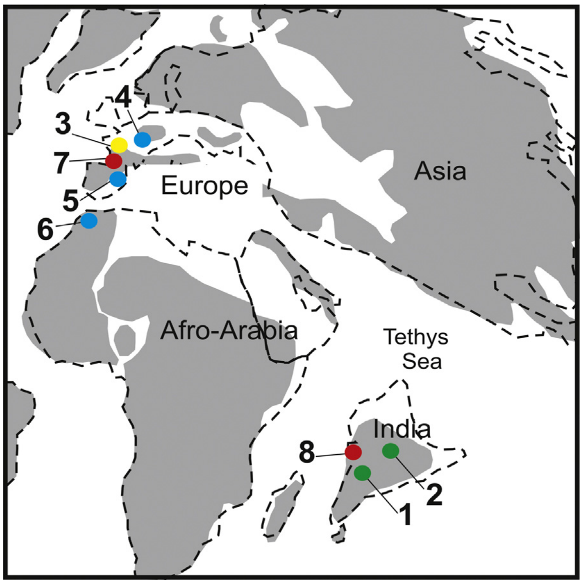

Fig. 1. Palaeogeographic map close to the K–Pg interval, showing localities yielding known adapisoriculid genera from across the globe as well as the present locality (Vastan, India) that yielded *Indolestes*. (1) Naskal (India), (2) Kisalpuri (India), (3) Hainin (Belgium), (4) Walbeck (Germany), (5) Cernay (France), (6) Adrar-Mgorn (Morocco), (7) Dormaal (Belgium) and (8) Vastan (India). Note: filled circles Green, Late Cretaceous; Yellow, early Paleocene; Blue, late Paleocene; Red, early Eocene. Map modified after Scotese (2006) with permission.

Fig. 1. Carte paléogéographique proche de l'intervalle K–Pg, montrant les localités qui ont fourni des genres d'adapisoriculidés connus à travers le globe et dans la présente localité (Vastan, Inde) qui a fourni *Indolestes*. (1) Naskal (Inde), (2) Kisalpiuri (Inde), (3) Hainin (Belgique), (4) Walbeck (Allemagne), (5) Cernay (France), (6) Adrar-Mgorn (Maroc), (7) Dormaal (Belgique) et (8) Vastan (Inde). À noter : cercles pleins vert, Crétacé supérieur ; jaune, Paléocène inférieur ; bleu, Paléocène supérieur ; rouge, Éocène inférieur. Carte modifiée d'après Scotese (2006), avec son autorisation.

$^{87}Sr/^{86}Sr$ (Clementz et al., 2011; Garg et al., 2008), indicate an age of ∼54.5 Ma for the Vastan mammal fauna, including the new adapisoriculid described in this paper.

3. Institutional abbreviations

Institutional abbreviations: (IITR) Department of Earth Sciences, Indian Institute of Technology Roorkee, Uttarakhand, India; (BSIP) Birbal Sahni Institute of Palaeosciences, Lucknow, Uttar Pradesh, India; (VPL/JU/) Vertebrate Palaeontology Laboratory, Department of Geology, University of Jammu, Jammu and Kashmir, India; (DUGF): Vertebrate Palaeontology Laboratory, Department of Geology, University of Delhi, Delhi, India; MNHN: Muséum national d'histoire naturelle, Paris, France.

4. Methods and repository

The dentary (VLM-804) described in this paper was photographed using Field Emission Scanning Electron Microscope (FESEM Model: JEOL 7610F) at BSIP, Lucknow. Measurements of the dentition (Figs. 4A and B) were taken using a camera mounted stereoscopic microscope with Leica Application Suite software (Leica LAS V4.8). The *Deccanolestes* dentary (DUGF/IM/1) illustrated in this paper was photographed by X-ray Computed Tomographic (CT) imaging at the AST-RX platform of the MNHN, Paris using a GE Sensing and Inspection Technologies phoenix x-ray-v-tome-x L240-180 CT scanner. A microfocus RX source 240 kV/320 W, detector 400 × 400 mm with a matrix of 2024 pixels (pixel size: 200 × 200 μm) was used. Further, data reconstruction was carried out using datos-x reconstruction software (Phoenix-x-ray, release 2.0) and then exported into a 16-bit TIFF image stack. Finally, the 3D models were reconstructed from the CT scans using the computer programs Materialise Mimics Innovation Suite 18.0 Research Edition (× 64) and Maxon Cinema 4DR15.

The phylogenetic analysis was performed by Tree analysis using New Technology (TNT) software (Goloboff et al., 2008).

The material described here is catalogued in the Vertebrate Palaeontology Laboratory, Department of Earth Sciences, Indian Institute of Technology Roorkee, Uttarakhand under the acronym IITR/SB/VLM.

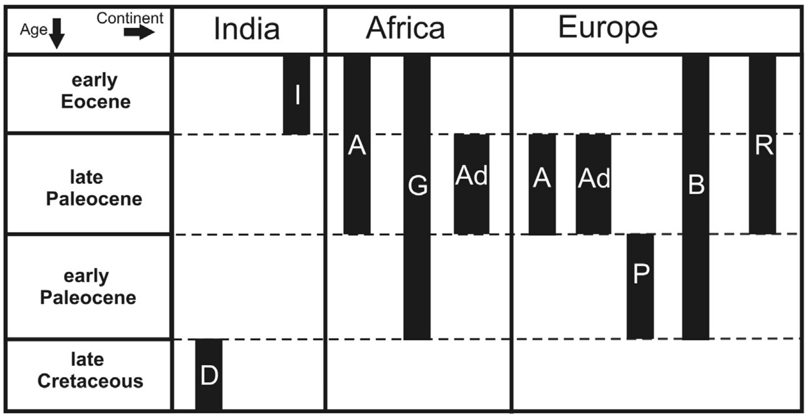

Fig. 2. Temporal range of known adapisoriculids from India, Africa and Europe. **A**: *Afrodon*; **Ad**: *Adapisoriculus*; **B**: *Bustylus*; **D**: *Deccanolestes*; **G**: *Garatherium*; **I**: *Indolestes*; **P**: *Proremiculus*; **R**: *Remiculus*.

Fig. 2. Domaine temporel des adapisoriculidés connus en Inde, Afrique et Europe. **A** : *Afrodon* ; **Ad** : *Adapisoriculus* ; **B** : *Bustylus* ; **D** : *Deccanolestes* ; **G** : *Garatherium* ; **I** : *Indolestes* ; **P** : *Proremiculus* ; **R** : *Remiculus*.

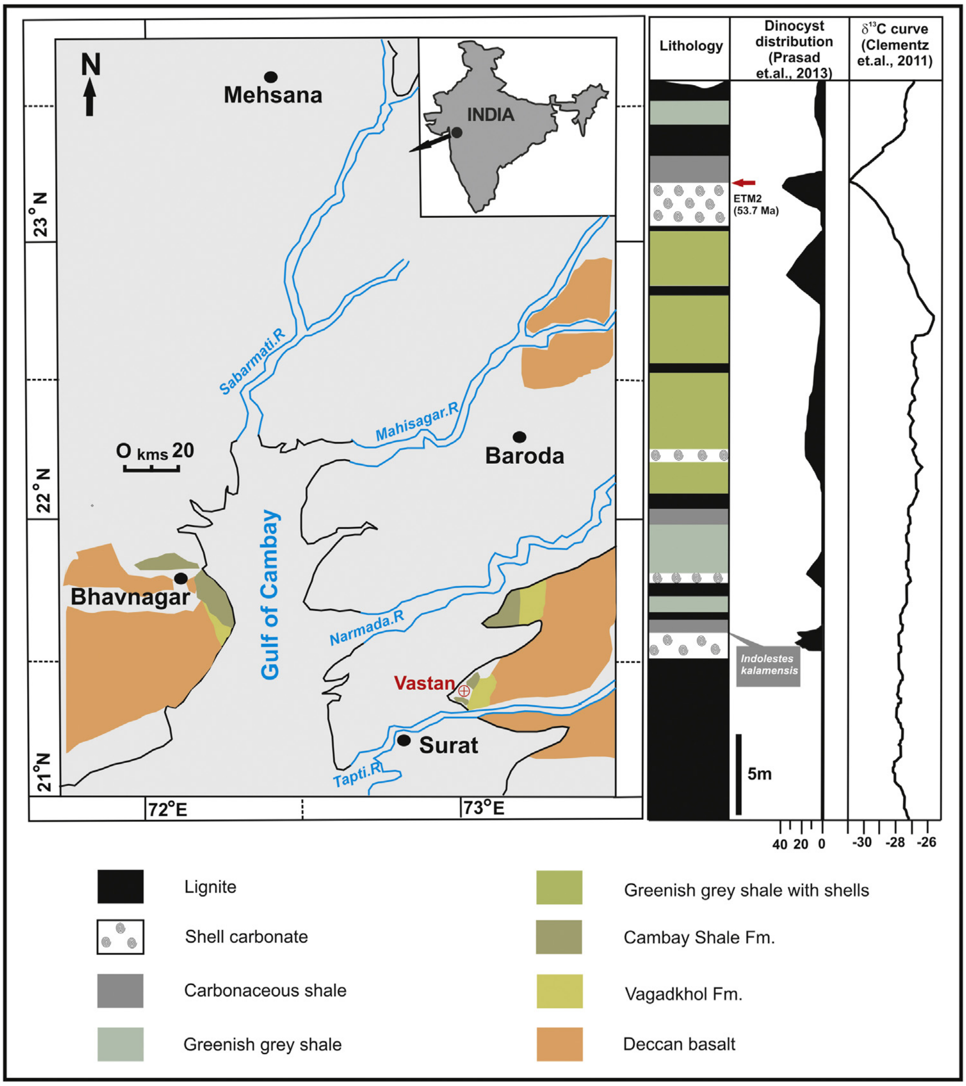

Fig. 3. Location map showing position of the fossil locality (Vastan, District Surat, Gujarat, western India) with a lithostratigraphic section showing *Indolestes kalamensis* gen. et sp. nov. yielding level. Note: ETM2 level is marked (red arrow) about 20 m above the mammalian level.

Fig. 3. Carte de localisation montrant la position de la localité fossilifère (Vastan, District de Surat, Gujarat, Inde occidentale) avec une section lithostratigraphique, avec un niveau à *Indolestes kalamensis* gen. et sp. nov. À noter que le niveau EDTM2 est marqué environ 20 m au-dessus du niveau à mammifères.

5. Systematic palaeontology

Class: Mammalia Linnaeus, 1758
Infraclass: Eutheria Gill, 1872
Order: Insertae sedis
Family: Adapisoriculidae Van Valen, 1967
Genus: *Indolestes* gen. nov.
Type and only species: *Indolestes kalamensis* gen. et sp. nov.

Derivation of name: The genus name is the combination of "*Indo*" for India and "*lestes*", a common suffix used for insectivorous mammals.

Diagnosis: A large adapisoriculid having the following features: double rooted p3 and p4; diastema between p3 and p4; mental foramen below p3; p4 with a small but distinct paraconid positioned anterolingual to the large protoconid; p4 metaconid absent; labiolingually compressed p4 protoconid; molar (m2 and m3) trigonid slightly wider than talonid, molar trigonid height almost twice the talonid height; lingual cusps in molars in line with each other, molar talonids with three cusps (entoconid, hypoconid and hypoconulid) with a highly salient hypoconid, positioned labially while hypoconulid positioned close to the entoconid; entoconid slightly more developed than hypoconulid; cristid obliqua moderately developed in molars (m2–m3), labial to the protocristid notch and ascends slightly on the posterior trigonid wall.

Differential diagnosis: *Indolestes* preserves large molars compared to well-known adapisoriculid genera (*Deccanolestes*, *Afrodon* and *Bustylus*). *Indolestes* molars differ from those of *Deccanolestes* (*D. hislopi*, *D. robustus*) and all known species of *Bustylus* in having molars with

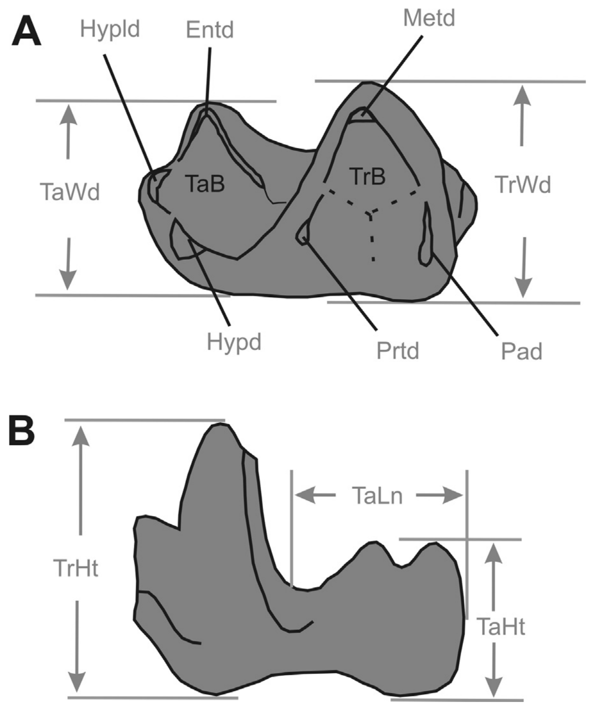

Fig. 4. A generalized sketch of the lower molar. **A**. Occlusal aspect. **B**. Lateral aspect. **Pad**: paraconid; **Metd**: metaconid; **Prtd**: protoconid; **Entd**: entoconid; **Hypld**: hypoconulid; **Hypd**: hypoconid; **TaB**: talonid basin; **TrB**: trigonid basin; **TaWd**: talonid width; **TrWd**: trigonid width; **TaLn**: talonid length; **TaHt**: talonid height; **TrHt**: trigonid height. Modified after Gheerbrant and Russell, 1991.

Fig. 4. Schéma général de la molaire inférieure. **A.** Aspect occlusal. **B.** Aspect latéral. **Pad** : paraconide ; **Metd** : métaconide ; **Prtd** : protoconide ; **Entd** : entoconide ; **Hypld** : hypoconulide ; **Hypd** : hypoconide ; **TaB** : bassin du talonide ; **TrB** : bassin du trigonide ; **TaWd** : largeur du talonide ; **TrWd** : largeur du trigonide ; **TaLn** : longueur du talonide ; **TaHt** : hauteur du talonide ; **TrHt** : hauteur du trigonide. Modifié d'après Gheerbrant et Russell, 1991.

slightly wider trigonid than talonid. Further, differ from those of *Deccanolestes* (*D. hislopi*, *D. robustus*), *Afrodon* (*A. chleuhi*) and *Bustylus* in having a prominent hypoconid, and from those of *Afrodon* (*A. gheerbranti*), *Bustylus* and *Adapisoriculus* (*A. minimus*) in lacking a p4 metaconid.

Age: early Eocene of India

Indolestes kalamensis sp. nov. (Figs. 5A–C and 6A–I)

Holotype: IITR/SB/VLM-804 (right dentary with alveoli for p2, p3 and m1; crowns for p4, m2 and m3 in place).

Derivation of name: The species is named in honor of late Dr. A.P.J. Abdul Kalam, former Indian president for his iconic contributions as an inspirational role model in science and technology in India.

Diagnosis: Same as for the genus

Type Locality: Vastan Lignite Mine, Taluka Mangrol, District Surat, Gujarat state, western India.

Type Horizon: Cambay Shale (early Eocene, ~54–55 Ma)

Description: The holotype is a right mandible preserving alveoli for p2, p3 and m1; in situ crowns for p4, m2 and m3. The only preserved mental foramen is observed at a depth of 0.89 mm below p3. The horizontal ramus is deep, ventrally convex with the greatest depth below the m2–m3 junction (see Table 2 for measurements). The ramus is convex lingually but nearly flat labially. The masseteric fossa is shallow. The coronoid process slopes upward at an angle of about 45° (Fig. 5A–C).

Although the alveoli anterior to p3 are damaged and do not preserve the bony partition (interalveolar septa), the bifurcated dorsal outline suggests that p2 was double-rooted, similar to p3-m3 (inferred from alveoli in the case of p3 and m1). A 0.62-mm diastema is observed between p3 and p4 (Fig. 5A1 and A2).

p4 is larger than p3 (as indicated by the size of alveoli) and is anteroposteriorly elongated, measuring 1.97 mm in length and 0.95 mm in width. A low but distinct paraconid is present anteriolingual to the protoconid. The protoconid is high and labiolingually compressed. The posterolingual portion of this tooth is damaged and a weak crest descends posterolingually from the protoconid towards this damaged region (Fig. 5A1 and A2; Fig. 6G–I).

Molars are robust and obliquely set in the dentary. Detailed measurements of the in situ molars in the holotype dentary are provided in Table 3.

The m2 trigonid is shorter as compared to the talonid and also about twice as high as the talonid. The trigonid is slightly wider than the talonid. An anterobuccal cingulid (precingulid) is seen to extend from the base of the paraconid to the base of the protoconid but no cusp is discernable. An anteriorly canted paraconid is positioned anteriolabial to the metaconid. Both these cusps are separated at their bases resulting in a lingual opening in the trigonid basin. The lingual cusps are in line with each other. The protoconid is the largest and the highest cusp, followed by metaconid and paraconid, respectively. The protoconid is labially convex. The metaconid is situated slightly posterolingual to the protoconid, resulting in obliquity of the posterior trigonid wall with respect to the transverse axis. The protolophid joining the protoconid and metaconid is notched (this feature is better observed in m3). The moderately developed cristid obliqua slightly ascends the trigonid wall but stays buccal to the protocristid notch thereby creating a wider talonid basin. The hypoflexid is deep. All three talonid cusps are better developed in m2 than in m3. Post-cingulid, labial cingulid and lingual cingulid are lacking. On the talonid, the hypoconid is the largest cusp, followed by the entoconid and hypoconulid. The hypoconid is labially positioned, thereby creating a deep and broad talonid basin. The posterolingually positioned hypoconulid is closer to the entoconid than to the hypoconid. Wear facets are best observed on this molar (for terminologies refer to Crompton and Kielan-Jaworowska, 1978). The narrow wear facet 1 is developed parallel to the posterior trigonid wall and lies along the ridge connecting the high protoconid and a slightly lower metaconid. However, this wear facet is disconnected at the protoconid-metaconid notch. Wear facet 2 extends posterolabially from the paraconid towards the protoconid. Wear facet 3 extends from the top of the hypoconid along the cristid obliqua while wear facet 4 extends posterolingually from the hypoconid ending well short of the hypoconulid. Wear facet 5 is not clearly observed but facet 6 is observed at the position

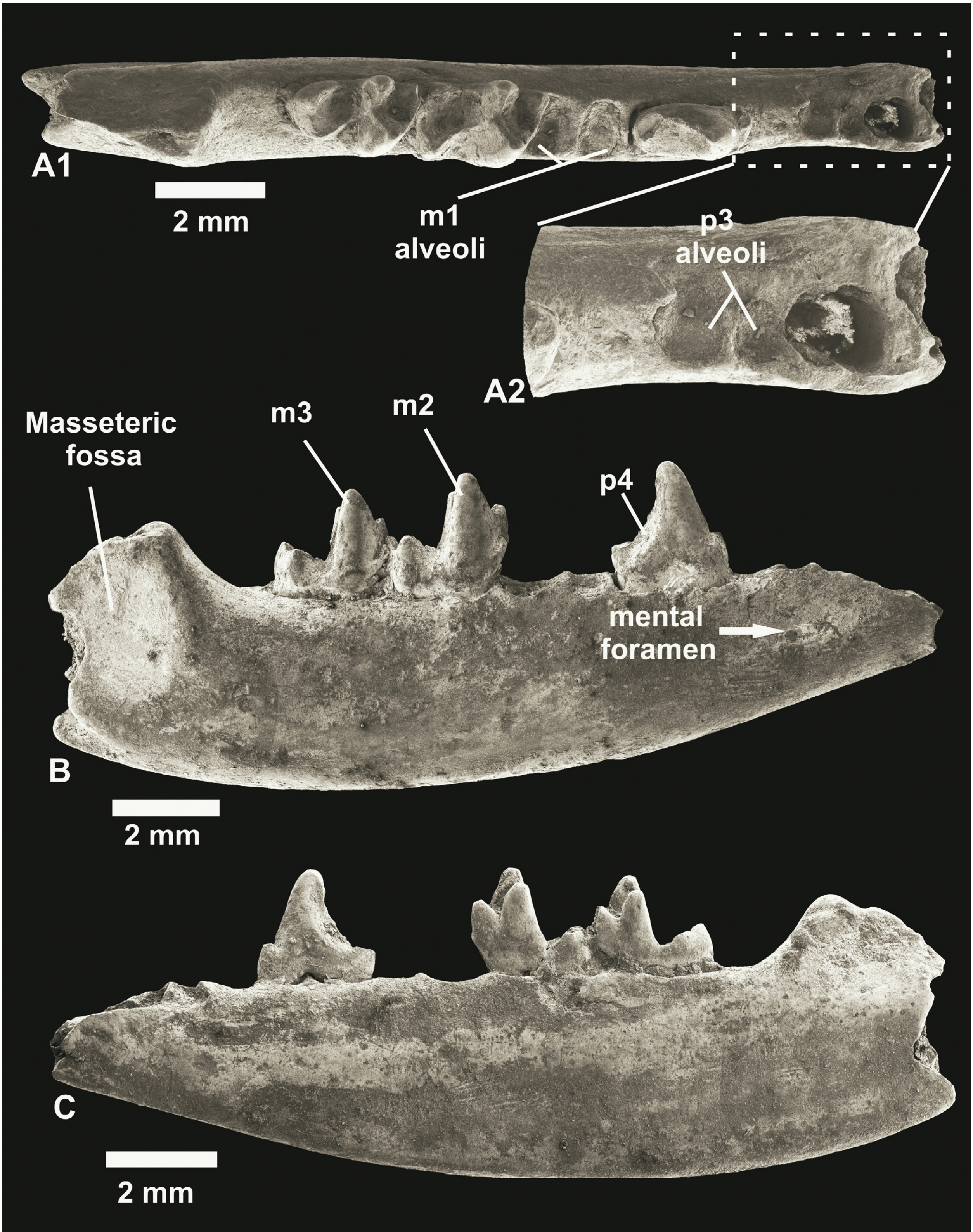

Fig. 5. *Indolestes kalamensis* gen. et sp. nov. (IITR/SB/VLM-804, holotype, right dentary with in situ p4, m2–m3): **(A1)** occlusal view; **(A2)** close-up view in occlusal aspect showing alveoli in front of p4; **(B)** labial view; **(C)** lingual view.

Fig. 5. *Indolestes kalamensis* gen. et sp. nov. (IITR/SB/VLM-804, holotype, dentaire droit avec p4, m2–m3 in situ) : **(A1)** vue occlusale ; **(A2)** gros plan en vue occlusale montrant des alvéoles en avant de p4 ; **(B)** vue labiale ; **(C)** vue linguale.

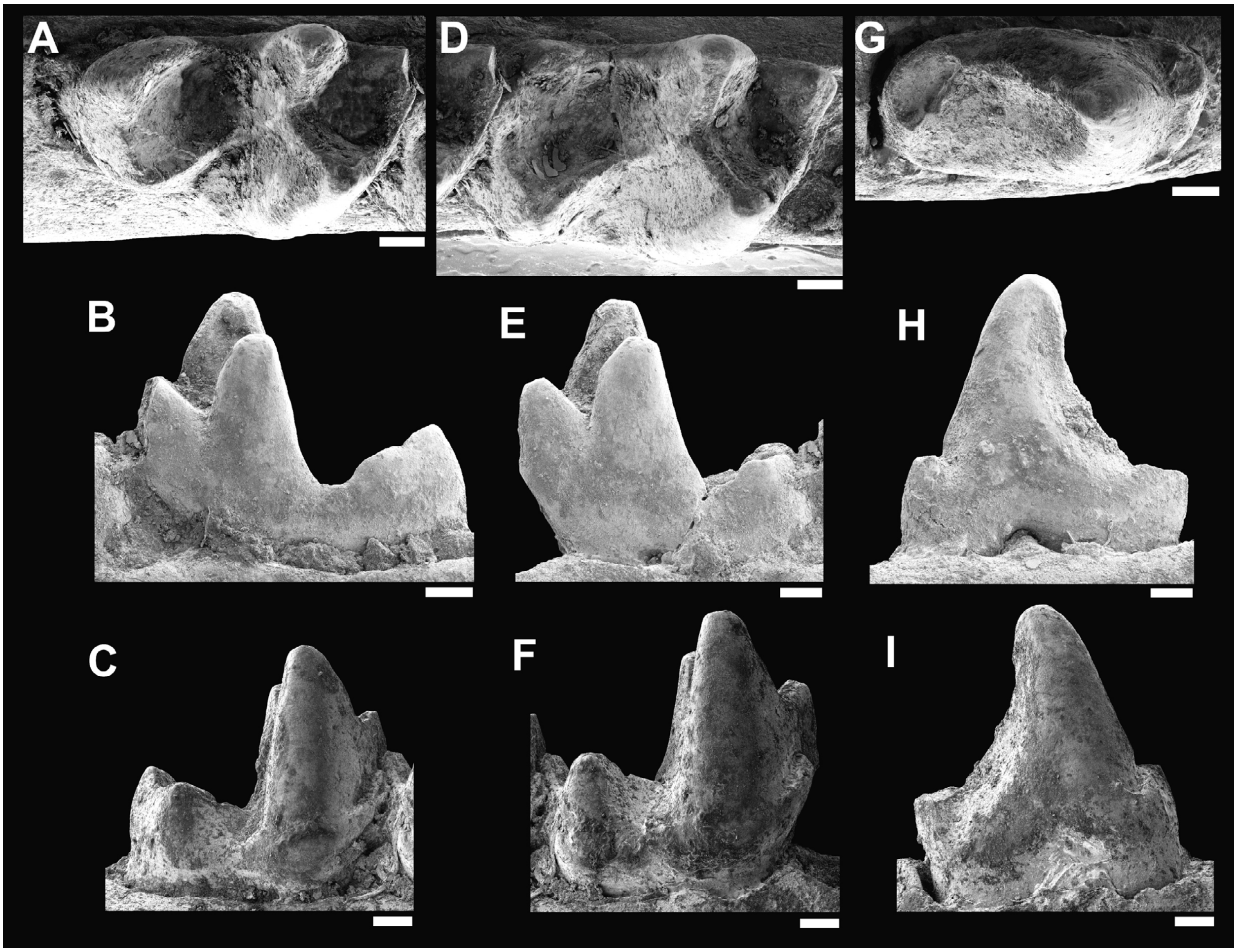

Fig. 6. *Indolestes kalamensis* gen. et sp. nov. (IITR/SB/VLM-804, holotype). **(A)** m3, occlusal view; **(B)** m3, lingual view; **(C)** m3, labial view; (**D**) m2, occlusal view; **(E)** m2, lingual view; **(F)** m2, labial view; (**G**) p4, occlusal view; **(H)** p4, lingual view; **(I)** p4, labial view. Scale bar equals 300 μm for all.
Fig. 6. *Indolestes kalamensis* gen et sp. nov. (IITR/SB/VLM-804, holotype. **(A)** m3, vue occlusale ; **(B)** m3, vue linguale ; **(C)** m3, vue labiale ; **(D)** m2, vue occlusale ; **(E)** m2, vue linguale ; **(F)** m2, vue labiale ; **(G)** p4, vue occlusale ; **(H)** p4, vue linguale ; **(I)** p4, vue labiale. La barre d'échelle représente 300 μm pour tous.

Table 2
Measurements (in mm) of the ramus depth in the dentary (IITR/SB/VLM-804) of *Indolestes kalamensis* gen. et sp. nov.
Tableau 2
Mesures (en millimètres) de la profondeur du ramus dans le dentaire (IITR/SB/VLM-804) d'*Indolestes kalamensis* gen. et sp. nov.

	p1	p2	p3	p4	m1	m2	Depth below m2–m3 junction	m3
IITR/SB/VLM-804 (holotype)	–	1.55[a]	1.94	2.91	3.32	3.57	3.62	3.50

[a] Estimate.

Table 3
Measurements (in mm) of molars in the holotype dentary (IITR/SB/VLM-804) of *Indolestes kalamensis* gen. et sp. nov. L: total length; TrLn: trigonid length; TrWd: trigonid width; TaLn: talonid length; TaWd: talonid width; TrHt: trigonid height; TaHt: talonid height.
Tableau 3
Mesures en millimètres des molaires du dentaire holotype (IITR/SB/VLM-804) de *Indolestes kalamensis* gen. et sp. nov. L : longueur totale ; TrLn : longueur du trigonide ; TrWd : largeur du trigonide ; TaLn : longueur du talonide ; TaWd : largeur du talonide ; TrHt : hauteur du trigonide ; TaHt : hauteur du talonide.

		L	TrLn	TrWd	TaLn	TaWd	TrHt	TaHt
IITR/SB/VLM-804 (holotype)	m2	2.13	1.04	1.44	1.09	1.18	2.02	0.98
	m3	2.00	0.95	1.34	1.05	0.99	1.76	0.96

of the posterolingual cusps (refer section 6 "Comparisons" and Fig. 9).

The m3 is broadly similar in crown morphology to m2 but smaller in size. The trigonid is less than twice the height of the talonid in this tooth (see Table 3). The apex of the paraconid is broken off but is anteriorly canted. The m3 talonid is narrower than that in m2 since the hypoconid is positioned less labially compared to that in m2. Compared to the condition in m2, the hypoconulid in m3 projects more posteriorly (although still close to the entoconid). The entoconid is smaller than in m2 and also labiolingually compressed. The wear pattern in m3 resembles that of m2 but is less prominent.

6. Comparisons

Comparison of *Indolestes* with possible lipotyphlans or proteutherians known from the Early Paleogene of the Indian Subcontinent reveals important differences. The p4 of *Pakilestes lathrius* from the middle Eocene Kuldana Formation of Pakistan (Russell and Gingerich, 1981) is 46% smaller and its protoconid is markedly convex labially and the tooth has a short, narrow and basined talonid, unlike the p4 of *Indolestes.* The *Pakislestes* molar (m1/m2) is about 60% smaller in size, with the paraconid projecting more anteriorly than in *Indolestes*. *Seia shahi* from Kohat region of Pakistan (Russell and Gingerich, 1981) is known from isolated upper molars (M1 and M2), therefore, direct morphological comparison with *I. kalamensis* is currently not possible. *Perizalambdodon*, described as a lipotyphalan by Thewissen et al. (2005) on the basis of an isolated lower molar (m1 or m2, H-GSP 92168) has a smaller m2 (about 80%) and lacks an entoconid and a talonid basin.

Previously described early Eocene insectivores from Vastan include an erinaceomorph *Vastania sahnia*, a palaeoryctid *Anthraryctes vastanensis* and a cimolestid *Suratilestes gingerichi* (Bajpai et al., 2005). *Indolestes* was also recovered from the same horizon at Vastan. *Vastania* can be easily distinguished from *Indolestes* in lacking a diastema between p3 and p4, having a smaller p4 (about 50%), a smaller m2 (about 60%) and a smaller m3 that lacks an entoconid. *Suratilestes*, described as a cimolestid, can also be clearly distinguished from *Indolestes* in having smaller (by about 60%) p4 without a paraconid, relatively smaller molars (m2 about 60% smaller and m3 about 54% smaller) with large difference in height between trigonid and talonid and having a wider talonid than trigonid. *Anthraryctes*, known from an isolated upper molar (M3) and the only record of a palaeoryctid from the early Eocene of India, cannot be directly compared with *Indolestes*.

Overall, the lower dentition (p4, m2 and m3) of *I. kalamensis* is reminiscent of the family Adapisoriculidae in exhibiting the following characters: mental foramen below p3 in the dentary, presence of a strong paraconid positioned anterolabially on the trigonid, a salient hypoconid positioned labially on the talonid, the hypoconulid shifted lingually close to the entoconid and a moderately developed cristid obliqua that ascends slightly on the posterior trigonid wall. Also, consistent with its younger stratigraphic record, *Indolestes* displays several characters that are derived relative to the oldest known adapisoroculid (*Deccanolestes*) and Paleocene taxa known from Africa (*Afrodon chleuhi*, *Afrodon gheerbranti*). These characters include larger size of lower molars with a talonid slightly less wide than the trigonid; deep and ventrally convex ramus; diastema between p3 and p4; m3 < m2 and cristid obliqua positioned slightly labial to the protoconid-metaconid notch.

I. kalamensis is a large adapisoriculid when compared to well-known adapisoriculids from India, Africa and Europe (e.g. *Deccanolestes*, *Afrodon* and *Bustylus*), with m2 size (length × width) approximately 30% larger than *A. gheerbranti*, 66% larger than *Bustylus marandati*, 58% larger than *Bustylus folieae*; m3 about 72% larger than *Deccanolestes narmadensis*, 68% larger than *Deccanolestes* cf. *hislopi* (isolated m3 ITV/R/Mm-12), 16% larger than *A. gheerbranti*, 47% larger than *Afrodon germanicus*, 68% larger than *B. marandati* and approximately 49% larger than *A. chleuhi* and *B. folieae*. Table 4 provides measurements of the lower dentition (p4-m3) of few known adapisoriculids while Fig. 7 provides a bivariate plot showing size comparisons between *Indolestes* and previously known adapisoriculids.

Molars of *I. kalamensis* were directly compared with the original specimens of Late Cretaceous Indian species *D. narmadensis* (VPL/JU/IM/6, VPL/JU/IM/7 and the holotype VPL/JU/IM/8) that is known only from lower molars. The two species are broadly similar in having lingual cusps in line with each other and the trigonid cusps forming an open triangle. However, *Indolestes* molars are more derived than those of *D. narmadensis* in having a slightly wider trigonid than the talonid; hypoconulid shifted lingually close to the entoconid and having a cristid obliqua positioned slightly labial to the protoconid-metaconid notch that ascends the posterior trigonid wall. It should be noted that the mandible fragments of adapisoriculids with *in situ* dentition are uncommon in the fossil record, making comparisons within the group difficult. Interestingly, the Late Cretaceous intertrappean locality at Naskal (South India), known for producing many isolated upper and lower teeth of *Deccanolestes* (Prasad and Sahni, 1988; Prasad et al., 1994, 2010), recently yielded a mandible fragment (DUGF/IM/1) with in situ p3, p4, m1 and m2 (Fig. 8A–C). This specimen is illustrated here for purposes of comparison (for measurements of dentition, refer to Table 4). The preserved dentary (DUGF/IM/1) referred here to *Deccanolestes hislopi*, is similar to *Indolestes* in the following characters: presence of a deep and ventrally convex ramus; lingually open molar trigonids; presence of a precingulid, protoconid being the largest cusp on trigonid; having a metaconid and protoconid that are separated at the base with the metaconid situated slightly posterolingual to the protoconid resulting in obliquity of the posterior trigonid wall with respect to the transverse axis. However, apart from being smaller in size, DUGF/IM/1 differs from *Indolestes* in the presence of a conspicuous diastema between p2 and p3, presence of a mental foramen below p4-m1 junction, having a ramus that is concave labially and convex lingually with greatest depth below m1-m2 junction. The not so well preserved p4 in DUGF/IM/1 has a large talonid unlike *Indolestes*. The molars of *D. hislopi* (DUGF/IM/1) are quite smaller (m2 about 69% smaller) compared to *Indolestes* and can be clearly differentiated

Table 4
Measurements of lower dentition (p4–m3) of known adapisoriculids including *Indolestes kalamensis* gen. et sp. nov. (IITR/SB/VLM-804). Data compiled from De Bast et al., 2012, 2013; Gheerbrant, 1988, 1991, 1993, 1995; Gheerbrant and Russell, 1989, 1991; Prasad and Sahni, 1988; Prasad et al., 1994, 2010.
Tableau 4
Mesures de la dentition inférieure (p4–m3) d'adapisoriculidés connus incluant Indolestes kalamensis gen. et sp. nov.(IITR/SB/VLM-804). Données compilées à partir de De Bast et al., 2012, 2013 ; Gheerbrant, 1988, 1991, 1993, 1995 ; Gheerbrant et Russell, 1989, 1991 ; Prasad et Sahni, 1988 ; Prasad et al., 1994, 2010.

Taxon	Specimen	Dentition	Length (mm)	Maximum width (mm)
Indolestes kalamensis gen. et sp. nov.	IITR/SB/VLM-804	p4	1.97	0.95
Indolestes kalamensis gen. et sp. nov.	IITR/SB/VLM-804	m2	2.13	1.44
Indolestes kalamensis gen. et sp. nov.	IITR/SB/VLM-804	m3	2.00	1.34
Deccanolestes narmadensis	VPL/JU/IM/8	m1 or m2	1.25	0.65
Deccanolestes narmadensis	VPL/JU/IM/7	m1 or m2	1.32	0.67
Deccanolestes narmadensis	VPL/JU/IM/6	m3	1.23	0.60
Deccanolestes hislopi	VPL/JU/NKIM/16	m1	0.95	0.58
Deccanolestes hislopi	DUGF/IM/1	p4	1.18	0.55
Deccanolestes hislopi	DUGF/IM/1	m1	1.33	0.85
Deccanolestes hislopi	DUGF/IM/1	m2	1.18	0.81
Deccanolestes cf. *hislopi*	ITV/R/Mm-7	m1 or m2	0.91	0.60
Deccanolestes cf. *hislopi*	ITV/R/Mm-10	m1 or m2	1.07	0.72
Deccanolestes cf. *hislopi*	ITV/R/Mm-11	m3	1.15	0.70
Deccanolestes cf. *hislopi*	ITV/R/Mm-12	m3	1.13	0.68
Deccanolestes robustus	VPL/JU/NKIM/14	m1	1.48	0.94
Afrodon gheerbranti	Q2-32/M1986	p4	2.12	1.08
Afrodon gheerbranti	N2-12	m1	2.24	1.20
Afrodon gheerbranti	O1-03	m1	2.16	1.02
Afrodon gheerbranti	N2-13/M1987	m1	2.14	1.12
Afrodon gheerbranti	Q1-06/M1988	m2	1.90	1.14
Afrodon gheerbranti	Q2-31	m2	1.88	1.20
Afrodon gheerbranti	Y1-06	m2	1.98	1.12
Afrodon gheerbranti	N2-06/M1989	m3	2.16	1.04
Afrodon chleuhi	THR 316	p4	1.25	0.87
Afrodon chleuhi	THR 051	m3	1.43	0.93
Bustylus germanicus	Wa/537	m1	1.35	0.72
Bustylus germanicus	WB 9	m1	1.40	0.83
Bustylus germanicus	CR-32-PN	m3	1.48	0.96
Bustylus marandati	N2-22/M1991	p4	1.18	0.56
Bustylus marandati	Q2-05/M1992	m1	1.20	0.64
Bustylus marandati	R1-27/M1993	m2	1.22	0.80
Bustylus marandati	R1-34	m2	1.24	0.84
Bustylus marandati	MZ1-01	m2	1.22	0.96
Bustylus marandati	Q2-42/M1994	m3	1.24	0.68
Bustylus folieae	N2-06b/M1998	p4	1.34	0.62
Bustylus folieae	R1-31/M2000	p4	1.26	0.60
Bustylus folieae	O1-08	p4	1.26	0.64
Bustylus folieae	N2-06b/M1998	m1	1.50	0.90
Bustylus folieae	P2-04/M2002	m1	1.50	0.86
Bustylus folieae	N2-07	m1	1.50	0.90
Bustylus folieae	O2-01	m1	1.44	0.80
Bustylus folieae	N2-06b/M1998	m2	1.38	0.94
Bustylus folieae	N1-01/M2003	m2	1.44	0.94
Bustylus folieae	R1-10/M2004	m3	1.48	0.80
Bustylus folieae	Q2-42	m3	1.24	0.68
Bustylus folieae	Q2-09	m3	1.36	0.78
Proremiculus lagnauxi	R1-38/M2007	m1	2.18	1.20
Proremiculus lagnauxi	R1-74/M2008	m1 or m2	2.04	1.30
Remiculus deutschi	CR 1170	m1 or m2	2.66	1.66

from the latter in the presence of a trigonid as wide as talonid; a crest like paraconid; cristid obliqua joining the posterior trigonid wall lingually and hypoconulid median in position.

Another taxon, *Sahnitherium rangapurensis*, was described from the Late Cretaceous intertrappean deposits of Rangapur, South India (Rana and Wilson, 2003), a locality about 4 km southeast of the famous mammal-yielding locality Naskal that yielded the first Cretaceous mammal of India i.e. *Deccanolestes*. *Sahnitherium* (known only from an isolated right upper molar, M1 or M2) is morphologically very close to the upper molars of *Deccanolestes* and detailed phylogenetic analysis suggests that this upper molar belongs to an adapisoriculid (Goswami et al., 2011). As *Indolestes* is known only from lower dentition, direct morphological comparisons with *Sahnitherium* cannot be made at this stage, however, *Indolestes* molar (m2) is larger (by about 56%) compared to the upper molar (specimen no. ITV/R/Mm-1) known for *Sahnitherium*.

The genus *Afrodon* can be clearly differentiated from *Indolestes* in having a submedian hypoconulid and cristid obliqua extending onto the lingual region of the posterior wall of the trigonid. *A. gheerbranti* differs from *Indolestes* in having smaller molars, a talonid as wide as trigonid,

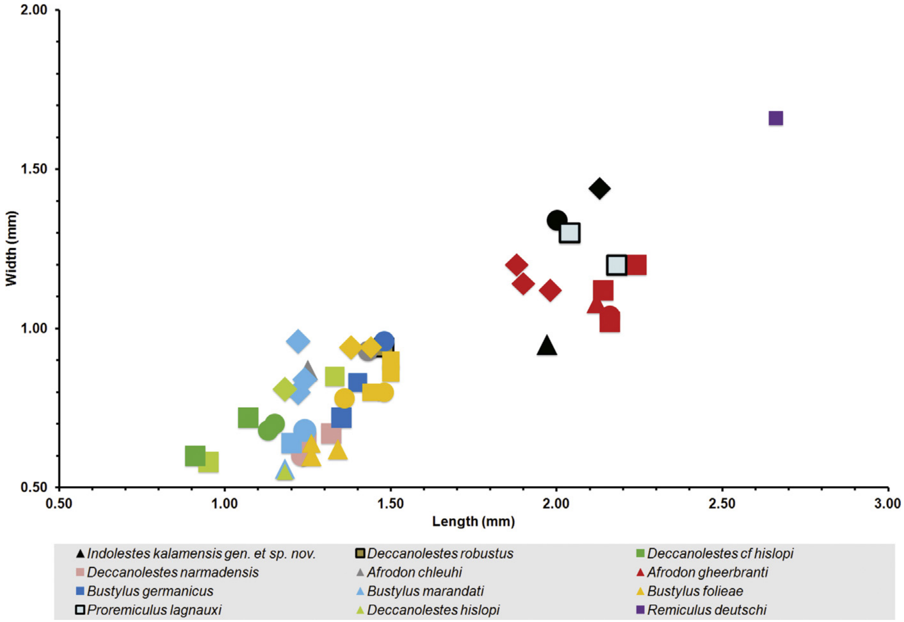

Fig. 7. Bivariate plot showing size variations in the lower dentition (ultimate premolar and lower molars) between *Indolestes kalamensis* gen. et sp. nov. from the early Eocene of India and well-recognized adapisoriculids from India, Africa and Europe based on data provided in Table 4 of this article. Note: a: Isolated lower molars identified by previous workers as "m1 or m2" for *Deccanolestes narmadensis*, *Deccanolestes* cf. *hislopi*, *Proremiculus lagnauxi* and *Remiculus deutschi* have been considered as m1 for plotting purpose only; b: p4 (triangle), m1 (square), m2 (diamond) and m3 (circle). Data on measurements compiled from De Bast et al., 2012, 2013; Gheerbrant, 1988, 1991, 1993, 1995; Gheerbrant and Russell, 1989, 1991; Prasad and Sahni, 1988; Prasad et al., 1994, 2010.

Fig. 7. Report graphique à double entrée montrant les variations de taille dans la dentition inférieure (dernière prémolaire et molaires inférieures) entre *Indolestes kalamensis* gen.et sp. nov. de l'Éocène inférieur d'Inde et les adapisoriculidés d'Inde, d'Afrique et d'Europe, basé sur des données fournies dans le Tableau 4 de cet article. À noter : a : les molaires inférieures isolées identifiées par des chercheurs antérieurs comme « m1 ou m2 » pour *Deccanolestes narmadensis, Deccanolestes* cf. *hislopi*, *Proremiculus lagnauxi* et *Remiculus deutschi* ont été considérées comme m1 uniquement dans un but de report graphique ; b : p4 (triangle), m1 (carré), m2 (losange) et m3 (cercle). Données sur les mesures compilées d'après De Bast et al., 2012, 2013 ; Gheerbrant, 1988, 1991, 1995 ; Gheerbrant et Russell, 1989, 1991 ; Prasad et Sahni, 1988 ; Prasad et al., 1994, 2010.

medially positioned hypoconulid, less salient hypoconid and presence of a p4 metaconid.

Molars of *Bustylus* are morphologically similar to *Indolestes* in the presence of a closely-spaced entoconid and hypoconulid. However, the latter differs in size (as discussed earlier) and in having a slightly larger hypoconid compared to the entoconid. Moreover, the genus *Bustylus* is typified based on the morphology of p4 that depicts a large paraconid, small and well-individualized metaconid (De Bast et al., 2013), unlike the p4 of *Indolestes.* A well-preserved dentary of *Bustylus* (*B. germanicus*) preserving a partial alveolus for c1, complete alveolus for p1, alveoli for biradiculate p2–p3 and in situ p4–m3, was recently reported from Maret, Belgium (Specimen no. IRSNB M2017, De Bast et al., 2013, Fig. 3G–K) and shows no diastema between the teeth, unlike in *Indolestes*.

Adapisoriculus (*A. minimus*) differs from *Indolestes* in being smaller (discussed earlier), having a p4 metaconid and in having molars that have a trigonid as wide as the talonid with a metaconid slightly more developed than the protoconid.

Garatherium is known from the late Paleocene and early Eocene of Africa (Crochet, 1984; Gheerbrant, 1988, 1995; Gheerbrant et al., 1998). However, this genus is known only by isolated upper dentition and thus, cannot be directly compared with *Indolestes* at this stage.

The molars in the European adapisoriculid genus *Remiculus* (Russell, 1964; Smith, 1997) have a significantly broader talonid than trigonid and a metaconid that is better developed than the protoconid, as opposed to that of *Indolestes*.

Proremiculus (*P. lagnauxi*) from the early Paleocene of Europe is known from isolated upper and lower molars (De Bast et al., 2012). The lower molars in this taxon are smaller (in size), have a wider talonid than the trigonid with three equidistant talonid cusps (hypoconulid median in position) and a hypoflexid that is shallow and wide.

Furthermore, it is observed that the position and pattern of wear facets (in particular 1, 2, 3, 4, 6) in the lower molar (m2) of *Indolestes* are similar to those generally found in the molars (m1–m2) of known adapisoriculids (see Fig. 9 of this article; also see Fig. 6 of De Bast et al., 2012). Facets 1 and 2 are the principal shearing surfaces on the trigonid. Facet 1 is better developed in *Indolestes* compared to *Deccanolestes* and *Afrodon*, but is less prominent compared to that in *Bustylus*. The wear pattern and morphology of the talonid (facets 3, 4 and 6) suggests that the talonid 'pestle' and protocone 'mortar' were used as a puncturing mechanism during feeding (*sensu* Luo, 2007), but this mechanism was less well developed in *Indolestes* compared to *Bustylus* and *Adapisoriculus*. In addition, the talonid morphology in *Indolestes* indicates that the upper molars of *Indolestes* should reveal a wider upper embrasure between the widely separated paracone and metacone (dilambdodonty) and a high and large protocone (generally observed in upper molars of adapisoriculids). The pres-

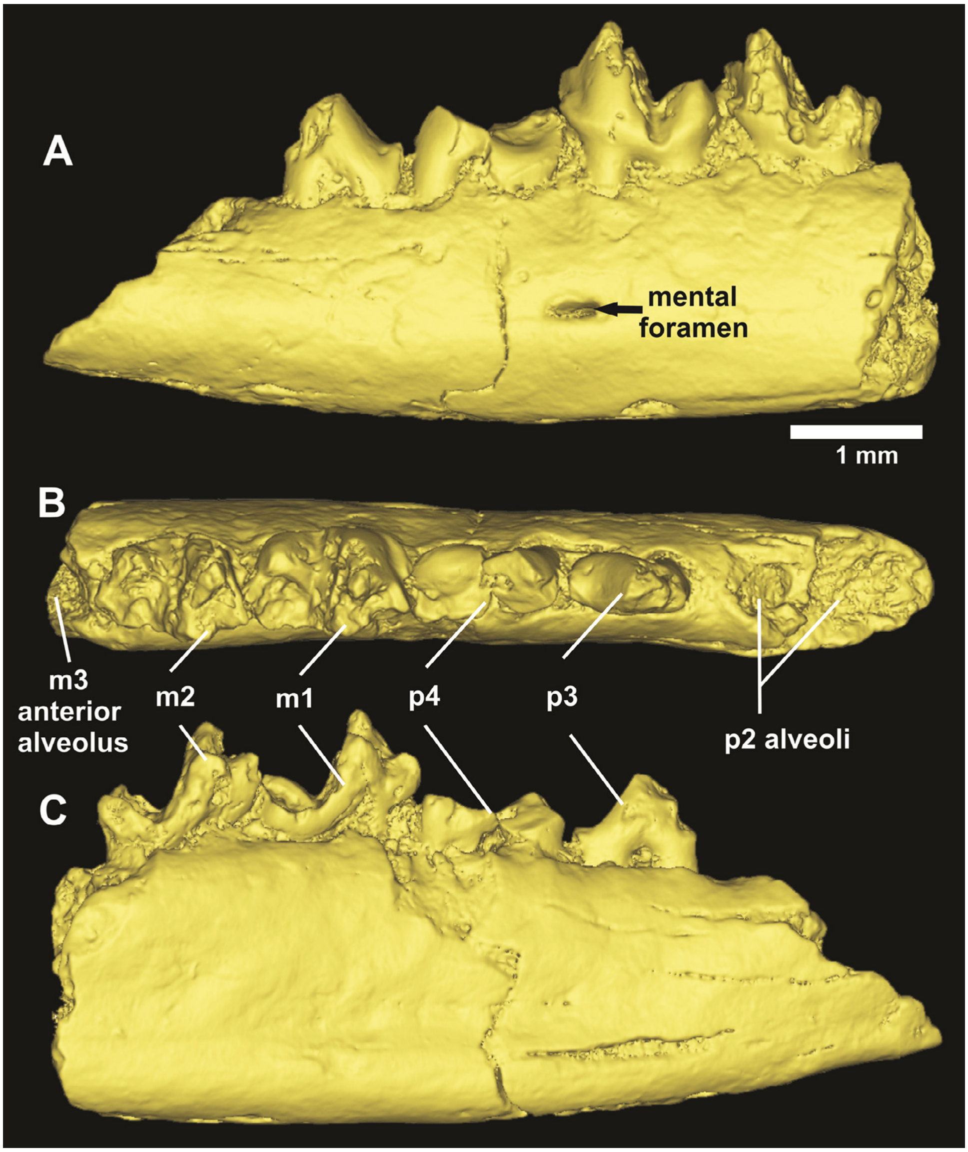

Fig. 8. CT images of *Deccanolestes hislopi* (DUGF/IM/1, left dentary with p3–m2). **(A)** labial view; **(B)** occlusal view; **(C)** lingual view.

Fig. 8. Images CT de *Deccanolestes hislopi* (DUGF/IM/1, dentaire gauche, avec p3-m2). Vues labiale (A), occlusale (B), linguale (C).

ence of a prominent precingulid in *Indolestes* and other known adapisoriculids (e.g., *Deccanolestes*) guarded the gum region from the metacone during shearing of food (*sensu* Crompton and Kielan-Jaworowska, 1978). Overall, the wear pattern and the tooth morphology of *Indolestes* are reminiscent of an adaptation for both shearing and puncturing of food. A detailed study on this aspect is beyond the scope of this paper, but will be taken up separately in the future.

7. Phylogenetic analysis

To assess the position of *I. kalamensis*, a preliminary phylogenetic analysis was conducted by adding this new taxon to the recently published matrix of De Bast et al. (2013) that includes the known Cretaceous–Paleogene (K–Pg) adapisoriculid taxa from India, Africa and Europe. De Bast et al. (2013) analysis is a simplified version of a previous analysis (De Bast et al., 2012) and excludes certain less well-known taxa (*D. narmadensis*, *Afrodon ivani* and *A. tagourtensis*). De Bast et al. (2013) also excluded *Remiculus* citing "possible convergences" with *Adapisoriculus*. In the present study, phylogenetic analysis was performed using Tree analysis using New Technology (TNT) software (Goloboff et al., 2008). The final matrix includes 12 taxa and 16 dental characters. A total of six dental characters based on lower dentition (IITR/SB/VLM-804) could be scored for *Indolestes*. "New Technology Search" function was run initially with the option to stabilize the consensus five times and setting the maximum branch length to 0 (i.e., collapsing rule 3). Subsequently, a "Traditional Search" with Tree Bisection and Reconnection (TBR) option was

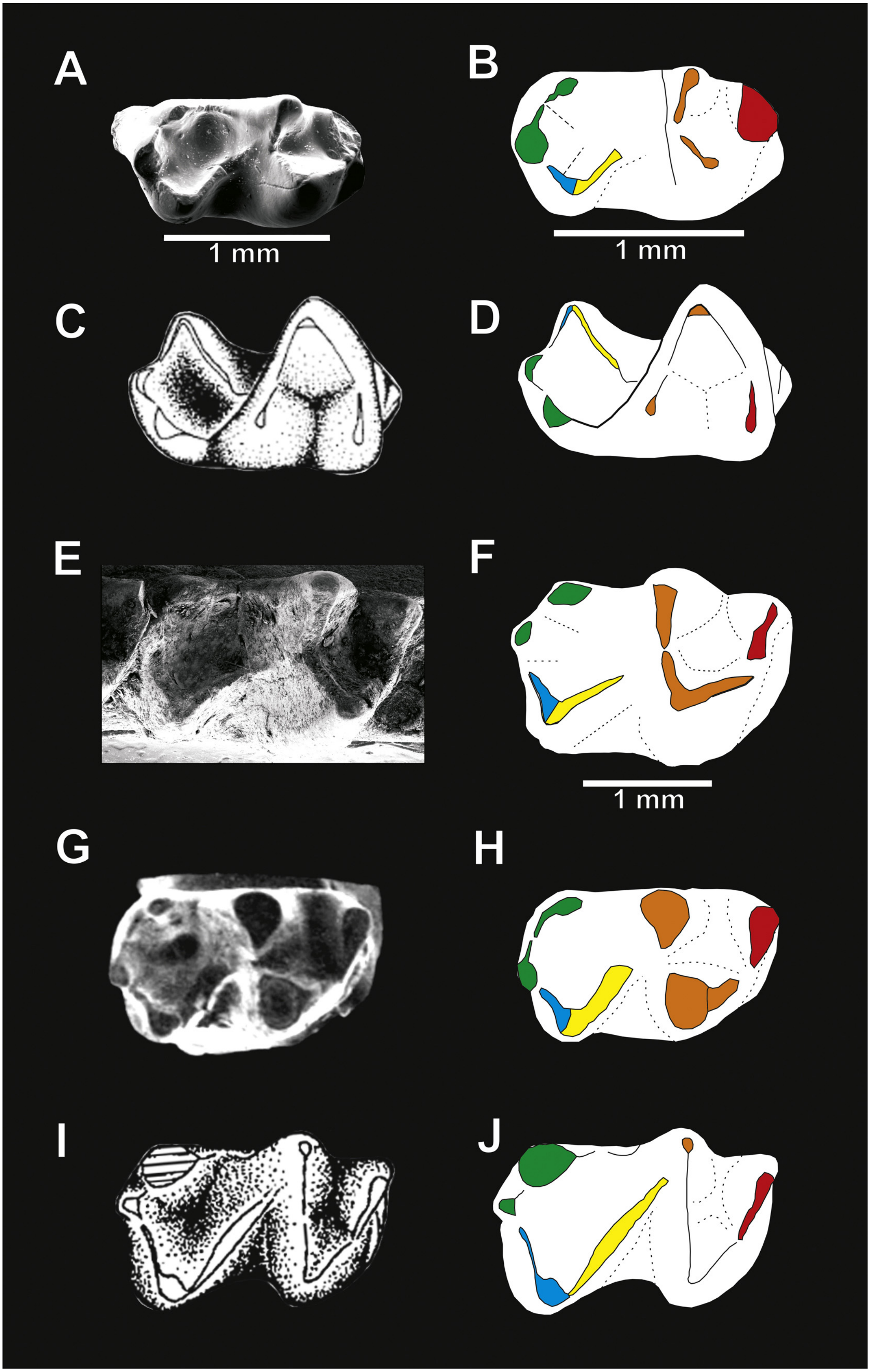
A
B
1 mm
1 mm
C
D
E
F
1 mm
G
H
I
J

Table 5
Character scores for *Indolestes kalamensis* gen. et sp. nov. For character definitions see Appendix 1 (De Bast et al., 2013). Note that "?" denotes missing or unknown characters.
Tableau 5
Scores des caractères pour *Indolestes kalamensis* gen. et sp. nov. Pour la définition des caractères, voir l'appendice 1 (De Bast et al., 2013). À noter que « ? » indique des caractères manquants ou inconnus.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Indolestes kalamensis gen. et sp. nov.	?	?	?	?	?	?	?	?	1	1	0	?	1	0	?	1

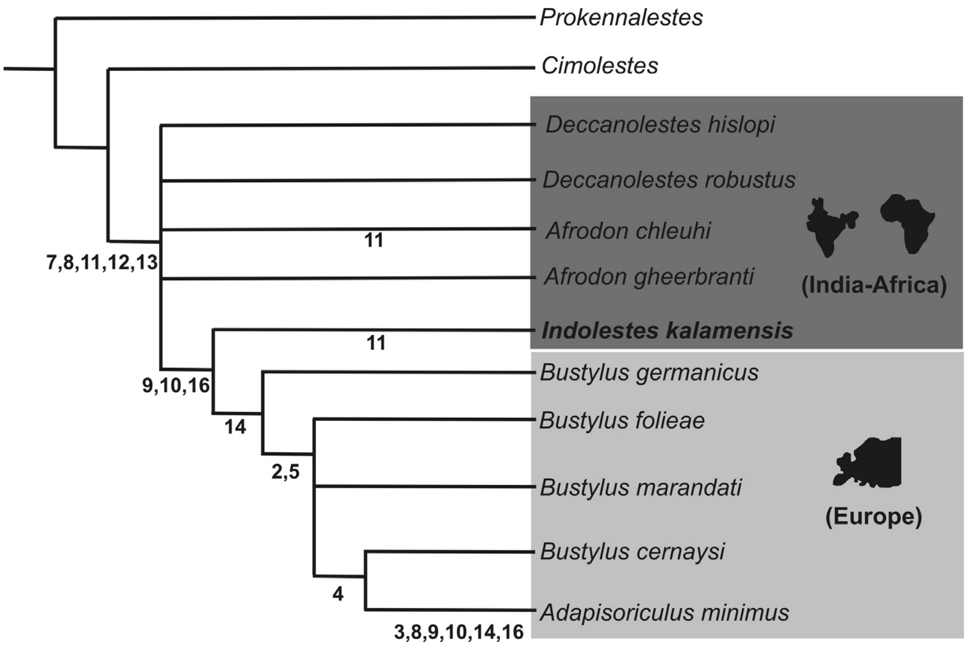

Fig. 10. Strict consensus tree of 8 maximum parsimonious trees (MPTs) with geographic affinities of the adapisoriculids used in the phylogenetic analysis. Synapomorphic characters are displayed at each node.
Fig. 10. Arbre de strict consensus de 8 arbres de parcimonie maximum (MPT), avec les affinités des adapisoriculidés utilisés dans l'analyse phylogénétique. Les caractères synapomorphiques sont indiqués à chaque nœud.

run, utilizing the trees produced in the previous search. The TNT software found eight Most Parsimonious Trees (MPTs) of Tree Length (TL) 22. The Consistency Index (CI) is 0.909 and the Retention Index (RI) is 0.949. The Strict Consensus tree is shown in Fig. 10. The character states for *Indolestes* are provided in Table 5 and details of these characters can be found in Appendix 1 of De Bast et al. (2013).

Overall, the results are in agreement with previous studies that suggest (a) *Deccanolestes* and *Afrodon* are primitive members of the family Adapisoriculidae, (b) *Bustylus germanicus* (= *Afrodon germanicus*) is more derived than other species of the genus *Afrodon*, (c) *Bustylus germanicus* is sister to the clade formed by *Adapisoriculus minimus* and all species of *Bustylus*. Our results suggest that *Indolestes* is more derived than *Deccanolestes* (*D. hislopi* and *D. robustus*) and *Afrodon* (*A. chleuhi* and *A. gheerbranti*) possibly due to the presence of a larger hypoconid as compared to entoconid (Character 9:1) and closer placement of molar hypoconulid and entoconid (Character 10:1). It is important to note that whereas both *A. chleuhi* and *I. kalamensis* gen. et sp. nov. have narrower molar talonids (than trigonid) (Character 11:0), this character is not shared by the clade formed by *Bustylus* (*B. germanicus*, *B. cernaysi*, *B. marandati*, *B. folieae*) and *A. minimus*. The presence of a p4 metaconid in the

Fig. 9. A diagrammatic sketch of lower molars (m1–2) of known adapisoriculids showing wear facets: 1 (orange), 2 (red), 3 (yellow), 4 (blue), and 6 (green). **(A–B)** *Deccanolestes narmadensis* (right m1 or m2, VPL/JU/IM/7); **(C–D)** *Afrodon chleuhi* (left m1?, THR 214); **(E–F)** *Indolestes kalamensis* gen. et sp. nov (right m2, IITR/SB/VLM-804); **(G–H)**. *Bustylus cernaysi* (right m1, CR 361 SLP); **(I–J)** *Adapisoriculus minimus* (right m2, Cr 301 Bn). Terminology of the wear facets follows Crompton and Kielan-Jaworowska (1978). For measurement scales of figures **C**, **D**, **G**, **H**, **I** and **J** refer Gheerbrant and Russell (1989, 1991). Figures reused and redrawn from Gheerbrant and Russell (1989, 1991) and Prasad et al. (2010) with permission from Elsevier.
Fig. 9. Schémas des molaires inférieures (m1–2) d'adapisoriculés connus, montrant des facettes d'usure : 1 (orange), 2 (rouge), 3 (jaune), 4 (bleu) et 6 (vert). **(A–B)** *Deccanolestes narmadensis* (m1 ou m2 droite, VPL/JU/DM/7) ; **(C–D)** *Afrodon chleuhi* (m1 ? gauche, THR 214) ; **(E–F)** *Indolestes kalamensis* gen. et sp. nov. (m2 droite, IITR/SB/VLM-804) ; **(G–H)** *Bustilus cernaysi* (m1 droite CR 361 SLP) ; **(I–J)** *Adapisoriculus minimus* (m2 droite, CR 301 Bn). La terminologie des facettes d'usure suit Crompton et Kielan-Jaworowska (1978). Pour les échelles des figures C, D, H, I et J, se référer à Gheerbrant et Russell (1989, 1991). Les figures réutilisées et redessinées sont issues de Gheerbrant et Russell (1989, 1991) et de Prasad et al. (2010), avec l'autorisation d'Elsevier.

latter clade is another character (Character 14:0) that suggests that this clade is more derived than *Indolestes*. In addition, the presence of several additional characters, such as a hypoconid slightly larger than entoconid (Character 9:1); hypoconulid positioned closer to the entoconid (Character 10:1); small size of p4 paraconid (Character 16:1) suggests a primitive dental morphology of *Indolestes* compared to European *A. minimus*.

It is to be noted that in all the eight MPTs produced, the position of *Indolestes* remains the same. Of the three hypotheses considered in the eight MPTs, for the phylogenetic relationships among *Indolestes*, *Deccanolestes*, *Afrodon*, *Bustylus* and *Adapisoriculus*, the first hypothesis suggests *A. chleuhi* is the most basal adapisoriculid and sister to the unresolved clade formed by *A. gheerbranti* + *Deccanolestes hislopi* + *D. robustus*. This unresolved clade is sister group to *Indolestes* + (*Bustylus* + *Adapisoriculus*) (Fig. 11A). The second hypothesis indicates *Deccanolestes*, *Indolestes* and *Bustylus* form successive sister taxa lineages to *Adapisoriculus* while *Afrodon* is the most basal adapisoriculid (Fig. 11B). The third hypothesis suggests that *Afrodon* + *Deccanolestes* are basal adapisoriculids and form an unresolved clade. This unresolved clade is sister group to *Indolestes* and (*Bustylus* + *Adapisoriculus*) (Fig. 11C). We favor the third hypothesis, as it matches better the stratigraphic position of *Deccanolestes.* However, the phylogenetic results presented here are tentative as the analysis is based only on dental characters and only 37% (6 out of 16) characters could be scored for *Indolestes*. Additional and more complete material (especially upper dentition and post-cranial elements) will help resolve the phylogenetic position of *Indolestes* among adapisoriculids with greater certainty.

8. Discussion

I. kalamensis gen. et sp. nov. adds significantly to the diversity of insectivores from Vastan as it represents a family hitherto not known from the Eocene of the Indian Subcontinent. Its lower dental morphology and wear facets are reminiscent of the family Adapisoriculidae and exhibit a pattern that played a role in both shearing and puncturing of food during feeding (Fig. 9). *Indolestes* is distinguishable from previously described Eocene insectivores from the Indian subcontinent including those known from Vastan (Bajpai et al., 2005).

Various proposals have been put forward with regard to the geographic region of origin of Adapisoriculidae. An African origin was proposed due to the presence of *A. chleuhi* (a primitive adapisoriculid) in the Paleocene of this region and a long history of this group in the erstwhile Gondwana (Gheerbrant and Russell, 1989) while a European origin for this family was suggested due to the presence of a highly diverse Paleocene adapisoriculid fauna in this region (De Bast et al., 2012). It should be noted that no adapisoriculids are known from the much explored European Cretaceous. However, De Bast et al. (2012) suggested that the high diversity of European adapisoriculids is an indication of the presence of a still unknown adapisoriculid clade in the Cretaceous of Europe that may have led to a *Deccanolestes*- and *Afrodon*-like taxa that eventually migrated to India (during the Cretaceous) and to Africa (during Paleocene), respectively. In another explanation, the high diversity of adapisoriculids in the Paleocene of Europe and the presence of *Afrodon* in both Europe and northern Africa were attributed to migrations between these continents around the K–Pg boundary (Smith et al., 2010).

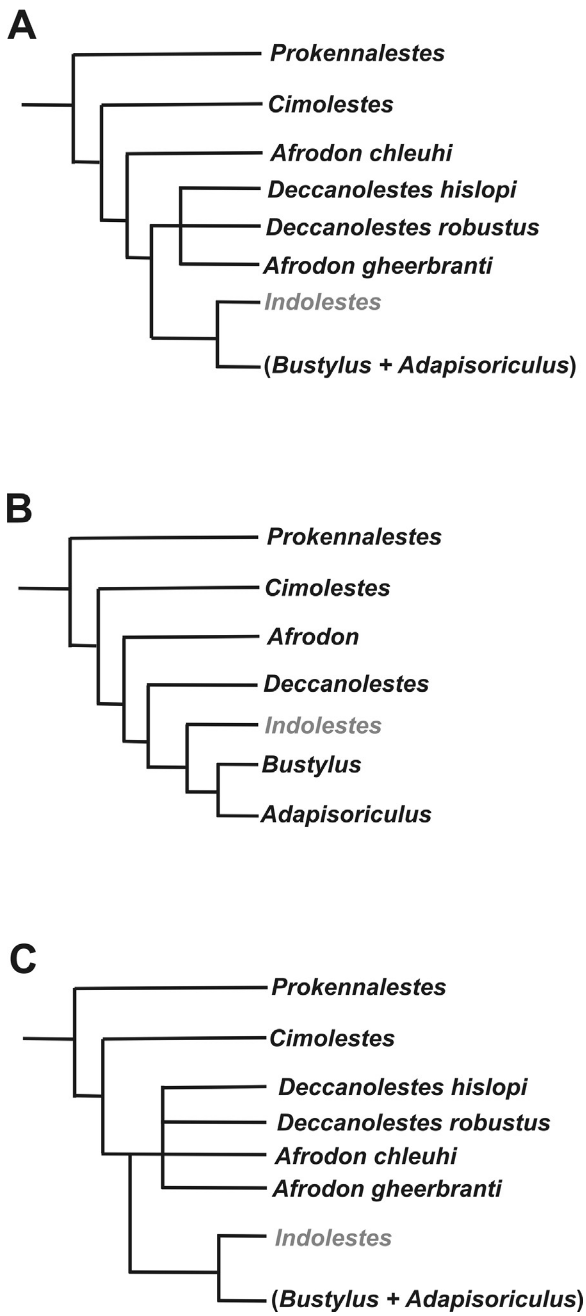

Fig. 11. Three different hypotheses of phylogenetic relationships among *Deccanolestes*, *Afrodon*, *Bustylus*, *Adapisoriculus* and *Indolestes* based on eight maximum parsimonious trees (MPTs).

Fig. 11. Trois hypothèses différentes de relations phylogénétiques entre *Deccanolestes*, *Afrodon*, *Bustylus*, *Adapisoriculus* et *Indolestes*, basées sur huit arbres de parcimonie maximum (MPT).

Fig. 12. Palaeogeographic map showing biotic exchanges between India and its surrounding landmasses involving adapisoriculids around the K–Pg interval. *Indolestes* yielding locality (Vastan) marked by a star. Mdr: Madagascar; Ker: Kerguelen. Map modified after Chatterjee and Scotese (2010) with permission.
Fig. 12. Carte paléogéographique montrant les échanges biotiques entre l'Inde et ses masses continentales environnantes incluant des adapisoriculidés autour de l'intervalle K–Pg. La localité fournissant *Indolestes* (Vastan) est marquée d'une étoile. Mdr : Madagascar ; Ker : Kerguelen. Carte modifiée d'après Chatterjee et Scotese (2013) avec l'autorisation des auteurs.

Recent data has shown that an Indian origin of adapisoriculids is more likely since the oldest (Late Cretaceous) stratigraphic record of adapisoriculids (*Deccanolestes*) is known from this region (Goswami et al., 2011; Prasad et al., 2010; Smith et al., 2010). Phylogenetic analysis shows that *Deccanolestes* is a sister taxon to *Afrodon* indicating an Out-of-India migration towards Africa and/or Europe (Goswami et al., 2011; Prasad et al., 2010). Goswami et al. (2011) have also suggested that adapisoriculids are part of a clade consisting of the basal eutherians and that a "ghost lineage" for adapisoriculids was present in the Gondwana for at least ~30 million years before *Deccanolestes*.

The discovery of *Indolestes* suggests continuation of the adapisoriculid lineage for more than 10 million years, after the Deccan volcanic episode during the terminal Cretaceous-earliest Paleocene. Also, *Indolestes* represents the first evidence for the presence of a mammal of Gondwanan lineage in the early Eocene of India. The primitive dental morphology of *Indolestes* relative to the European taxa (*Bustylus* and *Adapisoriculus*) weakens the possibility of India's biogeographic connection with Europe (in so far as the adapisoriculids are concerned). However, given the rich fossil record of adapisoriculids in the Paleocene of Africa and Europe, and the derived dental morphology of *Indolestes* relative to *Afrodon*, an in-to-India dispersal event during the Paleocene cannot be currently ruled out. The discovery of Paleocene mammals in India will help test this hypothesis. Prasad and Sahni (1999) suggested that, given the small size of these mammals, a trans-oceanic dispersal (*sweepstakes*) may have allowed faunal exchanges between India and Eurasia during the Late Cretaceous (~65 Ma). More recently, however, it has been proposed (Chatterjee and Bajpai, 2016; Chatterjee and Scotese, 2010; Chatterjee et al., 2013) that an island arc system (Oman-Kohistan-Dras) that existed north of the Indian Subcontinent during the Late Cretaceous acted as 'stepping stones' between India and Africa to facilitate faunal interchanges between these landmasses (Fig. 12). It is plausible that adapisoriculids may have used this migration route, as also suggested by Prasad et al. (2010). However, this hypothesis also needs to be tested rigorously, since the timing of contact between the Oman-Kohistan-Dras Island arc and the Indian plate is controversial, with several recent workers (e.g., Bouilhol et al., 2013; Jagoutz et al., 2015) favoring a much younger (~50 Ma) age for this contact.

Future discoveries from the Early Cretaceous interval of erstwhile Gondwanan and/or Laurasian continents and from the Paleocene of India will likely allow a better understanding of the phylogenetic relationships as well as paleobiogeographic reconstructions involving this interesting family of mammals that survived the K–Pg boundary events including the Deccan volcanic activity.

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