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Laurent Marivaux, Myriam Boivin

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Emergence of hystricognathous rodents: Palaeogene fossil record, phylogeny, dental evolution, and historical biogeography

Abstract

Although phylogenies imply Asia as the ancestral homeland of the Hystricognathi clade (Rodentia, Ctenohystrica), curiously the oldest known fossil occurrences of hystricognathous rodents are not from Asia but from Africa and South America, where they appear suddenly in the fossil record of both landmasses by the late middle Eocene. Here we performed cladistic and Bayesian (standard and tip dating analyses) assessments of the dental evidence documenting early ctenohystricans, including several Asian “ctenodactyloids”, virtually all Palaeogene Asian and African hystricognaths known thus far, and two representatives of the earliest known South American hystricognaths. Our results provide a phylogenetic context of early hystricognaths (with implications on systematics) and suggest that some Eocene Asian “ctenodactyloids” could be considered as stem hystricognaths and pre-hystricognaths, although they were not recognized as such originally. However, this view does not fill the gap of the Eocene Asian hystricognath record, as the proposed phylogeny implies many ghost lineages extending back to the middle Eocene for several Asian and African taxa. It also implies a complex early historical biogeography of the group, involving multiple dispersal events from Asia to Africa (and possibly from Africa back to Asia) and then to South America sometime during the middle Eocene. Based on these phylogenetic considerations, we discuss the emergence of hystricognathous rodents from a morpho-anatomical perspective, in analysing the differentiation of their masticatory apparatus and chewing movements, notably through the evolution of the dental pattern.

ADDITIONAL KEYWORDS: Africa – Asia – chewing movements – Ctenohystrica – dental morphology – Eocene – hystricognathy – Oligocene – South America.

INTRODUCTION

Modern African cane-, dassie- and mole-rats, Afro-Asian porcupines, and South American chinchillas, guinea pigs, spiny-rats, New World porcupines, etc., make up the natural group of the hystricognathous rodents (infraorder Hystricognathi Tullberg, 1899). Compared with living African hystricognaths (Phiomorpha Lavocat, 1967) and Afro-Asian porcupines (Hystricidae Fischer, 1817), South American hystricognaths (Caviomorpha Wood, 1955) are by far the most diverse today (e.g., [Wilson *et al.*, 2016](#)). For members of the Hystricognathi clade (except for caviid caviomorphs; see [Hautier *et al.*, 2011](#)), the hystricognathous condition (i.e., hystricognathy) is described on their lower jaw (mandible, dentary bone), which shows the origin of the angular process distinctly lateral to the plane of the incisor alveolus ([Tullberg, 1899](#)). All other rodents (members of the mouse-related clade and squirrel-related-clade, and ctenodactylomorphs; e.g., [Fabre *et al.*, 2015](#)) have in contrast a sciurognathous lower jaw, characterized by an angular process originating in the same plane that includes the incisor alveolus ([Tullberg, 1899](#)). A suite of morpho-anatomical traits (notably dental) and genetic data also define hystricognathous rodents (e.g., [Lavocat, 1976](#); [Bugge, 1985](#); [George, 1985](#); [Meng, 1990](#); [Martin, 1992, 1994](#); [Huchon & Douzery, 2001](#); [Huchon *et al.*, 2002, 2007](#); [Marivaux *et al.*, 2002, 2004a](#); [Montgelard *et al.*, 2008](#); [Blanga-Kanfi *et al.*, 2009](#); [Churakov *et al.*, 2010](#); [Hautier *et al.*, 2011](#); [Meredith *et al.*, 2011](#); [Fabre *et al.*, 2012, 2015](#); [Patterson & Upham, 2014](#)). Hystricognaths share a common ancestry with the modern African gundis (comb rats) or Ctenodactylidae and the Asian kha-nyou (Laotian rock rat) or Diatomyidae, the latter two being sciurognathous rodents. The current classification of modern rodents recognizes the suborder Ctenohystrica as the clade uniting ctenodactylids and diatomyids (= ctenodactylomorphs), together with hystricognaths (e.g., [Huchon *et al.*, 2000, 2007](#); [Dawson *et al.*, 2006](#); [Patterson & Upham, 2014](#); [Fabre *et al.*, 2015](#); [Wilson *et al.*, 2016](#)). From a palaeontological perspective, the origin of hystricognaths, as that of the kha-nyou and gundis, can be traced back to the Eocene of Asia, as they are nested within the Asian “ctenodactyloid” radiation, also including other extinct sciurognathous rodent families such as the Eocene Chapattimyidae, Yuomyidae, Tamquammyidae, Tataromyidae and Gobiomyidae (e.g., [Dawson, 1968, 2003](#); [Hussain *et al.*, 1978](#); [Dawson *et al.*, 1984](#); [Kumar *et al.*, 1997](#); [Wang, 2001](#); [Marivaux *et al.*, 2002, 2004a](#); [Li & Meng, 2015](#); [Li, 2017](#); [Li *et al.*, 2018](#)). From our current knowledge of the rodent fossil record, “ctenodactyloids” are only documented in Asia during the Palaeogene. Although phylogeny implies Asia as the ancestral homeland of the

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3 Hystricognathi clade, curiously the oldest known fossil occurrences of hystricognaths are not
4 from Asia, where they are so far known only from the latest Eocene (Marivaux *et al.*, 2000;
5 de Bruijn *et al.*, 2003), but from Africa and South America, where they appear suddenly in the
6 fossil record of both landmasses by the late middle Eocene (Antoine *et al.*, 2012; Marivaux *et*
7 *al.*, 2014a). This points out the incompleteness of the Eocene Asian fossil record for
8 hystricognaths, but also that this group rapidly achieved a widespread distribution from Asia
9 throughout Africa and South America, sometime during the middle Eocene (Antoine *et al.*,
10 2012; Marivaux *et al.*, 2014a; Barbière & Marivaux, 2015; Sallam & Seiffert, 2016).

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18 Earliest known hystricognaths **have been mostly documented** from North Africa, notably
19 from Egypt (historically: Osborn, 1908; Wood, 1968; Holroyd, 1994; but also more recently:
20 Sallam *et al.*, 2009, 2011, 2012; Sallam & Seiffert, 2016), Algeria (Jaeger *et al.*, 1985), Libya
21 (Fejfar, 1987; Jaeger *et al.*, 2010a; Coster *et al.*, 2010, 2012, 2015a), Tunisia (Marivaux *et al.*,
22 2014a), Morocco (Marivaux *et al.*, 2017a) and Oman (Thomas *et al.*, 1989, 1992), where they
23 are generally among the most common members of the late Eocene-early Oligocene mammal
24 faunas. Earliest African hystricognaths are recognized as stem members of the group (stem
25 Hystricognathi [# Protophiomyinae]), then by members of the Phiomyidae (stem Phiomorpha)
26 and Phiocricetomyinae (stem ?Phiomorpha), and by members of the Gaudeamuridae (stem
27 ?Hystricoidea). In Asia, the record of hystricognaths is clearly less abundant and limited to
28 the latest Eocene – early Oligocene “Baluchimyinae” from Peninsular Thailand (Marivaux *et*
29 *al.*, 2000) and Pakistan (Bugti Hills and Zinda Pir Dome, Balochistan; Flynn *et al.*, 1986;
30 Flynn & Cheema, 1994; Marivaux *et al.*, 2002; Marivaux & Welcomme, 2003), and the early
31 Oligocene Tsaganomyidae, a monogeneric family of odd hypsodontous species recorded in
32 Mongolia (e.g., Matthew & Granger, 1923; Bryant & McKenna, 1995). “Baluchimyines” or
33 stem hystricognaths are also recorded in Asia Minor, from Turkey, in deposits dating from the
34 Eocene/Oligocene transition (Süngülü, Lesser Caucasus; de Bruijn *et al.*, 2003). However, the
35 latter were not originally recognized as hystricognaths but as “ctenodactylids”
36 (Ctenodactylidae *sensu* de Bruijn *et al.*, 2003), although dental similarities with
37 “baluchimyines” and basal African phiomyids were underscored by the authors. The same is
38 true for “baluchimyines” from Pakistan, which were also originally considered as
39 “ctenodactylids” (subfamily of Chapattimyidae *sensu* Flynn *et al.*, 1986), although strong
40 affinities with early African phiomyids were appropriately advocated by Flynn *et al.* (1986).
41 The original non-recognition as hystricognaths of these Asian fossil rodents is partly due to
42 the meagre fossil documentation of early hystricognaths at that time, and to the little
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3 knowledge of their morphology as a result. Besides, it also relies on the fact that these Asian
4 species were exclusively documented by isolated teeth, without complete toothrow, and
5 notably without preservation of the dentary bone allowing the recognition of the Tullberg's
6 character (i.e., lateral displacement of the angular process relative to the plane of the incisors).
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8 However, even with a preserved dentary bone, a question arises as to whether the most basal
9 hystricognaths displayed a recognizable hystricognathous condition of their mandible, similar
10 to that observed in more recent or living forms. Based on well-preserved mandibles of African
11 hystricognaths (phiomorphs) from the early Oligocene of Egypt (e.g., [Wood, 1968](#)), the
12 additional discoveries of "baluchimyine" fossils from the Oligocene of Pakistan preserving
13 partial dentary bones (e.g., [Marivaux *et al.*, 2002](#)), and dental anatomy comparisons
14 associated with cladistic assessments of the dental evidence, it was then possible to identify
15 the Hystricognathi clade from a palaeontological point of view, and to formalize the dental
16 pattern of early and subsequent hystricognathous rodents (e.g., [Marivaux, 2000](#); [Marivaux *et*](#)
17 [al., 2002, 2004a](#)). The recognition of hystricognathous rodents based on isolated teeth was
18 therefore particularly critical, because most of Palaeogene fossil discoveries consist primarily
19 of isolated dental specimens. That was the case for most recent discoveries and descriptions of
20 Eocene and Oligocene rodents from Egypt ([Sallam *et al.*, 2009](#)), Libya ([Jaeger *et al.*, 2010a](#);
21 [Coster *et al.*, 2010, 2012, 2015a](#)), Tunisia ([Marivaux *et al.*, 2014a](#)) and Morocco ([Marivaux *et*](#)
22 [al., 2017a](#)), which were identified as early hystricognaths primarily on dental morphology
23 basis. The same is true for the earliest caviomorphs to be known from South America (late
24 middle Eocene: [Antoine *et al.*, 2012, 2016](#); [Boivin *et al.*, 2017a](#); ?late Eocene/early
25 Oligocene: [Frailey & Campbell, 2004](#); early Oligocene: e.g., [Vucetich *et al.*, 2010](#); [Boivin *et*](#)
26 [al., 2018](#), etc.), for which isolated teeth widely dominate their fossil record.

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Given the apparent and surprising Eocene gap (phylogenetically implied) for early
hystricognaths in the Asian fossil record, we decided here to re-investigate several Eocene
rodents from Asia, most of them known by isolated teeth and (initially) identified as
"Ctenodactyloidea", in order to assess if some of them could be in fact basal hystricognaths or
closely related to that group. For this purpose, we think that performing a cladistic assessment
(i.e., using the parsimony criterion) of the dental evidence documenting several early Asian
"ctenodactyloids" and virtually all Palaeogene African and Asian hystricognaths known thus
far (or recognized as such), should test the phylogenetic status of some species potentially
misidentified originally. With the same data set, Bayesian approaches (standard and tip-dating
analyses) will be also undertaken in order to compare the phylogenetic results and to identify

possible discrepancies. If consistent, the structures of such phylogenetic contexts should strengthen support for the recognition of possible early Asian hystricognathous rodents not originally recognized as such (as was the case for the “baluchimyines” from Pakistan and Turkey; Flynn *et al.*, 1986; de Bruijn *et al.*, 2003), and then to have a better idea of the palaeodiversity of the Eocene Asian hystricognathous rodents. These approaches will also attempt to formalize the phylogenetic relationships among Eocene and Oligocene African hystricognaths, notably in considering the numerous taxa recently discovered in Africa (see Table 1; e.g., Sallam *et al.*, 2009, 2011, 2012; Jaeger *et al.*, 2010a; Coster *et al.*, 2012, 2015a; Marivaux *et al.*, 2012, 2014a, 2017a; Sallam & Seiffert, 2016), and to depict the relationships between Palaeogene Asian and African (plus earliest South American) hystricognathous rodents. Based on these phylogenetic considerations, we will discuss the emergence of hystricognathous rodents from a morpho-anatomical perspective (differentiation of their masticatory apparatus). Phylogeny and stratigraphy will also be considered for assessing the ghost lineages phylogenetically implied, and the quality of the Palaeogene fossil record for early hystricognathous rodents. Finally, we will discuss the palaeobiogeographic implications deriving from this/these phylogenetic context(s), notably the faunal exchanges between South Asia and Africa (plus South America), in order to better specify the modalities, timing, and number of dispersals between these landmasses.

MATERIAL AND METHODS

SELECTED TAXA

For these phylogenetic analyses, we considered as in-group several Palaeogene Ctenohystrica species known from Asia (China, Inner Mongolia, Mongolia, Thailand, Pakistan, India, and Turkey; see Appendix S1) and Africa (Egypt, Libya, Tunisia, Algeria, Morocco, and Kenya; see Appendix S1), species for which it was possible to score at best a maximum of dental characters (on upper and lower teeth) based on original fossils, high resolution epoxy replicas, and/or fine illustrations. However, a few species, although not well-documented, were also included in the analyses as they provide dental morphologies that appear critical for

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3 understanding the evolutionary transformations of characters. Taxa were entered in the matrix
4 at the specific level. We sampled several genera and often several species of a same genus.
5 But we considered each species as a terminal taxonomic unit and did not introduce chimeric
6 species summarizing the morphology of several species of a genus.
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10 We selected as out-groups a basal Glires (*Tribosphenomys*) and two stem Rodentia
11 (*Archetypomys* and *Cocomys*), all three being recorded in the early Tertiary of Asia
12 (Appendix S2). Asian taxa of the in-group were primarily sampled by a set of
13 “ctenodactyloid” members, including representatives (originally recognized as such;
14 Appendix S2) of the Tataromyidae-Tamquammyidae (or stem Ctenodactylidae), Yuomyidae,
15 Gobiomyidae, Chapattimyidae, and by all known “baluchimyine” hystricognaths (recognized
16 as such; Appendix S2). As advocated in the introduction of this paper, given the apparent
17 Eocene gap in the Asian fossil record of early hystricognaths, we sampled Asian species
18 widely to assess if some “ctenodactyloids” could be in fact basal hystricognaths. For Africa,
19 sampled taxa were exclusively hystricognaths (recognized as such; Appendix S2), the only
20 ctenohystricans found in Africa during the Palaeogene. We have notably included several taxa
21 from the latest Eocene of Egypt and the earliest Oligocene of Morocco that were recently
22 described by Sallam & Seiffert (2016) and Marivaux *et al.* (2017a), respectively. Palaeogene
23 Asian and African hystricognaths were sampled as thoroughly as possible (all genera so far
24 known, and nearly all species) in order to have a better idea of the phylogenetic relationships
25 among early African taxa known (for systematics purposes), and between African and Asian
26 taxa in order to decipher how early African hystricognaths are related to non-African forms
27 and vice versa (for systematics and palaeobiogeographic purposes). We have also sampled
28 two early hystricognaths from South America, among the oldest (but perhaps not the earliest)
29 caviomorphs to be known thus far (Appendix S2), to determine in which Old World
30 hystricognath group they are nested, or which are their African (or Asian) sister group and
31 closest out-group.
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52 SELECTED CHARACTERS

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56 We employed most of the dental characters and character states listed by Marivaux in Antoine
57 *et al.* (2012). However, some characters were re-interpreted or added in order to better
58 describe the extent and variation of the character states within the Palaeogene Ctenohystrica
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(see updated dental nomenclature; Fig. 1, modified after [Marivaux *et al.*, 2004a, 2014a, 2017a; Boivin *et al.*, 2017a,b, 2019; Boivin & Marivaux, 2018](#)). As in [Antoine *et al.* \(2012\)](#), some multistate characters were considered as ordered if changes from one state to another required passing through intermediate states ([Slowinski, 1993](#)). With such an *ad hoc* assumption, character state assignments do not convey *a priori* judgments about character polarity (unconstrained parsimony). However, for these new analyses, the additive multistate characters were scaled by the number of character states, such that the sum of the steps in the morphocline equals “1”. For some characters, multistate taxa were considered and characters were scored primarily as polymorphism (0 and 1 [0+1]; i.e., morphological variability within a given species) or as uncertain (0 or 1 [0/1]; i.e., when a character state observed within a species/individual was ambiguous). The description of characters (including added + amended characters), character states, and the scaling value (sv) for each character are presented as Supplementary Material online (Appendix S3). For the taxa preserved from the original matrix published by [Antoine *et al.* \(2012\)](#), we have rechecked all the former scores, and adjusted/modified and completed the score of the upper and lower tooth characters according to our amendments. Characters were polarized via the out-group comparison method ([Watrous & Wheeler, 1981](#)).

The final character-taxon matrix included 198 characters and 60 taxa (*contra* 182/39 in [Antoine *et al.*, 2012](#)). The data matrix (Nexus format) was edited with NDE (Nexus Data Editor v. 0.5.0; [Page, 2001](#)).

PHYLOGENETIC ANALYSES

For estimating the relationships of the taxa, the final data matrix was subjected to both cladistic (using the maximum parsimony criterion) and Bayesian (based on the likelihood concept) phylogenetic analyses. For the cladistic analyses, the phylogenetic reconstructions were performed with PAUP* 4.0b10 ([Swofford, 2002](#)). Polymorphic (0+1; {01} under PAUP) *versus* uncertain (0/1; {01} under PAUP) character states (multistate taxa) were considered and both treated distinctly by PAUP (options MSTaxa= Variable). Given the high number of selected taxa, analyses were carried out using the Heuristic search method (Hsearch), with a random step-wise addition (1,000 replications with randomized input order of taxa) and tree-bisection-reconnection (TBR) branch swapping options. The clade robustness was measured

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3 by the Bremer Index (Bremer, 1988) and the Bootstrap percentages (BP) in equally weighted
4 maximum-parsimony (after 1,000 iterations comprising two replications with randomized
5 input order of taxa). The character-taxon matrix plus the assumptions (Nexus format) for the
6 cladistic analyses are provided as Supplementary Material online (Appendix S4).
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10 Two types of Bayesian analyses were performed with MrBayes 3.2.6 (Ronquist *et al.*,
11 2012a), using the public resource CIPRES Science Gateway V. 3.3. (Miller *et al.*, 2015;
12 <https://www.phylo.org/>): a standard Bayesian approach and a Bayesian tip-dating approach
13 (Ronquist *et al.*, 2012b). For the two Bayesian analyses, we selected the conditional version
14 of the Markov-*k* model (Mk_v; Lewis, 2001) for our total dataset, which included only
15 morphological data, with the assumption of a gamma-distributed rate variation across
16 characters, thereby with coding set to “variable”. For the standard Bayesian (SB) analysis,
17 two independent runs were performed simultaneously with four Markov Chain Monte Carlo
18 (MCMC) chains for 25 million generations. Each run had one cold chain and three heated
19 chains (temp= 0.02). The chains were sampled every 1,000 generations and the first 25% of
20 the trees were discarded as the “burn-in” period. The remaining trees were summarized via an
21 “allcompat” consensus tree (majority-rule plus compatible groups). The effective sample sizes
22 (ESSs) and standard deviation of the mean of split frequencies in the final generation were
23 checked in order to assess convergence. The ESSs were checked using Tracer 1.7.1 (Rambaut
24 *et al.*, 2018). The character-taxon matrix and the command lines for this standard Bayesian
25 analysis are provided as Supplementary Material online (Appendix S5).
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39 We also estimated simultaneously both phylogeny and divergence dates among taxa in
40 performing a Bayesian tip-dating (BTD) analysis, which takes into account the ages of fossil
41 taxa and rates of character evolution (e.g., Pyron, 2011; Ronquist *et al.*, 2012b; Borths *et al.*,
42 2016; Sallam & Seiffert, 2016). The independent gamma rates (IGR) relaxed-clock model
43 was applied to account for variation in morphological evolutionary rates among branches. The
44 fossilized birth-death (FBD) process was used as a tree prior on branch lengths in setting
45 “samplestrat” to “fossiltip”, thereby considering that tips left no descendants. Each tip was
46 calibrated with a uniform prior on age, corresponding to minimum and maximum ages of each
47 taxon (i.e., error range of an absolute radiometric age, upper and lower bounds of geological
48 stages or Palaeogene Land Mammal Ages to which a fossil has been assigned, or stratigraphic
49 range of a taxon; see Appendix S1). Given that the FBD process begins at some time to > 0
50 Myr in the past (here *ca.* 56 Myr, i.e., the root of the Rodentia clade) and ends when t = 0
51 (today), we added an extant hystricognathous taxon, *Thryonomys swinderianus* (African cane
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3 rat; Phiomorpha Thryonomyidae), to our data matrix, which so far included only extinct
4 Palaeogene taxa for the purpose of this paper. Considering the addition of this living taxon
5 (calibrated with a fixed prior on age, i.e., modern days: fixed(0)), the percentage of extant
6 species sampled in the analysis (“sampleprob”) was set to 0.005 (Sallam & Seiffert, 2016).
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8 The root node was constrained to fall within a broad uniform prior on node age from 50 Myr
9 to 60 Myr, beyond which no ctenohystrican (or even rodent and rodentiaform) has been
10 recognized in the fossil record (e.g., Meng & Wyss, 2001; Marivaux *et al.*, 2004a; Meng *et*
11 *al.*, 2007). We opt for flat beta priors (1.0, 1.0) associated to the FBD process
12 (“fossilizationpr” and “extinctionpr”). The prior on the net speciation rate (“speciationpr”)
13 was set to exp(50). Regarding the gamma distribution from which the branch lengths are
14 drawn (“igrvarpr”), this prior was set to exp(3). The prior on the “base substitution” rate
15 (morphological changes), measured in number of changes per “site” per Myr (“clockratepr”),
16 was set to normal(0.25, 0.05). MCMC analyses consisted of two independent runs of four
17 chains (one cold and three heated; temp = 0.01), sampling every 1,000 generations for 50
18 million generations per run, with a burn-in percentage of 25%. An “allcompat” consensus tree
19 was generated, summarizing all post-burn-in sampled trees. Convergence was also assessed
20 here by checking the ESSs and the average standard deviation of split frequencies in the final
21 generation. The character-taxon matrix plus its assumptions for this Bayesian tip-dating
22 analysis are provided as Supplementary Material online (Appendix S6). Several additional
23 analyses with various perturbations of the priors, notably “speciationpr”, “igrvarpr” and
24 “clockratepr” (see Appendix S7) returned similar topologies and age estimates. Results of
25 these additional analyses with different prior values are not reported here.
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47 RESULTS

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51 Taxa above the generic level (families or subfamilies) are not defined here and not formally
52 endorsed, but are indicated when evident by informal terminations of “-id(s)” or “-ine(s)”,
53 reflecting previous usage.
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Heuristic searches yielded two equally most parsimonious trees of 1042.46 steps each (Consistency Index, CI= 0.373; Retention Index, RI= 0.637). The cladogram presented in Figure 2 corresponds to a strict consensus tree of the two trees generated. In this phylogeny, the numerous Asian “ctenodactyloid” taxa illustrating tamquammyids, yuomyids, chapattimyids, gobiomyids and “ctenodactyloids” *incertae sedis* (see Appendix S2) are separated from taxa so far recognized as early hystricognaths and forming the Hystricognathi clade (i.e., all Palaeogene Asian [*Ottomania* and *Confiniummys*, plus “baluchimyines”] and African [protophiomyines, phiocricetomyines, metaphiomyines, phiomyids, and gaudeamurids] taxa, plus *Canaanimys* and *Cachiyacuy* [the two early South American taxa]). Here, the monophyly of the yuomyids is not recovered but the sampled members (*Yuomys*, *Petrokozlovia*, *Advenimus*, and *Saykanomys*) of this apparent paraphyletic family are found closely related to each other nonetheless. Interesting is the position of the two species of *Dianomys* (*D. obscuratus* and *D. exiguus*) as well as *Anadianomys*, which appear as the closest out-groups of the Asian taxa so far considered as basal members of the Hystricognathi clade (i.e., *Ottomania*, *Confiniummys*, and some other “baluchimyines”). The two species of *Dianomys* were originally considered as representatives of the Yuomyidae (Wang, 1984), later Ctenodactyloidea without familial attribution (Wang, 2001). Given the phylogenetic position of *Dianomys* and *Anadianomys*, a taxonomic enlargement regarding the basal content of the Hystricognathi clade is envisaged below.

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Regarding the phylogenetic structure within the Hystricognathi clade, several subclades are revealed, clustering taxa that illustrate families and/or subfamilies (with revisited content of some), or that could suggest new taxonomic units (Fig. 2). In contrast, some of the taxonomic units are not identified, appearing as paraphyletic or even polyphyletic. It is notably the case of the Asian “baluchimyines” (*Baluchimys*, *Lindsaya*, *Hodsahibia*, *Bugtimys*, *Lophibaluchia*, plus *Ottomania* and *Confiniummys*), for which certain taxa form subclades ([*Baluchimys*, *Lindsaya*] and [*Ottomania*, *Confiniummys*]) that are sequentially arranged at the base of the Hystricognathi clade, while other taxa ([*Hodsahibia*, *Bugtimys*] and *Lophibaluchia*) are nested separately within the basal African taxa (Marivaux *et al.*, 2002, 2004a; Sallam *et al.*, 2011, 2012; Coster *et al.*, 2010, 2012; Antoine *et al.*, 2012; Sallam & Seiffert, 2016). Such a scattered phylogenetic distribution of “baluchimyines” at the base of the Hystricognathi clade requires the recognition of distinct taxonomic units of Asian hystricognaths. Indeed, *Hodsahibia* plus *Bugtimys*, as well as *Lophibaluchia*, being placed

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3 apart and hierarchically higher on the tree with respect to the other “baluchimyines”, are
4 considered here as advanced “baluchimyines” (*sensu* Sallam & Seiffert, 2016), and as such
5 could represent new higher taxonomic units (Fig. 2). Interesting is the clade clustering the
6 different species of *Protophiomys* (*P. algeriensis*, *P. aegyptensis*, and *P. durattalahensis*, to
7 the exception of *P. tunisiensis* [see below]) plus *Waslamys attiai*, inasmuch as it constitutes a
8 clade of late Eocene African taxa occupying an intermediate position nested within the Asian
9 “baluchimyines” (basal + advanced). *Waslamys* has been often regarded as a possible junior
10 synonym of *Protophiomys* (Coster *et al.*, 2012; Marivaux *et al.*, 2014a, 2017a), a taxonomic
11 option which is emphasized here by our phylogenetic results. Regardless of the possible
12 synonymy of *Waslamys*, the phylogenetic position of the African protophiomysines (*sensu*
13 Coster *et al.*, 2012), nested within Asian taxa, has important biogeographic implications, not
14 only for the protophiomysines, but also for the Asian advanced “baluchimyines” (African
15 origin?). We analyse and discuss below those biogeographic aspects that imply seemingly
16 complex dispersals between Asia and Africa.

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28 Within the Hystricognathi clade, phiocricetomyines can be recognized as a subclade
29 clustering markedly cuspidate and low crested African taxa, exemplified by *Phiocricetomys*,
30 *Talahphiomys* and *Neophiomys*, to which are also associated here *Mubhammys*, *Birkamys*,
31 *Phenacophiomys* and *Protophiomys tunisiensis*. *Mubhammys* and *Birkamys* were originally
32 interpreted as advanced phiomorph taxa of an indeterminate family, closely related to the
33 extant *Thryonomys* (cane-rat) and some other Miocene taxa such as *Paraphiomys*, and
34 sequentially arranged after the Palaeogene phiomorph taxa such as *Phiomys*, *Acritophiomys*,
35 *Turkanamys*, *Metaphiomys*, etc. (see Sallam & Seiffert, 2016: fig. 10). Our results propose
36 distinct affinities for *Mubhammys* and *Birkamys*, considering these bunodont and low crested
37 taxa from the latest Eocene/earliest Oligocene of North Africa (Sallam & Seiffert, 2016;
38 Marivaux *et al.*, 2017a) as phiocricetomyines, clearly set apart from the phiomysids and the
39 stem thryonomyids (?metaphiomysines). Concerning *Phenacophiomys*, this taxon was recently
40 recognized as a distinct phiomysid genus from the earliest Oligocene of Morocco, notably by a
41 suite of dental traits which would place this taxon between *Phiomys/Acritophiomys* and
42 *Protophiomys/Waslamys* (see Marivaux *et al.*, 2017a). *Phenacophiomys* is here
43 phylogenetically interpreted as the basalmost phiocricetomyine taxon (the earliest offshoot of
44 the large clade considered here as the phiocricetomyine clade; Fig. 2). A phiocricetomyine
45 status is also proposed here for *Protophiomys tunisiensis*, the oldest African representative of
46 the Hystricognathi clade to be known thus far (late middle Eocene of Tunisia; Marivaux *et al.*,
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3 2014a). The teeth of this species are still moderately cuspidate (main cusps and cuspids not
4 strongly bulbous but still well-defined) and low crested, with upper molars mostly
5 tetralophodont, but with some specimens exhibiting an incipient pentalophodonty (presence of
6 a very short mesolophule). Originally, this species was tentatively attributed to the genus
7 *Protophiomys*, the well-known genus documented by species dating from the late Eocene of
8 Algeria and Egypt (*P. algeriensis* and *P. aegyptensis*, respectively; Jaeger *et al.*, 1985; Sallam
9 *et al.*, 2009). However, *P. tunisiensis* appearing morphologically less advanced than the
10 Egyptian and Algerian (even Libyan; Jaeger *et al.*, 2010a) species, it was regarded as
11 documenting a primitive morph of that lineage. Our phylogenetic analyses clearly set the
12 Tunisian species apart from the other species of *Protophiomys*, and rather propose a
13 phiocricetomyine status for that species. Given these results (consistent with those of Sallam
14 & Seiffert, 2016), “*Protophiomys*” *tunisiensis* should be then attributed to another genus,
15 probably a new genus. The same is true for *Neophiomys paraphiomyoides*, which is found
16 here within the phiocricetomyine clade clearly separated from the other species of that genus
17 (*N. minutus* and *N. dawsonae*). *Neophiomys* had been included among the Thryonomyidae
18 (e.g., Coster *et al.*, 2015a), but our phylogenetic results rather opt for a phiocricetomyine
19 status of *Neophiomys*.

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22 Finally, within the Hystricognathi clade (Fig. 2), another large subclade, rooted here by
23 *Lophibaluchia* (Asian taxon), clusters species of *Metaphiomys* (metaphiomyines), followed by
24 a subclade recognized here as the phiomyid clade clustering the different species of *Phiomys*
25 with *Acritophiomys* and *Turkanamys*, and sister to another subclade uniting the species of
26 *Gaudeamus* (gaudeamurids) with *Canaanimys* and *Cachiyacuy*, two taxa being among the
27 oldest South American representatives of the Hystricognathi clade (i.e., stem Caviomorpha;
28 Antoine *et al.*, 2012; Boivin, 2017; Boivin *et al.*, 2019). Regarding what we identify here as
29 the Phiomyidae clade, we could then envisage that *Acritophiomys* and *Turkanamys* are junior
30 synonyms of *Phiomys*, as recently suggested and discussed for *Acritophiomys* by Marivaux *et*
31 *al.* (2017a). From these phylogenetic results, gaudeamurids and caviomorphs seem to share a
32 common ancestry. Several phylogenetic results have already advocated the possible
33 relationships between gaudeamurids and caviomorph rodents (e.g., Coster *et al.*, 2010; Sallam
34 *et al.*, 2011, 2012; Antoine *et al.*, 2012; Sallam & Seiffert, 2016), whereas others envisage
35 gaudeamurids as potentially stem representatives of the Hystricoidea clade (a lineage, leading
36 to the extant Afro-Asian *Hystrix* and African *Atherurus*; i.e., porcupines; Sallam *et al.*, 2011;
37 Barbière & Marivaux, 2015; Marivaux *et al.*, 2017a). The dental pattern of *Gaudeamus* is
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3 very specialized as early as the latest Eocene, the first occurrence known for that genus (L-41,
4 Fayum, Egypt; [Sallam et al., 2011](#)), and somewhat evolutionarily advanced over that of the
5 coeval African or Asian genera known. Furthermore, there is so far no precursor known in
6 Africa (middle and late Eocene), which would exhibit a dental morphology clearly indicating
7 transformations toward a *Gaudeamus* dental pattern. Curiously, the dental morphology of
8 *Gaudeamus* is strikingly very similar to that of *Eoincamys*, a coeval **taxon** from the New
9 World (Peruvian Amazonia; [Frailey and Campbell, 2004](#); [Coster et al., 2011](#); [Boivin, 2017](#);
10 [Boivin & Marivaux, 2018](#); [Boivin et al., 2018, 2019](#)). *Gaudeamus*, as *Eoincamys*, displays
11 some dental features, which are otherwise found primarily in *Cachiyacuy* and *Canaanimys*,
12 but at a different degree of development in the latter (e.g., on upper teeth: presence of a well-
13 defined mesostyle associated with a buccal mesoloph, well-marked parastyle; on lower teeth:
14 moderately long and high posterior arm of the metaconid, well-defined mesostylid associated
15 with the development of a neomesolophid, absence of hypoconulid). One noteworthy point is
16 that some of these dental features can be also observed, to some extent (i.e. less marked; e.g.,
17 mesostyle, mesostylid, and neomesolophid), in certain specimens of phiomyids (*Phiomys*,
18 *Acritophiomys*, and *Turkanamys*). Although tenuous, these dental traits suggest that
19 gaudeamurids share an ancient common ancestry with the caviomorph ancestor and
20 phiomyids, ancestry which would be so far undocumented in the fossil record of Africa. In
21 this context, the strong dental similarities between *Gaudeamus* and *Eoincamys* would indicate
22 that these two lineages evolved in parallel from a more ancient African common ancestry.
23 Given the age of the first known species of *Gaudeamus* and *Eoincamys* (i.e., latest
24 Eocene/earliest Oligocene) and the presence of much more ancient hystricognathous species
25 in South America (recorded in the late middle Eocene; [Antoine et al., 2012](#); [Boivin, 2017](#);
26 [Boivin et al., 2017a, 2019](#)), the hypothesis of a close *Gaudeamus-Eoincamys* phylogenetic
27 relationships would necessarily imply an extra (second, later) dispersal from Africa to South
28 America during the latest Eocene, in addition to the dispersal (likely the first) of the ancestor
29 of the earliest caviomorphs known from Peruvian Amazonia (*Cachiyacuy*, *Canaanimys*,
30 *Eobranisamys*, *Eoespina*, *Pozomys*, etc.; [Antoine et al., 2012](#); [Boivin, 2017](#); [Boivin et al.,](#)
31 [2017a, 2019](#)). The latter palaeobiogeographic scenario is rather difficult to conceive. In sum,
32 the phylogenetic view considering a common ancestry between gaudeamurids, proto-
33 caviomorphs and phiomyids (plus metaphiomyines) does not favour a gaudeamurid-hystricid
34 link (but see constrained alternative hypothesis of [Sallam et al., 2011](#); see also [Barbière &](#)
35 [Marivaux, 2015](#)). Indeed, if we take into consideration molecular phylogenies, hystricids are
36 not closely related to South American caviomorphs, but would have diverged before the
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3 Caviomorpha/Phiomorpha split (e.g., Huchon *et al.*, 2002, 2007; Blanga-Kanfi *et al.*, 2009;
4 Sallam *et al.*, 2009; Meredith *et al.*, 2011; Patterson & Upham, 2014; Fabre *et al.*, 2015). In
5 other words, Hystricidae are regarded as the earliest offshoots of the crown Hystricognathi
6 clade. From a palaeontological point of view and based on our phylogenetic results, stem
7 hystricids (if they had been known and sampled here) would then be expected outside the
8 clade uniting proto-caviomorphs, gaudeamurids and phiomyids, **the latter assumed** to be the
9 unique stem representatives of the extant Phiomorpha clade (see below). In this context, the
10 root of the Hystricidae should perhaps be sought within the phiocricetomyines or perhaps
11 within the protophiomyines, or even the bugtimyids and the basal “baluchimyines”, inasmuch
12 **as all are** stem groups of the Hystricognathi clade, preceding the Phiomorpha-Caviomorpha
13 split. The possibility also exists that hystricids are not closely related to **these known stem**
14 **hystricognaths**, and that their **earliest representatives** remain undocumented in the Palaeogene
15 fossil record (either of Asia or Africa).

26 Finally, in this phylogenetic context, another critical issue is the recognition of the stem
27 Phiomorpha. Gene-based phylogenies (e.g., Huchon *et al.*, 2007; Blanga-Kanfi *et al.*, 2009;
28 Patterson & Upham, 2014; Fabre *et al.*, 2015; Upham & Patterson, 2015) support a close
29 relationship between extant Phiomorpha (including Thryonomyidae plus Petromuridae, and
30 Bathyergidae plus Heterocephalidae) and extant Caviomorpha (including Octodontoidea plus
31 Chinchilloidea, and Cavioidae plus Erethizontoidea). According to our phylogenetic results,
32 phiomyids **(as sister of the gaudeamurid-caviomorph clade; Fig. 2)** **would be the only group**
33 recognized as stem Phiomorpha. The Phiomorpha-Caviomorpha split would be then
34 illustrated here by the split between the ancestor of *Phiomys* (plus *Acritophiomys* and
35 *Turkanamys*) and the African ancestor of *Cachiyacuy/Canaanimys* (plus *Gaudeamus*, the
36 latter would be an African caviomorph?; see also Coster *et al.*, 2010). The two lineages would
37 have then subsequently evolved separately on the two landmasses leading to the modern
38 diversity of both groups. In this context, gaudeamurids, as African sister of the stem
39 caviomorphs, would have rapidly become extinct in Africa. But such a view regarding the
40 Phiomorpha-Caviomorpha split is overly simplistic and **weakly supported** because we are far
41 from having an exhaustive late middle and late Eocene fossil record in Africa documenting
42 that phylogenetic event (**see section below** dedicated to the analysis of the quality of the fossil
43 record). Furthermore, in this study, we have voluntarily limited our taxonomic sampling to
44 Palaeogene taxa. A more comprehensive phylogenetic analysis associating Palaeogene taxa
45 with more recent and extant taxa (among phiomorphs and caviomorphs) would certainly
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3 provide a broader framework for deciphering the phylogenetic pattern related to the
4 emergence of crown taxa. However, although our taxonomic sampling is limited, interesting
5 evolutionary aspects are revealed nonetheless. For instance, **one key dental** synapomorphy of
6 crown Phiomorpha is the retention throughout life of the deciduous premolars (DP4 and dp4;
7 i.e., the eruption of the permanent premolars being suppressed; e.g., [Wood, 1968](#)). If
8 phiomysids are stem Phiomorpha, as our phylogenetic results suggest, it is worth noting that
9 their representatives (*Phiomys*, *Acritophiomys*, etc.) did not show a retention of the deciduous
10 premolars, thereby indicating that this dental feature was achieved subsequently in more
11 recent representatives of the Phiomorpha clade. In describing *Mubhammys* and *Birkamys* from
12 the latest Eocene of Egypt (L-41), [Sallam & Seiffert \(2016\)](#) have shown that these two taxa
13 were already characterized by the suppression of lower and upper permanent premolar
14 eruption, an observation thereby strengthening support for the phiomorph status of these two
15 fossil taxa (both being nested within Phiomorpha in the proposed phylogeny of [Sallam &](#)
16 [Seiffert, 2016: 29-30](#)). Based on our phylogenetic results, *Mubhammys* and *Birkamys* would
17 be **rather phiocricetomyines**, i.e., stem hystricognaths, not phiomorphs. If the retention of the
18 deciduous premolars characterizes crown Phiomorpha (but not all stem members of the clade)
19 but also the extinct metaphiomysines (species of *Metaphiomys*) and some members of the
20 phiocricetomyines (*Mubhammys* and *Birkamys*), accordingly this dental feature was achieved
21 independently several times among African stem and crown hystricognaths. The iterative
22 pattern of this dental feature is emphasized even more by the fact that several extinct and
23 extant representatives of crown caviomorphs (**octodontoids**) also have suppressed the eruption
24 of permanent lower and upper premolars, whereas a replacement of the deciduous premolars
25 is observed in most stem caviomorphs for which these dental loci are documented (e.g.,
26 [Frailey & Campbell, 2004](#); [Vucetich et al., 2010](#); [Antoine et al., 2012](#); [Boivin et al., 2017a,](#)
27 [2018, 2019](#); [Pérez et al., 2019](#); except for *Eobranisamys romeropittmanae*, see [Frailey &](#)
28 [Campbell, 2004](#)).

STANDARD BAYESIAN PHYLOGENETIC ANALYSIS

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56 The “allcompat” consensus tree (majority-rule plus compatible groups) of 25,000 post-burn-in
57 trees retained by the Bayesian (SB) analysis is provided in [Figure 3](#). As for the results of the
58 cladistic analyses, the Bayesian inferences reveal a neat separation of most Asian
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“ctenodactyloid” taxa illustrating tamquammyids, yuomyids, chapattimyids, gobiomyids and “ctenodactyloids” *incertae sedis*, from taxa recognized as early hystricognaths and forming the Hystricognathi clade. Although the global phylogenetic structure is similar between the results of the two analyses, there are, however, some points of disagreement. Among the “ctenodactyloid” taxa, there are some rearrangements, notably regarding the stem members of the extant Ctenodactylidae (i.e., tamquammyids and tataromyids), which are successively arranged (except *Protataromys*) at the base of the tree, rather than forming a clade (Fig. 3). *Protataromys*, while closely related to the tamquammyids in the cladistic results, is found situated hierarchically higher in the tree, near the Hystricognathi clade. The gobiomyids occupy a hierarchically lower position in the tree, situated sequentially after the paraphyletic “yuomyids”. Next come chapattimyids, forming again a monophyletic group (including some internal rearrangements), to which agglomerates *Stelmomys* forming the basalmost branch of the clade. As for the cladistic results, the two Asian species of *Dianomys* (*D. obscuratus* and *D. qujingensis*) are particularly interesting for reconsidering the basal content of the Hystricognathi clade. Indeed, the two species occupy here a critical position in being no more considered as the closest out-groups of the Hystricognathi clade, but in being deeply nested “within” the Hystricognathi clade. Indeed, the two species form a clade closely related to some basal “baluchimyines” ([*Ottomania*, *Confiniummys*] plus *Baluchimys krabiense*). That clade is sister to the African protophiomysines, which clusters here only *Protophiomys algeriensis*, *P. aegyptensis* and *Waslamys attiai*. *Protophiomys durattalahensis*, which was the basalmost member of the protophiomysines in the results of the cladistic analyses (Fig. 2), occupies here a phylogenetic position hierarchically much higher, in being closely related to the clade uniting the basal phiomorphs and caviomorphs (see below). The possibility that this taxon represents a distinct genus, outside of the protophiomysines, was already advocated by Marivaux *et al.* (2014a), who regarded the dental morphology of “*P.*” *durattalahensis* as more derived with respect to that of the other protophiomysines. In contrast, Sallam *et al.* (2012) then Sallam & Seiffert (2016) considered “*P.*” *durattalahensis* as closely related to *Waslamys*, and phylogenetically distinct to the other species of *Protophiomys* (*P. algeriensis* and *P. aegyptensis*). The Bayesian inferences here are rather in favour of the recognition of “*P.*” *durattalahensis* as a distinct genus (new) from *Protophiomys* and *Waslamys*. This conclusion and the cladistic results support the assumption according to which *Waslamys* would be a junior synonym of *Protophiomys* (following Coster *et al.*, 2012; Marivaux *et al.*, 2014a, 2017a). As for the cladistics results, these Bayesian inferences reveal again the polyphyly of the “baluchimyines”. If some members (*Ottomania*, *Confiniummys*, and *Baluchimys*

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3 *krabiense*) are closely related to *Dianomys* (as discussed above), other taxa (*Lindsaya* and
4 *Baluchimys barryi*) form a clade situated at the root of the Hystricognathi clade, whereas
5 *Hodsahibia*, *Bugtimys* and *Lophibaluchia* form another clade situated higher in the tree, and
6 sister to the clade uniting the basal phiomorphs and caviomorphs (see below). Here, unlike the
7 cladistic results, *Lophibaluchia* is agglomerated with *Hodsahibia* and *Bugtimys*. As advocated
8 previously with the cladistic results, such a scattered phylogenetic distribution of
9 “baluchimyines” really requires the recognition of distinct taxonomic units of Asian
10 hystricognaths, notably units for the different basal “baluchimyines” and another unit for the
11 advanced “baluchimyines” (bugtimyids; Figs 2, 3).

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19 A large phiocricetomyine clade is also well identified here (Fig. 3), clustering the same
20 taxa grouped by the cladistic analyses (Fig. 2). These results corroborate the phiocricetomyine
21 status of *Mubhammys*, *Birkamys* and “*Protophiomys*” *tunisiensis*, underscoring the need to
22 provide a new generic attribution to “*P.*” *tunisiensis*. Although the content of this clade is here
23 similar to that obtained by the cladistic analyses, there are, however, some taxonomic
24 rearrangements, notably in revealing a closer phylogenetic relationship between
25 *Talahphiomys* (*T. lavocati* and *T. libycus*) and *Phiocricetomys*, and a closer relationships
26 between *Birkamys* and *Neophiomys* (*N. minutus* and *N. dawsonae*). *Birkamys* and
27 *Phiocricetomys* were positioned hierarchically lower on the tree generated by the parsimony
28 analyses (Fig. 2). Given these results, it is not excluded that additional dental material for
29 these fossil taxa (notably for *Neophiomys*, *Talahphiomys*, and *Phiocricetomys*), demonstrates
30 that *Birkamys* is potentially a junior synonym of *Neophiomys* (as suggested by Marivaux *et*
31 *al.*, 2017a). *Talahphiomys* may also be a junior synonym of *Phiocricetomys*, although less
32 certainly given the highly derived and specialized dental pattern of *Phiocricetomys* (see
33 Wood, 1968; Coster *et al.*, 2012; Marivaux *et al.*, 2017a) with respect to *Talahphiomys*.

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46 The last large subclade identified within the Hystricognathi clade, is that clustering
47 metaphiomyines, phiomyids, stem caviomorphs and gaudeamurids. Unlike the cladistic
48 results, this clade also includes at its base “*Protophiomys*” *durattalahensis*, and here
49 phiomyids are sequentially arranged (i.e. appearing paraphyletic). Indeed, the two sampled
50 species of *Phiomys* (*P. andrewsi* and *P. hammudai*) are not associated to the subclade uniting
51 *Acritophiomys* and *Turkanamys*, but are successively positioned before that subclade. The
52 critical issue raised previously (see cladistic results) regarding the recognition of the stem
53 Phiomorpha is here even more complicated to assess given the sequential arrangement of “*P.*”
54 *durattalahensis*, metaphiomyines, “phiomyids”, stem caviomorphs and gaudeamurids. Dental
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3 characters are perhaps not sufficient for identifying a Phiomorpha clade, which could cluster
4 “*P.*” *durattalahensis*, *Metaphiomys*, *Phiomys*, *Acritophiomys* and *Turkanamys* (allied with
5 more recent, e.g., *Paraphiomys*, *Lavocatomys*, *Diamantomys*, etc., see Lavocat, 1973, and
6 crown phiomorph taxa). Based on our phylogenetic results (cladistics or Bayesian), the
7 problem here is that caviomorphs are nested within a clade that could be identified as the
8 Phiomorpha clade, thereby making the latter paraphyletic. Among extant hystricognaths, if
9 crown phiomorphs (*Thryonomyidae*, *Petromuridae*, *Bathyergidae*, and *Heterocephalidae*)
10 form a clear monophyletic group, sister to crown Caviomorpha, to the exclusion of the
11 Hystricidae, this simple dichotomous pattern deriving from gene-based phylogenies is far
12 from well established by palaeontological data, which includes extinct lineages.
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23 BAYESIAN TIP-DATING ANALYSIS WITH THE FOSSILIZED BIRTH-DEATH PRIOR

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28 The “allcompat” consensus tree (majority-rule plus compatible groups) of 50,000 post-burn-in
29 trees retained by the Bayesian tip-dating (BTD) analysis is provided in Figure 4. Here, we
30 only describe and discuss the phylogenetic relationships in comparison with the results of the
31 cladistic and standard Bayesian (SB) analyses. We discuss the estimated node ages later (see
32 “Discussion” section about the adaptive radiation and historical biogeography of
33 hystricognaths). As for the cladistic and SB analyses, the results of the BTD analysis point out
34 a net separation of the “ctenodactyloid” taxa from the large Hystricognathi clade, for which
35 the *Dianomys* clade occupies a well-supported (PP = 1) sister taxon position. The position of
36 the *Dianomys* clade is similar to that found by the cladistic analyses (Fig. 2), and contrasts
37 with the SB results where the *Dianomys* clade is outright nested within the basal
38 hystricognaths (Fig. 3). Regarding the internal relationships of the “ctenodactyloids”, as for
39 the cladistic results (Fig. 2), the BTD analysis recovers the monophyly of the tamquammyid
40 group situated at the base of the ctenohystrican tree, whereas the SB analysis has failed to
41 recover the monophyly of this group (Fig. 3). As for the cladistic and SB analyses, the
42 monophyly of the Yuomyidae is also not demonstrated by the BTD analysis. In the previous
43 analyses, if the “yuomyid” taxa were found closely related, forming two successive clades
44 arranged after the tamquammyids (Figs 2, 3), here some taxa (*Advenimus* plus *Saykanomys*)
45 form a basal clade situated consistently after the tamquammyid clade, and the other taxa
46 sampled (*Yuomys* and *Petrokozlovia*) occur surprisingly arranged successively higher in the
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3 tree, close to the *Dianomys* clade (Fig. 4). The BTM analysis recovers the chapattimyid clade
4 similar to the results of the cladistic analyses (Fig. 2). This clade was also found by the SB
5 analysis, but with the addition of *Stelmomys*, which appears in these results as the first
6 offshoot of the chapattimyid clade (Fig. 3). Here, *Stelmomys* is found outside of the
7 chapattimyid clade, and positioned higher in the “ctenodactyloid” tree, appearing as basal to a
8 clade uniting the Gobiomyidae and *Xueshimys* (as for the cladistic results) plus a clade uniting
9 *Anadianomys* and *Protataromys* (Fig. 4). In the cladistic results, *Protataromys* was found
10 much lower in the “ctenodactyloid” tree, and nested within the tamquammyids (Fig. 2). In
11 both Bayesian analyses, this taxon is found higher in the trees, and close to the root of the
12 Hystricognathi clade.

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15 Concerning the large Hystricognathi clade, the results of BTM analysis are similar to
16 those of the cladistic and SB analyses in identifying the main hystricognath subclades
17 corresponding to the basal baluchimyines, protophiomyines, advanced “baluchimyines”
18 (bugtimyids), phiocricetomyines, gaudeamurids, “phiomyids”, “metaphiomyines” (or
19 thryonomyids) and stem caviomorphs (Fig. 4). However, the high-level relationships between
20 these subclades are resolved differently by the BTM approach. It is particularly noteworthy
21 that the basal Asian baluchimyines (i.e., *Baluchimys krabiense*, *B. barryi*, *Lindsaya*,
22 *Ottomania*, and *Confiniummys*) are found here, for the first time, forming a monophyletic
23 group, sister to the African protophiomyines. The baluchimyine-protophiomyine clade is itself
24 sister to the bugtimyid clade (Fig. 4). Given the latter clustering obtained by the BTM
25 analysis, the phylogenetic position of the bugtimyid clade then contrasts with the results of the
26 cladistic and SB analyses, being here neither sister to the large subclade clustering the
27 “phiomorphs”, gaudeamurids and caviomorphs (as resolved by the SB analysis; Fig. 3), nor
28 sister of the former large subclade plus phiocricetomyines (as resolved by the cladistic
29 analyses; Fig. 2). As for the SB analysis (Fig. 3), *Lophibaluchia* is placed at the base of the
30 bugtimyid clade, contrary to the cladistic results (Fig. 2), where it was set apart from that
31 clade, and placed as a succeeding branch. The position of the phiocricetomyines also contrasts
32 with that found by the cladistic and SB analyses. Phiocricetomyines are here sister to the large
33 clade clustering baluchimyines, protophiomyines plus bugtimyids (Fig. 4), whereas their
34 position was resolved as sister of the clade clustering the “phiomorphs”, gaudeamurids and
35 caviomorphs by the cladistic analyses (Fig. 2), or as a basal subclade of the Hystricognathi
36 clade by the SB analysis (Fig. 3). Within the phiocricetomyine clade, with the BTM approach
37 there are also few changes regarding the position of some taxa, notably at the root nodes of
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3 the clade, compared with the results of the cladistic and SB analyses. “*Protophiomys*”
4 *tunisiensis* occupies here the basalmost position of the phiocricetomyine clade in place of
5 *Phenacophiomys* as proposed by the cladistic and SB analyses. *Phenacophiomys* and
6 “*Neophiomys*” *paraphiomyoides* form a succeeding clade to “*P.*” *tunisiensis*, rather than being
7 positioned as successive basal branches in the results of the cladistic and SB analyses.
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12 The large clade uniting the phiomyids, metaphiomyines (plus here *Thryonomys*) and the
13 gaudeamurids plus the two stem caviomorphs is here resolved hierarchically less highly
14 nested within the Hystricognathi clade than in the results of the cladistic and SB analyses
15 (Figs 2, 3). With the BTM approach (Fig. 4), this clade appears basal and at the same
16 hierarchical level as the phiocricetomyine clade and the bugtimyid-protophiomyine-
17 baluchimyine clade. As for the cladistic and SB results, gaudeamurids remain the African
18 diverging group of the South American caviomorphs (gaudeamurids would be the African
19 caviomorphs?), and together form a distinct clade, sister to the clade uniting “*Protophiomys*”
20 *durattalahensis*, the different phiomyid taxa (the two species of *Phiomys*, *Acritophiomys*, and
21 *Turkanamys*) and the metaphiomyines (the two species of *Metaphiomys*) plus here
22 *Thryonomys* (thryonomyids) (Fig. 4). These results do not support the monophyly of the
23 phiomyids and metaphiomyines, but this large subclade gathering “*P.*” *durattalahensis*, the
24 “phiomyid” and “metaphiomyine” taxa plus *Thryonomys* could represent here a more
25 inclusive Phiomorpha clade than that deriving from the cladistic analyses, where only
26 phiomyid taxa were considered as representing phiomorphs (Fig. 2). From the SB analysis (as
27 here), “phiomyids” were not resolved as a monophyletic group (Fig. 3). Based on the cladistic
28 and SB results, applying this more inclusive taxonomic association describing basal
29 phiomorphs as suggested by the BTM results, would make the phiomorphs paraphyletic
30 inasmuch as basal caviomorphs would then appear to be nested within that more inclusive
31 phiomorph clade (Figs 2, 3; see previous discussions on cladistic and SB results).
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52 DISCUSSION AND CONCLUSIONS

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57 The phylogenetic inferences deriving from the cladistic and Bayesian (SB and BTM) analyses
58 are consistent for many taxonomic relationships, but they differ in some cases, notably in the
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3 position of certain taxa, which are either considered as members of a given clade or outside
4 that clade, but often remaining closely related to that given clade. The monophyly of some
5 main taxonomic units (families and/or sub-families) is not systematically recovered when
6 parsimony results are compared with Bayesian results. Therefore, establishing a precise and
7 formal phylogenetic systematics of basal ctenohystrican rodents may appear somewhat
8 premature. We must keep in mind that most of taxa sampled here are documented only by
9 dental remains, most often by isolated teeth (not complete tooththrows). In addition, some
10 dental loci are simply not documented (not recovered or not fossilized). But such is the
11 current nature of the fossil record for early representatives of the Ctenohystrica clade.
12 However, although incomplete, these fossil data are crucial as they provide unique glimpses
13 into the past diversity and evolution of that rodent group. The establishment of a phylogenetic
14 context is a prerequisite for better understanding morphological transformation/evolution, and
15 for identifying homoplasies. We must keep in mind that the phylogenetic relationships
16 proposed here represent current hypotheses, based on palaeontological data available today
17 and on the dataset we have assembled and employed. This dataset will certainly grow and will
18 be modified as the knowledge of early ctenohystrican rodents accumulates. For these reasons,
19 we do not provide here a fixed systematics of early ctenohystricans, but underscore the main
20 groups and main relationships that seems to emerge from these phylogenetic assessments of
21 the dental evidence. The names proposed on the main groups (former names or new
22 declination, and new ones; Figs 2-4; Appendix S2) are only indicative of possible future
23 formalization of families and/or subfamilies, which would be tested by additional
24 morphological supports.

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42 The phylogenetic approaches employed here separate the numerous “ctenodactyloid” taxa
43 as tamquammyids, “yuomyids”, chapattimyids, gobiomyids and “ctenodactyloids” *incertae*
44 *sedis*, from taxa so far recognized as early hystricognaths and forming the Hystricognathi
45 clade (i.e., all Palaeogene African and Asian taxa, plus *Canaanimys* and *Cachiyacuy*, the two
46 early South American taxa). The latter clade is nested within the “Ctenodactyloidea”, thereby
47 making this superfamily paraphyletic (“ctenodactyloids”). Particularly interesting is the
48 phylogenetic position of the two Asian species of *Dianomys* (*D. obscuratus* and *D.*
49 *qujingensis*), which led us to envisage a taxonomic enlargement regarding the basal content of
50 the Hystricognathi clade. These two species were originally considered as representatives of
51 the Yuomyidae (Wang, 1984), than subsequently to the Ctenodactyloidea, without familial
52 attribution (Wang, 2001). From the results of our cladistic analyses (Fig. 2) and BTDA analysis
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(Fig. 4), these two species form a clade closely related to the Asian taxa (*Ottomania*, *Confiniummys*, and other basal “baluchimyines”) considered as basal members of the Hystricognathi clade. From the results of the SB analysis (Fig. 3), they form a clade nested within the Hystricognathi clade (closely related to the same aforementioned Asian taxa considered as early hystricognaths). Given these phylogenetic results, a reconsideration of the systematic status of *Dianomys*, i.e., stem Hystricognathi (rather than “Ctenodactyloidea”), can be envisaged. Furthermore, as the two species of *Dianomys* always form a distinct clade, they could be recognized as representing a distinct family (i.e., Dianomyidae) of stem hystricognaths. We will evaluate the Hystricognathi taxonomic option for *Dianomys* later in the text, through a detailed comparative examination of its dental morphology and the possible chewing movements associated. The dental morphology and chewing pattern of other taxa such as *Anadianomys*, *Xueshimys* and *Gobiomys*, also occupying a phylogenetic position close to the Hystricognathi clade (Fig. 2), will be scrutinized as well.

HYSTRICOGNATHY VS MASTICATORY APPARATUS WITHIN CTENOHYSTRICA

Given that the Hystricognathi clade is nested within the paraphyletic radiation of the Eocene “ctenodactyloids”, and considering the close phylogenetic relationships between modern Ctenodactylidae+Dianomyidae (Ctenodactylomorphi) and Hystricognathi (e.g., Dawson *et al.*, 2006; Huchon *et al.*, 2007; Fabre *et al.*, 2015), the morphological differentiation of hystricognathous jaws derives *de facto* from the primitive sciurognathous condition. This is a somewhat simplistic view from a macroevolutionary perspective, inasmuch as the hystricognathy is not a unique character defined by the apparent lateral displacement of the angular process of the mandible, but a suite of morpho-anatomical attributes of the whole masticatory apparatus. Furthermore, among modern hystricognaths, the lateralization of the angular process is shaped differently from one family (sub-family) to another, and diverse morphotypes exist as a result (e.g., Vassalo & Verzi, 2001; Hautier *et al.*, 2011). The other characters associated to the lateralization of the angular process and its multiple morphotypes are notably the position and shape of the mandibular condyles (generally occupying a low to moderately high position with respect to the occlusal tooth plane, i.e., above of the toothrow; Vassalo & Verzi, 2001; Hautier *et al.*, 2011), the correlated arrangements/developments of the masticatory muscles (notably masseter and internal pterygoid muscles), and various dental

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3 patterns (see below). All of these morpho-anatomical features are related to the mechanics of
4 the masticatory apparatus for performing primarily oblique chewing movements, but also
5 other types of movements (e.g., [Butler, 1980, 1985](#); [Vassalo & Verzi, 2001](#); [Hautier *et al.*,
6 2010, 2011](#)). Further extant Hystricognathi indisputably form a natural group supported by a
7 corpus of morphological and molecular data, but that clade does not rely chiefly on the
8 recognition of the “hystricognathous” condition of their mandible. Modern caviid
9 caviomorphs for instance, although classified among the hystricognathous rodents, display a
10 mandible that is very similar to that of some sciurognathous rodents ([Hautier *et al.*, 2011](#)).
11 Indeed, their mandibles are characterized by a weak lateralization of the angular process, by a
12 lower position of the mandibular condyles with respect to the tooth plane (compared to other
13 caviomorphs and other hystricognaths [i.e., phiomorphs and hystricids]), and they bear high
14 crowned **teeth with** flat occlusal surfaces, resulting in a chewing mode unusual among
15 hystricognaths (i.e., nearly propalinal mastication rather than oblique; see [Vassalo & Verzi,
16 2001](#); [Hautier *et al.*, 2010, 2011](#)). It is clear that the inclusion of caviids within the
17 Hystricognathi clade relies on characters other than that of the mandibular morphology.
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32 DENTAL PATTERNS OF EARLY “CTENODACTYLOIDS” AND CHEWING MOVEMENTS 33 34 35 36

37 From an evolutionary palaeontological perspective, the morphological differentiation of
38 hystricognathous jaws (or sciurognathous-hystricognathous switching) may imply gradual
39 modifications of the whole masticatory apparatus and its mechanics through time,
40 modifications which were constrained by the need of preserving continuously efficient dental
41 occlusion. Molars of early “ctenodactyloids” (e.g., chapattimyids, “yuomyids”,
42 tamquammyids/ctenodactylids, or “ctenodactyloids” *incertae sedis*; see [Fig. 5A-D](#)) were
43 cuspidate (bearing bulbous cusps and cuspids) and low crested (when crests and cristids are
44 present). Upper molars have generally a strong and rounded protocone, a moderately
45 developed and rounded hypocone (smaller than the protocone), well-defined and strong
46 paracone and metacone, and bear prominent, even inflated conules (especially the
47 metaconule; [Fig. 5A-D](#)). The mesialmost and distalmost transverse crests are not elevated and
48 trenchant, remaining at a stage of cingulum (not loph), the metaloph is discreet, often limited
49 to a short and low buccal branch (situated between the metacone and the metaconule), and its
50 lingual branch being either absent ([Fig. 5B](#)) or often very thin and incomplete (from the
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3 metaconule, it reaches or does not reach the protocone; Fig. 5A, C-E). The same is true for the
4 protoloph, which is low and often incomplete (buccal part between the protoconule and the
5 paracone, often absent; Fig. 5B). The protoloph can also be complete and transverse (links the
6 paracone to the protocone) when the protoconule is reduced to absent, but it remains relatively
7 low compared to the height of the main cusps (Fig. 5A, C-D). The anterior arm of the
8 hypocone is low, thin, short or moderately long, and always longitudinal, i.e., directed toward
9 the distal flank of the protocone or its short posterior outgrowth (thereby forming an
10 endoloph; Fig. 5A-D). With this configuration of the protocone and the hypocone with its
11 anterior arm, there is no internal sinus (no hypoflexus), and the lingual margin of upper teeth
12 is walled-off. Only a shallow groove is present, formed by the coalescence of the distal flank
13 of the protocone with the mesial flank of the hypocone. Lower molars also exhibit well-
14 defined and rounded main cuspids (metaconid, protoconid, entoconid and hypoconid, and
15 often a well-marked hypoconulid), and the main transverse cristids (metalophulid I,
16 metalophulid II, hypolophid, and posterolophid) are thin and low with respect to the cuspid
17 height, and often incomplete or absent (notably the hypolophid and metalophulid II). The
18 longitudinal cristids (ectolophid and posterior arm of the metaconid) are thin, often short,
19 mesially interrupted and not trenchant (Fig. 5A-D). The dental pattern of early
20 “ctenodactyls” is basically comparable to that characterizing other primitive rodents such
21 as the Eocene ischyromyids and paramyids (members of the Ischyromyiformes clade, *sensu*
22 *Marivaux et al., 2004a*). For those latter basal rodents, in comparing the attrition facets with
23 those of extant sciurids, which harbour a primitive ischyromyoid-like dental pattern, Butler
24 (1980, 1985) suggested that the lower jaw movements in these fossils were more or less
25 transverse, and chewing involved a two-phase movement (“Grade A” *sensu* *Butler, 1985:*
26 *383*): firstly, lower molars pass medially across the upper in a relatively transverse direction
27 (buccal phase), then obliquely forward (lingual phase). Given the dental pattern similarities
28 between early ischyromyiforms and early ctenohystricans (bunodont, and low or not crested
29 upper and lower teeth), it may be then expected that early “ctenodactyls” had similar or
30 close chewing patterns (i.e., two-phase type), with a marked forward component in the lingual
31 phase.

DENTAL PATTERNS OF EARLY HYSTRICOGNATHS AND CHEWING MOVEMENTS

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3 If we analyse the dental transformations through the cladogram obtained here (Fig. 2), and
4 notably those of the branches and nodes corresponding to the early offshoots of the
5 Hystricognathi clade, we can report a suite of dental traits that allows for a clear distinction of
6 early hystricognaths from within early “ctenodactyloids”. Basically, the dental patterns of
7 early hystricognaths (Fig. 5) are much more crested, display less protruding main cusps and
8 cuspids, the conules decrease in size and can disappear (they become indistinct, being
9 subsumed within transverse crests, or lost), some crests and cristids change orientation and
10 connection, and additional transverse and longitudinal crests and cristids can appear. These
11 changes in cusp (-id) and crest (cristid) developments and arrangements were likely
12 associated to a significant change in the masticatory movements through time. On upper teeth,
13 the anterior and posterior crests are much more elevated than in “ctenodactyloids”, appearing
14 as loph (anteroloph and posteroloph, respectively). The anterior arm of the hypocone is better
15 differentiated, it increases in length, and is displaced toward the centre of the crown (oblique,
16 mesio buccally oriented). In some taxa, the mesial extremity of the anterior arm of the
17 hypocone reaches the short and relictual lingual metaloph or enterocrest (Fig. 5J-K, M), or
18 can directly connect to the reduced metaconule, which is slightly displaced mesially (e.g., Fig.
19 5L, N-X). In the latter case, the lingual metaloph is lost. In contrast, due to the slight mesial
20 displacement and size reduction of the metaconule, but also the slight reduction in size of the
21 metacone, the buccal metaloph is much more differentiated. It forms a well-defined transverse
22 or slightly oblique crest, the lingual extremity of which can remain free (without connection;
23 Fig. 5W-X), or can connect either to the metaconule (Fig. 5J-N, S, V) or connected backward
24 to the posteroloph (Fig. 5O-P). Some taxa display a double connection of the metaloph
25 (metaconule + posteroloph; Fig. 5Q-R, T). In more advanced hystricognath taxa, a short
26 longitudinal crest can appear from the metaconule or from the mesialmost extremity of the
27 anterior arm of the hypocone (when the metaconule is lost). This longitudinal crest, called
28 mure (Fig. 1), can reach mesially the protoloph (Fig. 5L, P-U), and together, with the oblique
29 anterior arm of the hypocone and the hypocone itself (slightly mesiodistally compressed),
30 hence provide additional cutting edges. The same is true with the protocone, which becomes
31 slightly mesiodistally compressed and obliquely oriented, and develops a more or less long
32 posterior outgrowth, thereby forming an oblique ridge (Fig. 5L, N-W). In some taxa (on the
33 M1 of *Ottomania proavita*, on the M2 of *Protophiomys algeriensis*, *P. aegyptensis* and
34 *Waslamys attiai*, and on the molars of *Baluchimys krabiense*; Fig. 5J, K, M), the posterior
35 outgrowth of the protocone can be long with an unusual distobuccal orientation, and connects
36 to the anterior arm of the hypocone. Except for the latter taxa, in the other early
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3 hystricognaths, the mesiodistally compressed and oblique protocone and hypocone are no
4 more in connection, and are separated by a valley (i.e., internal sinus or hypoflexus; Fig. 1).
5 From the metaconule or, if the latter is no more distinct, at the mesial extremity of the anterior
6 arm of the hypocone (i.e., the location where a metaconule would normally occur), an
7 additional transverse crest, the mesolophule (Fig. 1), variably develops among taxa (Fig. 5J-T,
8 X). This new crest can reach in some cases the buccal margin of the crown (connected or not
9 to a mesostyle or a short mesoloph; Fig. 1). Lower molars also display important
10 modifications. In addition to the development of stronger and higher transverse (metalophulid
11 I, hypolophid, and posterolophid) and longitudinal (ectolophid and posterior arm of the
12 metaconid) cristids, the buccal cuspids (protoconid and hypoconid), are mesiodistally
13 compressed and somewhat mesio-distolingually oriented, thereby forming oblique and
14 parallel ridges. The anterior arm of the hypoconid is well defined and can be long, joining
15 both the buccal extremity of the hypolophid and the distal branch of the ectolophid (Figs 1, 5).
16 The ectolophid tends to be centrally displaced, and together with the oblique protoconid and
17 hypoconid ridges, plus the anterior arm of the hypoconid, they delimit a wide external valley
18 (i.e., sinusid or hypoflexid; Fig. 1). The posterior arm of the protoconid is variably developed
19 in length. In some cases, it can reach the lingual margin of the crown, thereby forming a
20 complete and trenchant transverse cristid (= metalophulid II), but often it remains moderately
21 developed (short), and may be limited to a short buccal spur. An accessory central cristid
22 (mesolophid or neomesolophid, or both; Fig. 1 and Fig. 5J, L, Q, S-U) can also occur in some
23 taxa.

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25 All these numerous apparent changes in the dental morphology can be only appreciated
26 when fossils are placed in their temporal and phylogenetic contexts. Considering the changes
27 on upper molars, characterized notably by the addition of a central crest (mesolophule), the
28 presence of a better differentiated metaloph, a stronger protoloph, the development of
29 elevated and trenchant anteroloph and posteroloph, associated with the development of
30 stronger and equally elevated ectolophid, metalophulid I, hypolophid and posterolophid (and
31 sometimes metalophulid II and neo/mesolophid) on lower molars, it is obvious that such
32 incremental dental transformations, whatever their configuration (i.e., various morphotypes
33 across species), have progressively increased the efficiency of the grinding function during
34 the lingual phase of chewing (involving oblique forward movements of the lower jaw). For
35 most species documented here (Fig. 5G-T, V-W), only the paracone and metacone on upper
36 molars, and the metaconid and entoconid on lower molars, although reduced, still rise above
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3 from the plane of these grinding surfaces of upper and lower teeth. This recalls Butler's
4 (1985) "Grade B", performed by rodents having upper and lower teeth developing crests and
5 cristids, with protocone and hypocone on upper molars, and protoconid and hypoconid on
6 lower molars tending to form oblique ridges, the whole providing an increased grinding
7 function of teeth, whereas buccal cusps on upper molars and lingual cuspids on lower molars,
8 still standing up to the plane of the grinding surfaces. For this "Grade B", Butler (1985)
9 noticed that the buccal phase movement is more oblique than in "Grade A", tending to line up
10 with the oblique forward lingual phase movement. Butler (1985) also described "Grade C",
11 when the entire crown surface forms a flattened grinding area (i.e., by reduction in height of
12 the upstanding buccal cusps on upper molars and lingual cuspids on lower molars). In the
13 latter case, chewing is simplified to a single oblique movement, and the teeth usually become
14 hypsodont (as observed for instance in different species of *Gaudeamus*; Fig. 5U).

EMERGENCE OF THE HYSTRICOGNATHY

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32 The acquisition of a pentalophodont pattern (notably on upper molars) and other anatomical
33 details (see above) increasing the efficiency of the grinding function of teeth, associated with
34 a modified chewing action involving primarily oblique movements, have likely also implied
35 re-arrangements/developments of the masticatory muscles (notably masseter and internal
36 pterygoid muscles). Greaves (1980) showed that maintaining oblique chewing movements of
37 the mandible requires a high position of the articular joint (condyles), above the occlusal
38 plane of the toothrow. Extant hystricognaths (except some cavioids) have indeed mandibular
39 condyles occupying a moderately high position with respect to the occlusal plane of lower
40 molars (Vassallo & Verzi, 2001; Hautier *et al.*, 2011). The posterior part of the dentary is
41 rarely preserved in early hystricognaths for which the mandible is documented, but based on
42 dental morphology, we show that enhanced oblique chewing movements are expected in the
43 early representatives of the infraorder, thereby suggesting a relatively high position of the
44 mandibular condyles in these extinct early forms. The few partially preserved dentary
45 specimens of *Acritophiomys bowni*, *Gaudeamus aslius* and *G. hylaeus* (latest Eocene, Egypt;
46 Sallam *et al.*, 2011, 2012) or *Metaphiomys schaubi* and *Neophiomys paraphiomysoides* (early
47 Oligocene, Egypt; Wood, 1968), indeed displayed condyles situated well above the occlusal
48 tooth plane. In modern hystricognath taxa (except in some cavioids), a moderately high
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3 position of the condyles has been interpreted as enhancing the medial force component of the
4 masseter and pterygoid muscles, acting hence against their lateral force component (Greaves,
5 1980; Hautier *et al.*, 2010, 2011). From palaeontological and biomechanical perspectives, the
6 decrease of the lateral component of these muscle forces could have been linked to (or could
7 have involved) the lateralization of the angular process of the mandible (Hautier *et al.*, 2011).
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12 The case of some cavioids, which show a very weak lateralization of the angular process
13 (being rather distally positioned) and a lower position of the mandibular condyles with respect
14 to the occlusal tooth plane (compared to other caviomorphs and other hystricognaths [i.e.,
15 phiomorphs and hystricids]) indicate examples of evolutionary reversals (see Hautier *et al.*,
16 2011). Caviids display a very specialized dentition characterized by high crowned teeth
17 (euhypsonodonts) with flat occlusal surfaces, and associated with chewing movements not
18 oblique but nearly propalinal (i.e., anteroposterior; Vassalo & Verzi, 2001). Butler (1985)
19 described this derived mode of mastication as “Grade D”, wherein individual relations
20 between upper and lower teeth are lost. These chewing movements are associated with an
21 increase of the antero-posterior component of the masseter and internal pterygoid muscle
22 forces (Vassalo & Verzi, 2001; Hautier *et al.*, 2010). Among Ctenohystrica, anteroposterior
23 masticatory movements (i.e., nearly propalinal mastication) are also observed in extant
24 Ctenodactylidae, which display a sciurognathous mandible with indeed condyles occupying a
25 low position compared to the occlusal tooth plane. They also bear high crowned teeth with
26 flat occlusal surfaces, thereby suggesting loss of the individual relations between upper and
27 lower teeth. Such a specialized dental pattern was already achieved in early Miocene forms,
28 although much lower crowned, such as *Prosayimys* and *Sayimys* (e.g., Baskin, 1996; López-
29 Antoñanzas *et al.*, 2004, 2016; López-Antoñanzas & Knoll, 2011). Early to middle Eocene
30 tamquammyids, which are commonly regarded as the early representatives of the
31 Ctenodactylidae lineage, likely performed a chewing mode with a two-phase movement (see
32 discussion above). In more advanced members of that lineage, notably in Oligocene forms
33 (e.g., *Tataromys*, *Yindirtemys*, *Karakoromys*; Wang, 1997; Schmidt-Kittler *et al.*, 2007;
34 Vianey-Liaud *et al.*, 2006), based on the direction of the attrition facets observed on several
35 specimens, Vianey-Liaud *et al.* (2006) noted that oblique movements could have been
36 performed in some species (e.g., *Tataromys sigmodon*, *Yindirtemys ulantatalensis*). Basically,
37 Oligocene ctenodactylid species were moderately low crowned, still slightly cuspidate (in
38 early stages of wear) and not strongly crested. However, these species never developed a
39 pentalophodont dental pattern, the buccal cusps on upper teeth and lingual cusps on lower
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3 teeth appear mesiodistally compressed and form ridges in continuity with the transverse crests
4 and cristids, and they do not stand out distinctly after wear. In fact, in these fossil taxa, the
5 grinding area occupied nearly the entire occlusal surface of the crowns, a configuration which
6 could then roughly correspond to “Grade B” or even “Grade C” modes of chewing defined by
7 Butler (1985). Although a detailed study of attrition facets should be made on ctenodactylids,
8 it appears that this group of ctenohystrican rodents likely achieved rapidly a “Grade D” mode
9 of chewing with anteroposterior movements. During the Eocene epoch, their dental pattern
10 was rapidly specialized and clearly distinct from that of the early hystricognaths, which would
11 indicate an ancient divergence between these two groups (as estimated by gene-based
12 phylogenies; e.g., Fabre *et al.*, 2012). In that context, it is clear that the “Grade D” mode of
13 mastication observed in extant ctenodactylids and extant caviids resulted from an adaptive
14 convergence.

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17 Finally, among ctenohystricans, diatomyids are particularly interesting for pointing out
18 the difficulty/ambiguity in the recognition of the mandible condition (sciurognathous *versus*
19 hystricognathous). *Laonastes*, the only extant representative of that family was initially
20 recognized as a member of the Hystricognathi clade, based on morpho-anatomy and
21 mitochondrial sequences (*Laonastidae sensu Jenkins et al.*, 2005). However, based on fossil
22 evidence, notably dental evidence, *Laonastes* was subsequently considered as the unique
23 extant relative of the Diatomyidae (Dawson *et al.*, 2006), an Asian “ctenodactyloid” family
24 (formerly believed as extinct), among which the Miocene forms (*Diatomys*) display a
25 sciurognathous mandible with low condyles (Dawson *et al.*, 2010). Additional nuclear gene-
26 based phylogenetic assessments on *Laonastes* (Huchon *et al.*, 2007) have corroborated the
27 non-Hystricognathi status of that taxon, and supported a close phylogenetic relationship
28 between the Diatomyidae and the Ctenodactylidae (Ctenodactylomorphi). Interestingly, the
29 mandible of *Laonastes*, in addition to its own characteristics, exhibits a combination of
30 intermediate features between sciurognathous and hystricognathous morphologies, associated
31 with a strong tendency to anteroposterior masticatory movements (see Hautier *et al.*, 2011: 7-
32 8). The mandible of *Laonastes*, like that of *Diatomys*, has indeed low condyles and bears
33 highly crowned cheek teeth with some degree of transverse bilophodonty, without individual
34 occlusal relations between upper and lower teeth (flat occlusal crown; i.e., “Grade D” of
35 Butler, 1985). Such a dental specialization was acquired very early in the diatomyid lineage,
36 as demonstrated by its early representatives documented from the early Oligocene (*Fallomus*;
37 Flynn *et al.*, 1986; Marivaux & Welcomme, 2003; Marivaux *et al.*, 2004b; Flynn, 2007;
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3 Marković *et al.*, 2018) and possibly from the late middle Eocene (Dawson *et al.*, 2010). These
4 early diatomyids show much lower crowned teeth, bearing bulbous and buccolingually
5 coalescent cusps and cuspids with discreet crests and cristids, forming transverse lobes in
6 early stages of wear. The inclusion of early diatomyids, i.e., the different species of *Fallomus*,
7 within the matrix for the cladistic analyses, suggests affinities of the group with gobiomyids
8 (not shown here). However, these phylogenetic relationships are unstable and poorly
9 supported given the meagre character scoring related to their simplified dental morphology.
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11 Regrettably, these Palaeogene diatomyid fossils are known only by isolated teeth, which does
12 not allow for a detailed analysis of the dentary morphology. As underscored by Hautier *et al.*
13 (2011), given the peculiar mandibular morphology of the living *Laonastes*, which exhibits an
14 original combination of features considered as intermediate between sciurognathous and
15 hystricognathous morphologies, mandibles of these early diatomyids would certainly
16 contribute to further our understanding of this morphological transition.
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29 EARLIEST STEM HYSTRICOGNATHS OR PRE-HYSTRICOGNATHOUS “CTENODACTYLOIDS”

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33 Thanks to available fossil evidence in a phylogenetic context, we have pointed out the main
34 structural changes in the dental patterns differentiating early “ctenodactyloids” (i.e., Asian
35 chapattimyids, “yuomyids”, tamquammyids/ctenodactylids, or “ctenodactyloids” *incertae*
36 *sedis*) from early hystricognaths (see discussion above). Therefore, we focus here on taxa,
37 such as *Dianomys* (Fig. 5H-I), *Anadianomys* (Fig. 5G), and eventually *Gobiomys* (Fig. 5F)
38 and *Xueshimys* (Fig. 5E), which are very close to the taxa considered as belonging to the
39 Hystricognathi clade (cladistic results; Fig. 2) based on compatible dental pattern (i.e.,
40 “baluchimyines”). The case of the late Eocene *Dianomys* is particularly interesting inasmuch
41 as the dental pattern of its two referred species (*D. qujingensis* and *D. obscuratus*; Fig. 5H-I)
42 includes anatomical details (and tendencies) that are otherwise found only in hystricognathous
43 rodents. Indeed, the main cusps and cuspids are not bulbous, notably the protocone and
44 hypocone on upper molars, and the protoconid and hypoconid on lower molars. These cusps
45 and cuspids are rather mesiodistally compressed and obliquely positioned, thereby appearing
46 as oblique ridges in continuity with the transverse crests and cristids. The two latter are
47 particularly well defined and moderately high (i.e., not as high as the apices of the main cusps
48 and cuspids), and form lophes and lophids (upper molars: anteroloph, protoloph, metaloph, and
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3 posteroloph; lower molars: metalophulid I, metalophulid II [or composite cristid; see after],
4 hypolophid, and posterolophid). On upper molars, the anterior arm of the hypocone is well
5 defined and moderately long, appearing elevated (as high as the transverse crests), slightly
6 oblique (not distomesially oriented), and not connected to the distal flank of the protocone (as
7 observed in “ctenodactyloids”). Due to its obliquity, it connects to a short and somewhat
8 relictual lingual metaloph (see below), and in some cases it further connects to the distal
9 extremity of a thin and distobuccally oriented posterior outgrowth of the protocone. The latter
10 is variably developed in length, and often absent on M2 and M3 (especially in *D. qujingensis*;
11 see Wang, 2001: plates I and II). Its absence generates a proverse internal sinus (hypoflexus),
12 the mesial and distal margins of which are formed by the protocone ridge and the hypocone
13 ridge plus its oblique anterior arm (M2 and M3 of *D. qujingensis*; Fig. 5H). When the sinus is
14 present, it remains open buccally (transversally open) due to the absence of longitudinal mure.
15 In the middle of the occlusal surface, a small, somewhat discreet (faintly visible) metaconule
16 is present, but the latter is still distally positioned as in “ctenodactyloids”, rather than
17 displaced mesiolingually as in hystricognaths. The metaconule is buccally connected to a thin
18 but well-defined and moderately long buccal metaloph, and lingually to the lingual branch of
19 the metaloph. The latter is not directed toward the protocone and connected to it as in
20 “ctenodactyloids”, but (as we already mentioned above) is connected to the mesial extremity
21 of the anterior arm of the hypocone (as observed on the M1 of *Ottomania* or the M1 and M2
22 of *Baluchimys krabiense*; Fig. 5J-K). Interestingly, in some upper molars referred to *D.*
23 *qujingensis* (Fig. 5H), the metaconule is rather mesiodistally compressed, and in some
24 specimens (see Wang, 2001: Plate II) it bears a short spur originating from its buccomesial
25 aspect. This spur is buccally directed and corresponds here to an incipient mesolophule. The
26 presence of this neocrest, although discreet, illustrates a first step toward the development of a
27 pentalophodont pattern, as that characterizing subsequent early hystricognaths (Fig. 5J-T).
28 The configuration of the anterior arm of the hypocone (well-defined, long, and slightly
29 obliquely oriented) and of the protocone (oblique, with the development of a short posterior
30 outgrowth), the presence of a lingual branch of the metaloph linking the mesial extremity of
31 the anterior arm of the hypocone (not the protocone), and the appearance in some specimens
32 of an internal sinus, also illustrate early stages toward the dental pattern characterizing upper
33 molars of hystricognaths. Lower molars also exhibit features compatible with the conditions
34 characterizing early hystricognaths. This is particularly shown in their marked lophate pattern
35 characterized by the development of trenchant and elevated transverse (metalophulid I and II,
36 hypolophid, and posterolophid) and longitudinal (ectolophid) cristids, and more discreet

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3 buccal cuspids (protoconid and hypoconid), which are mesiodistally compressed, appearing as
4 parallel oblique ridges. These two transformed buccal cuspids, together with the complete,
5 centrally displaced and high ectolophid, delimit a large and deep external sinusid (=
6 hypoflexid; Fig. 1). The hypoconulid is also much more discreet, being mesiodistally
7 compressed and virtually entirely subsumed within the posterolophid. The second transverse
8 cristid is particularly well developed and buccolingually complete. The configuration and
9 composition of this cristid are interesting inasmuch as they recall those observed in lower
10 molars of *Ottomania* (Fig. 5J), *Phiomys* (Fig. 5Q), *Acritophiomys* (Fig. 5R), *Gaudeamus* (Fig.
11 5U), and of the stem caviomorphs *Cachiyacuy* (Fig. 5T) and *Canaanimys* (Fig. 5S), although
12 across these taxa, these conditions were likely achieved iteratively. Similarly in *Dianomys*
13 (Fig. 5H-I), the second transverse cristid is in fact composed of two joint branches, one
14 corresponding to a short posterior arm of the protoconid, the other corresponding to a
15 moderately long neomesolophid (stemming from a mesostylid; Fig. 1). In sum, *Dianomys*
16 exhibits a composite dental pattern combining “ctenodactyloid” features with several
17 characters illustrating early stages of early hystricognaths. Given its transitional dental
18 morphology, which reflects its transitional phylogenetic position, for us *Dianomys* can
19 accordingly be regarded as a stem Hystricognathi, representing an early offshoot of that clade.
20 Although *Dianomys* was originally attributed to the Yuomyidae (Wang, 1984), de Bruijn
21 (1986) suggested possible affinities of this Asian Eocene taxon with the African Phiomysidae
22 (but without a detailed comparison of the few available isolated teeth). In her study of
23 additional fossil material attributed to *Dianomys qujingensis*, Wang (2001: 39, fig. 1) reported
24 a fragment of mandible that she described as sciurognathous. If the observation of Wang is
25 correct, and if our phylogenetic assumption regarding *Dianomys* makes sense (i.e., stem
26 Hystricognathi; Figs 2-4), then *Dianomys* could illustrate a case where the morphology of the
27 mandible is still not sufficiently differentiated for describing a hystricognathous condition.
28 The combination of intermediate dental features characterizing *Dianomys* teeth, probably
29 illustrates a transitional masticatory pattern between the “Grade A” and “Grade B” described
30 by Butler (1980, 1985). This transitional pattern would not yet have involved a marked
31 transformation of the dentary bone (lateralization of the angular process). The distal part of
32 the *Dianomys* mandible is not preserved, which prevents any indication regarding the position
33 of the condyles. However, given the dental pattern including well-developed transverse crests
34 and cristids, and the configuration of the lingual cusps and buccal cuspids (mesiodistally
35 compressed and oblique), it may be expected that the chewing movements included a marked
36 oblique component, thereby suggesting that the mandibular condyles had a rather high
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3 position with respect to the occlusal tooth plane. Therefore, it should be particularly
4 interesting to analyse in detail the attrition facets of the dental material available for the two
5 species of *Dianomys*, to assess if they showed a tendency to increased oblique masticatory
6 movements.
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11 The late middle Eocene *Anadianomys* (*A. declivis*; Fig. 5G; Tong, 1997: plate IX 17-22)
12 from China is clearly much less advanced morphologically than *Dianomys*, in having bulbous
13 cusps and cuspids (not mesiodistally compressed), very low anterior and posterior crests of
14 upper molars (being still at a cingulum state), a well-defined metaconule, which is slightly
15 mesially displaced, but nearly twinned with the metacone, thereby making the buccal
16 metaloph virtually indistinct. In contrast, the lingual metaloph, stemming from the
17 metaconule, is short, low but well defined, and not strictly directed toward the protocone
18 apex, but slightly displaced distally toward the distal extremity of a short, gently sloping and
19 buccodistally oriented (slightly oblique) posterior outgrowth of the protocone (Fig. 5G, but
20 also see Tong, 1997: plate IX 18-19, 22). The protoloph is complete, slightly arcuate and
21 relatively elevated (trenchant). The anterior arm of the hypocone is particularly well marked,
22 being long, moderately high and slightly buccally displaced/mesiobuccally oriented (i.e.,
23 slightly oblique). The latter reaches the distal extremity of the posterior outgrowth of the
24 protocone, near the lingual extremity of the lingual metaloph. There is no hypoflexus, but the
25 lingual margin of the crown is markedly grooved due to the slightly distobuccal orientation of
26 the posterior outgrowth of the protocone and of the slight obliquity of the anterior arm of the
27 hypocone. The lower molars have also protruding cuspids. The cristids are present, complete
28 (metalophulid I, hypolophid, posterolophid, and ectolophid), but moderately elevated, and the
29 protoconid and hypoconid are not obliquely positioned. In sum, the dental pattern of
30 *Anadianomys* is far from that of early hystricognathous rodents or even *Dianomys*, but few
31 characters such as the development and orientation of the anterior arm of the hypocone, the
32 orientation of the lingual metaloph, and the position of the metaconule are not
33 “ctenodactyloid” dental features, but rather tendencies toward early stages characterizing teeth
34 of early hystricognaths and *Dianomys*. *Anadianomys* may document a lineage close to the
35 emergence of the Hystricognathi clade. Additional palaeontological data documenting this
36 taxon would be critical for better understanding the morphological transformation and
37 chewing mode involved, illustrating an early step toward the differentiation of hystricognaths.
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58 The Gobiomyidae (*Gobiomys exiguus* and *G. neimongolensis*; Fig. 5F) and *Xueshimys*
59 *dissectus* (Fig. 5E) form a clade in our cladistic phylogenetic results (Fig. 2), appearing as the
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3 closest out-group of the Hystricognathi clade plus *Anadianomys*. In contrast, following the
4 standard Bayesian phylogenetic inferences (Fig. 3), the Gobiomyidae are nested within the
5 “ctenodactyloid” radiation, closely related to the “Yuomyidae” and the Chapattimyidae,
6 whereas *Xueshimys* is sister to *Anadianomys*. From the tip-dating Bayesian inferences (Fig.
7 4), the Gobiomyidae appear closely related to *Xueshimys*, and together form a clade sister to
8 the clade uniting *Anadianomys* and *Protataromys*. This large clade is rooted by *Stelmomys*,
9 and is nested within the “ctenodactyloid” radiation, appearing hierarchically lower due to the
10 presence of “yuomyids” (*Petrokozlovia* and *Yuomys*) occupying an unexpected and surprising
11 position, sister to the Hystricognathi clade (Fig. 4). Gobiomyidae and *Xueshimys*, as
12 *Anadianomys*, display upper molars with bulbous cusps, with crests (anterior and posterior,
13 protoloph and metaloph) somewhat more elevated, and bear on some specimens a well-
14 marked metaconule (see Wang, 2001: plates I and II; Tong, 1997: plate IX 1-8). However,
15 upper molars do not display a well-defined anterior arm of the hypocone, and the lingual
16 metaloph is often absent. Lower molars display also bulbous cuspids, without noticeable
17 mesiodistal compression of the protoconid and hypoconid, and the cristids, notably the
18 hypolophid, are often low and incomplete. On *Gobiomys exiguus*, the ectolophid is
19 incomplete (does not reach the protoconid), and a well-defined mesoconid is still present (Fig.
20 1). *Gobiomys neimongolensis* is documented by a mandible described as sciurognathous
21 (Wang, 2001: plate I2), the distal part of which is preserved but broken at the level of the
22 condyle. Despite this breakage, based on the preserved portion, it can be expected that the
23 condyle was relatively low with respect to the occlusal tooth plane, a position which indicates
24 in turn that oblique chewing movements were probably rather limited in this taxon. The
25 pattern of attrition recalls that of early “ctenodactyloids” (e.g., tamquammyids, yuomyids, and
26 chapattimyids), rather indicating more or less transverse chewing movements. Given their
27 dental morphology and their phylogenetic position (cladistic results; Fig. 2), the Gobiomyidae
28 and *Xueshimys* are therefore considered here as pre-hystricognathous “ctenodactyloids” (Fig.
29 5E-F).

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32 Finally, we consider a unique specimen (Fig. 6) published by Hussain *et al.* (1978: 100,
33 Plate 6, fig. 9) as M2 of “*Saykanomys*” *sondaari* (i.e., *Birbalomys sondaari sensu Kumar et*
34 *al.*, 1997). In its original description, this specimen was recognized as “aberrant”, and the
35 authors did not exclude the possibility that it could represent a different taxon. The occlusal
36 pattern of this unique upper molar from the middle Eocene of Pakistan (Kala Chitta Range,
37 Punjab) clearly illustrates for us a distinct genus, and besides, undoubtedly outside of the
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3 Chapattimyidae. In its less cuspidate main cusps, strongly oblique and long anterior arm of
4 the hypocone that is connected to a reduced (not inflated), faintly visible metaconule, and in
5 the long and well-defined metaloph, this tooth can be clearly set apart from chapattimyids
6 (e.g., *Chapattimys*, *Birbalomys*, and *Basalomys*). In contrast, this suite of morphological
7 details is observed in early taxa considered as basal hystricognaths (e.g., *Dianomys*,
8 *Ottomania*, *Confiniummys*, *Baluchimys*, etc.). This tooth preserves a trace of the lingual
9 metaloph, which is thin, very low, and linking the lingual aspect of the metaconule to the
10 median part of the long posterior outgrowth of the protocone (Fig. 6). Although long and
11 extending distally, the posterior outgrowth of the protocone does not reach the hypocone
12 (damping distally), so the lingual margin is open lingually by a narrow and shallow notch.
13 The posterior outgrowth of the protocone plus the oblique and long anterior arm of the
14 hypocone generate an internal sinus (= hypoflexus; Fig. 1). There is no well-differentiated
15 mure (only a small, very short and faintly visible longitudinal spur stemming from the
16 metaconule), and the hypoflexus is open transversally, being only limited lingually by the
17 relict of the lingual metaloph. The mesialmost transverse crest is still at a stage of cingulum
18 (anterocingulum, not anteroloph), which remains not connected to the protocone. There is a
19 narrow but still well-defined protoconule, which is connected to the lingual extremity of a
20 moderately long buccal protoloph. Although the transverse crests are low, the tooth displays a
21 clear tetralophodont pattern, without incipient pentalophodonty. There is, indeed, neither
22 mesolophule nor mesoloph stemming from the metaconule and mesostyle, respectively. Their
23 absence illustrates a dental pattern that appears evolutionarily less advanced compared to that
24 characterizing early hystricognaths (*Dianomys*, *Ottomania*, *Confiniummys*, and *Baluchimys*).
25 Given the special morphology of this unique tooth (Fig. 6) and the antiquity of this taxon,
26 additional fossil material would be particularly interesting for better appreciating its
27 phylogenetic status. If this taxon is an early stem hystricognath, then its dental pattern and the
28 associated masticatory mechanics could illustrate an early evolutionary stage of the
29 masticatory apparatus differentiation of the group.
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52 QUALITY OF THE ASIAN-AFRICAN FOSSIL RECORD OF EARLY HYSTRICOGNATHS

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57 The strict consensus tree of the cladistic analyses (Fig. 2) was transposed onto a
58 chronostratigraphical context (Fig. 7). First, regardless of the phylogenetic topology, a general
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3 overview (direct reading) of the stratigraphic occurrences or extensions of known
4 hystricognaths highlights a fossil record primarily concentrated over a time interval ranging
5 from the early late Eocene to the late early Oligocene (Priabonian-Rupelian; see also
6 Appendix S1). Only a few hystricognaths are documented in older strata: “*Protophiomys*”
7 *tunisiensis* from Central Tunisia (Djebel el Kébar), found in deposits dated at *ca.* 39.5 Myr
8 (41-38 Myr, late middle Eocene, early Bartonian; Marivaux *et al.*, 2014a,b), and *Canaanimys*
9 and *Cachiyacuy* (plus other taxa) from Peruvian Amazonia (Contamana), found in deposits
10 dated *ca.* 41 Myr (42-40 Myr, early Bartonian, Barrancan South American Land Mammal
11 Age; Antoine *et al.*, 2012, 2016; Boivin *et al.*, 2017a, 2019). These taxa from North Africa
12 and South America are so far the oldest known hystricognaths. The incredible widespread
13 geographic distribution of these taxa suggests a greater antiquity of the Hystricognathi clade,
14 and an early diversification of the group, which would have occurred during a short time
15 interval. This is graphically striking when we apply the phylogeny on the stratigraphic
16 occurrences of known Palaeogene hystricognaths (Fig. 7). Based on the results of the cladistic
17 analyses, the topology of the Hystricognathi clade and both the great antiquity and
18 hierarchically high positions within that clade of “*P.*” *tunisiensis* and *Canaanimys* plus
19 *Cachiyacuy*, imply numerous extensive ghost lineages, notably for the Asian basal and
20 advanced “baluchimyines”, but also for the African protophiomyines, metaphiomyines,
21 phiomyids, gaudeamurids, and phiocricetomyines. For all of these groups, the ghost lineages
22 extend back to the middle middle Eocene (late Lutetian; Fig. 7), whereas their first known
23 occurrence dates only from the late middle Eocene (early Bartonian; for phiocricetomyines),
24 the early late Eocene (early Priabonian; for protophiomyines), the latest Eocene (latest
25 Priabonian; for “baluchimyines”, phiomyids, and gaudeamurids), and the early Oligocene
26 (early Rupelian; for bugtimyids and metaphiomyines). Gaps in the hystricognath fossil record
27 are also observed when considering the datings of the internal nodes estimated by the
28 Bayesian tip-dating analysis (BTD; Fig. 8) with the fossilized birth-death prior (taking into
29 consideration the ages of related species, the rates of evolution, the phylogenetic relationships,
30 and the patterns of speciation and fossilization). However, the root ages estimated for some
31 hystricognath groups appear somewhat less ancient than those estimated from the cladistic
32 phylogenetic results. Indeed, baluchimyines, protophiomyines and gaudeamurids are
33 estimated to have originated during the early Bartonian (Fig. 8), while bugtimyids,
34 phiocricetomyines as well as phiomorphs (such as taxonomically depicted by the BTD
35 analysis) are estimated to have originated during the late Lutetian (Fig. 8).

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3 Based on our phylogenetic results and dental pattern analyses, the two species of
4 *Dianomys* (*D. obscuratus* and *D. qujingensis*) from China (Caijiachong; Wang, 1984, 2001)
5 are considered here as basal members of the Hystricognathi clade. These two species come
6 from deposits that are middle late Eocene in age (Ergilian Asian Land Mammal Age;
7 Appendix S1). *Dianomys* increases our knowledge of the past diversity of early Asian
8 hystricognaths, but given its age (if valid), it does not fill the gap of the Asian fossil record
9 documenting ancient hystricognathous rodents in Asia. Indeed, given the age of the *Dianomys*
10 clade and its position within the phylogeny, an extensive ghost lineage extending back to the
11 middle middle Eocene is implied (middle Lutetian; Fig. 7). The dating of the origin of the
12 *Dianomys* clade deriving from the BTM analysis provides a similar estimation, dating the root
13 of this clade from the middle Lutetian (Fig. 8), thereby underscoring a nearly 10 Myr ghost
14 lineage for this clade in Asia.
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24 In summary, these results (deriving from cladistic and Bayesian tip-dating analyses)
25 indicate that the origin of the Hystricognathi clade likely occurred *ca.* 45 Myr (middle
26 Lutetian; Figs 7, 8; consistent with estimates deriving from molecular data; e.g., see Upham &
27 Patterson, 2015), followed by a rapid radiation (high-level taxonomic diversification) of the
28 group during the middle Eocene, and was associated with intercontinental dispersal events
29 during this time window (see discussion after). Colonizations of large continents where strong
30 rodent competitors were seemingly missing, might have involved rapid early diversifications
31 (and morphological changes) associated with filling of open niche space (see Sallam &
32 Seiffert, 2016: 3). However, despite these assumptions and a somewhat new vision regarding
33 the timing of the emergence of hystricognaths and the internal distinct groups, it must be
34 noted that this expected Eocene basal radiation of the group is still undocumented in Asia and
35 scarcely documented in Africa and South America.
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46 Remark: As discussed previously, the morphology of the unique tooth (Fig. 6) from the
47 middle Eocene of Pakistan might illustrate an early stage of the dental pattern of
48 hystricognaths. This taxon could then testify to a very ancient record of the groups in South
49 Asia, but to be valid, this assumption requires further morphological support than current data
50 allow. Even if this taxon is among the earliest members of the Hystricognathi clade, we must
51 recognize that the Eocene fossil record of the apparent ancestral homeland (Asia) of
52 hystricognathous rodents remains so far particularly under-documented.
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PALAEOBIOGEOGRAPHIC IMPLICATIONS

Palaeontological data are scarce and often limited, but in association with an accurate temporal context, they reveal some aspects of the past evolutionary history of a group, and provide critical evidence and constraints regarding its historical biogeography. But understanding the macroevolutionary events and consequent palaeobiogeographic scenarios requires a phylogenetic context, which within a temporal context provides the baseline for any interpretations. Despite the incompleteness of the fossil record in Asia and Africa for early hystricognathous rodents (Figs 7, 8), the widespread Palaeogene geographic distribution of currently available fossil data from South Asia, North Africa and equatorial South America, testifies to the existence of intercontinental dispersals. However, whatever the phylogenetic inferences considered (deriving from cladistic or Bayesian analyses), the topologies imply a complex early historical biogeography of the group, notably between Asia and Africa. Based on these phylogenetic topologies (Figs 2-4), and using the parsimony optimization for reconstructing ancestral biogeographic states (under Mesquite 2.75; Maddison & Maddison, 2011), several alternative hypothetical scenarios of hystricognathous rodent dispersals between Asia and Africa can be envisaged. Considering an Asian origin of the Hystricognathi clade:

- Three African clades (*i.* protophiomyines, *ii.* Phiocricetomyines, and *iii.* “metaphiomyines-phiomyids-gaudeamurids-caviomorphs”; Figs 2-4) appear patchy nested within the paraphyletic Asian radiation. This would imply the existence of multiple (a least three) unidirectional dispersals to Africa from Asia of the Asian ancestors of these three African clades (Fig. 9A and Fig. 10A, C; Appendix S8A, D, F);
- Two African clades (*i.* protophiomyines and *ii.* “phiocricetomyines-metaphiomyines-phiomyids-gaudeamurids-caviomorphs”) appear patchy nested within the paraphyletic Asian radiation. In this case, at least two colonisations of Africa from Asia could be expected (Fig. 9B; Appendix S8B). However, in this context, one dispersal event occurred to Asia from Africa (considering here an African taxon [ancestor of the Asian *Lophibaluchia*] colonizing Asia; interpretation deriving only from the results of the cladistic analyses);
- The African clades (plus some Asian clades*) form a monophyletic group, nested within the paraphyletic Asian radiation. This view would imply only one dispersal event

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3 to Africa from Asia of the Asian common ancestor of all African taxa (Fig. 9C and Fig.
4 10B, D; Appendix S8C, E, G). But in this context, the Asian clades* nested within the
5 monophyletic African radiation (* i.e., bugtimyids and *Lophibaluchia* from the cladistic
6 results [Fig. 9C; Appendix S8C]; bugtimyids and “baluchimyines-dianomyids” from the
7 standard Bayesian results [Fig. 10B; Appendix S8E]; bugtimyids and baluchimyines
8 from the Bayesian tip-dating results [Fig. 10D; Appendix S8G]) would have an African
9 origin, thereby indicating at least two dispersal return events to Asia from Africa (see
10 also Sallam & Seiffert, 2016).
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20 Whatever the scenario considered, these dispersals between Asia and Africa seem to have
21 occurred during the initial adaptive radiation of the group, i.e., during the middle middle
22 Eocene and the late middle Eocene (late Lutetian – early Bartonian; see Figs 7, 8). Given that
23 all Asian and African hystricognath taxonomic units seem to have emerged during this time
24 interval, we would be then rather in favour of the hypothesis of multiple unidirectional
25 dispersals from Asia to Africa of the Asian ancestors of at least three African clades (Fig. 9A
26 and Fig. 10A, C; Appendix S8A, D, F). Indeed, it is hard to consider the possibility of several
27 “round-trips” between Asia and Africa during this estimated time window (i.e., Asian origin
28 of the African clades and African origin of some Asian clades [= quick back to Asia]; Fig. 9C
29 and Fig. 10B, D; Appendix S8C, E, G). Dispersals from Africa toward South Asia at that time
30 were, however, not impossible inasmuch as such a dispersal scenario (direction) is suggested
31 for interpreting the Afro-Asian distribution of the late middle - early late Eocene anomaluroid
32 rodents, based on the hypothesis of their ancient African antiquity (see Marivaux *et al.*,
33 2005a, 2011, 2015, 2017b; Sallam *et al.*, 2010; but see Coster *et al.*, 2015b). As surprising as
34 it might seem, it is worth noting that if ancestral Asian hystricognaths dispersed across the
35 Tethys Sea to invade Africa sometime during the middle Eocene (Figs 7, 8), they were also
36 able to continue their pattern of intercontinental dispersal across the Atlantic Ocean to
37 colonize South America, perhaps only shortly before their first appearance in the fossil record
38 there (i.e., ca. 41 Myr, late middle Eocene; Antoine *et al.*, 2012; Antoine *et al.*, 2016; Boivin
39 *et al.*, 2017a, 2019). The results of the Bayesian tip-dating analysis would suggest that the
40 dispersal from Africa to South America of the ancestor of caviomorphs (including
41 Gaudeamuridae) most likely occurred ca. 42-43 Myr (the Phiomorpha-Caviomorpha split
42 would have occurred ca. 43-44 Myr; Fig. 8; consistent with estimates deriving from molecular
43 data; e.g., see Upham & Patterson, 2015). However, although the time window during which
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3 the Asio-African and Afro-South-American dispersals occurred seems to be better bracketed,
4 the modalities and pathways of these dispersals remain unresolved. Interestingly, the
5 historical biogeography of hystricognaths is strikingly similar and can be put in parallel with
6 that of anthropoid primates, for which an Asian origin is also demonstrated (e.g., [Beard *et al.*, 1996](#);
7 [Jaeger *et al.*, 1999](#); [Beard, 2004, 2006, 2016](#); [Beard & Wang, 2004](#); [Marivaux *et al.*, 2003, 2005b](#);
8 [Jaeger & Marivaux, 2005](#); [Seiffert, 2012](#)), associated with (several) dispersal(s)
9 to Africa sometime during the middle Eocene (e.g., [Jaeger *et al.*, 2010b](#); [Chaimanee *et al.*, 2012](#);
10 [Marivaux *et al.*, 2014b](#); [Beard, 2016](#)), then to South America (e.g., [Bond *et al.*, 2015](#);
11 [Marivaux *et al.*, 2016](#)). Today, many questions remain as to whether the colonization of
12 Africa and South America by hystricognathous rodents and anthropoid primates took place
13 synchronously or in a temporally staggered fashion (e.g., [Chaimanee *et al.*, 2012](#); [Beard, 2016](#);
14 [Upham & Patterson, 2015](#) and references cited). The extensive marine barriers that
15 separated Asia from Africa (e.g., [Barrier *et al.*, 2018](#)), and Africa from South America (e.g.,
16 [de Oliveira *et al.*, 2009](#)) at that time, and the absence of ecological continuity (land corridor)
17 between each landmass as a result, have likely required “extraordinary” overwater dispersals
18 (sweepstakes dispersal on natural rafts; e.g., [Houle, 1998, 1999](#)). Regardless of the modalities
19 of these dispersals (that remain speculative), the success of the African and South American
20 colonizations of anthropoid primates and hystricognathous rodents **suggests** that the three
21 landmasses had very similar and favourable tropical palaeoenvironmental conditions at that
22 time (at least South Asia, North Africa, and equatorial South America). Another critical
23 question also remains as to whether the middle Eocene Climate Optimum (MECO; e.g.,
24 [Zachos *et al.*, 2008](#)) recorded at *ca.* 40-41 Myr, might have played a role in these dispersals
25 and/or in early diversifications in both Africa and South America of these two mammal
26 groups (e.g., [Antoine *et al.*, 2012](#); [Chaimanee *et al.*, 2012](#); [Marivaux *et al.*, 2014a,b](#); [Beard, 2016](#);
27 [Boivin *et al.*, 2019](#)). Many critical issues remain on the early evolution and historical
28 biogeography of both groups, which should be highlighted by additional palaeontological and
29 neontological evidence, and a better knowledge of the palaeoenvironmental constraints.
30 Palaeontological field efforts must then be strongly sustained in the tropical regions of South
31 Asia, Africa and South America in order to substantially document and further our
32 understanding of the early evolutionary history and palaeodiversity of hystricognathous
33 rodents, anthropoid primates and other groups.
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SUPPORTING INFORMATION

Additional supporting information may be found online in the supporting information tab for this article:

Appendix S1. List of selected taxa.

Appendix S2. List of selected taxa and systematics (original and proposed).

Appendix S3. Characters and character states used in the phylogenetic analyses.

Appendix S4. Matrix for the cladistic analyses (for PAUP* 4.0b10).

Appendix S5. Matrix for the standard Bayesian analysis (for MrBayes 3.2.6).

Appendix S6. Matrix for the Bayesian tip-dating analysis (for MrBayes 3.2.6).

Appendix S7. List of prior perturbations performed with the Bayesian tip-dating analyses.

Appendix S8. Color-coded non-simplified tree illustrating the hypothetical scenarios of hystricognathous rodent dispersals between Asia, Africa and South America during the Eocene. **A-C**, cladistic results (strict consensus); **D-E**, inferences resulting from the standard Bayesian analysis (Allcompat consensus tree); **F-H**, inferences resulting from the Bayesian tip-dating analysis (Allcompat consensus tree).

Figure legends

Figure 1. Dental terminology (updated and modified after [Marivaux *et al.*, 2004, 2014a, 2017a; Boivin & Marivaux, 2018](#)). Abbreviations for upper teeth: **Aah**, anterior arm of the hypocone; **Aam**, anterior arm of the metacone; **Al**, anteroloph (or anterocingulum); **Ay**, anterostyle; **H**, hypocone; **Hfx**, hypoflexus; **Lac**, lingual anterocingulum; **Lmel**, lingual metaloph (= enterocrest); **M**, metacone; **Mcu**, metaconule; **Mel**, buccal metaloph; **Mel (+)**, buccal metaloph and its possible lingual connections (+); **Msfx**, mesoflexus; **Ms**, mesostyle; **Msl**, Mesoloph; **Msul**, mesolophule; **Mr**, mure; **P**, protocone; **Pa**, paracone; **Pafx**, paraflexus; **Pap**, posterior arm of the paracone; **Pcu**, protoconule; **Pop**, posterior outgrowth of the protocone (Pop + longitudinal Aah = endoloph); **Prl**, protoloph; **Psfx**, posteroflexus; **PsI**, posteroloph; **Py**, parastyle. Abbreviations for lower teeth: **Aahd**, anterior arm of hypoconid; **Acd**, anterocingulid; **Ad**, anteroconid; **Afxd**, anteroflexid (= paraflexid); **Ecd**, ectolophid (Ecd mesial + Ecd distal); **Et**, entoconid; **Hd**, hypoconid; **Hfxd**, hypoflexid; **Hld**, hypolophid (= entolophid); **Hud**, hypoconulid; **Mcd**, mesoconid; **Md**, metaconid; **Med. I**, metalophulid I (= ancestral paralophid); **Med. II**, metalophulid II (= protolophid or long posterior arm of the protoconid); **Msd**, mesolophid; **Msfxd**, mesoflexid; **Mstd**, mesostylid; **Mtfxd**, metaflexid; **Nmsd**, neo-mesolophid; **Pamd**, posterior arm of the metaconid; **Prd**, protoconid; **Psd**, posterolophid. Arrowheads point mesiolingually to indicate the orientation of the teeth on the jaws (mesiolingual).

Figure 2. Results of the cladistic phylogenetic analyses. Strict consensus tree of two equally most parsimonious trees of 1042.46 steps each (CI= 0.373; RI= 0.637). Bootstrap (BP) and Bremer (B) values are indicated by the numbers labelled above and under internal branches, respectively (BP > 15; B ≥ 0.5). The solid line arrow indicates the Hystricognathi clade (including taxa formerly considered as such, plus *Dianomys* as proposed and discussed here). The dashed arrows indicate the possibilities of taxonomic enlargements regarding the basal content of the Hystricognathi clade (considering *Anadianomys* and gobiomyids; but see discussion in the main text). Quotation marks mean paraphyletic taxonomic unit.

Figure 3. Results of the Bayesian phylogenetic analysis. Allcompat consensus tree (majority-rule plus compatible groups) of 25,000 post-burn-in trees retained by the Bayesian analysis. Numbers at nodes represent posterior probabilities (PP; in percent). The solid line arrow indicates the Hystricognathi clade (including taxa formerly considered as such, plus *Dianomys*, which is nested here within the Hystricognathi clade). Bal, baluchimyines (-ids); Bug, bugtimyids; Cav, stem caviomorphs; Chp, chapattimyids; Coc, cocomyids; Dia, dianomyids; Gau, gaudeamurids; Gob, gobiomyids; Met, metaphiomyines (-ids); Phc, phiocricetomyines (-ids); Phi, phiomyids; Pro, protophiomyines (-ids); Taq, tamquammyids; Yuo, yuomyids. Quotation marks mean paraphyletic taxonomic unit.

Figure 4. Results of the Bayesian phylogenetic tip-dating analysis with the fossilized birth-death prior. Allcompat consensus tree (majority-rule plus compatible groups) of 50,000 post-burn-in trees retained by the tip-dating analysis. Numbers at nodes represent posterior probabilities (PP; in percent). The solid line arrow indicates the Hystricognathi clade (including taxa formerly considered as such, plus *Dianomys* as proposed and discussed here). Bal, baluchimyines (-ids); Bug, bugtimyids; Cav, stem caviomorphs; Chp, chapattimyids; Coc, cocomyids; Dia, dianomyids; Gau, gaudeamurids; Gob, gobiomyids; Met, metaphiomyines (-ids); Phc, phiocricetomyines (-ids); Phi, phiomyids; Pro, protophiomyines (-ids); Taq, tamquammyids; Yuo, yuomyids. Quotation marks mean paraphyletic taxonomic unit.

Figure 5. Phylogeny and dental patterns. The circular tree corresponds to the strict consensus tree topology of the cladistic analyses (Fig. 2). The computerized schematic line drawings of upper and lower teeth illustrate the dental patterns of selected ctenohystrican taxa of the main subclades. All the line drawings illustrate left upper and lower molars (some drawings were reversed from the corresponding original fossil specimens), and primarily represent M2 and m2, respectively. The upper molars (and the lower molars associated) are scaled to have equal buccolingual width. For some taxa recognized here as members of the Hystricognathi clade (e.g., *Dianomys* and *Ottomania*), we have illustrated additional upper and lower specimens (*Dianomys obscuratus* and *D. qujingensis*: M1-3 and m1-3; *Ottomania proavita*).

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3 **Figure 6.** Schematic line drawing of the unique upper molar (M2) documenting a taxon from
4 the middle Eocene of Pakistan (Kala Chitta Range, Punjab). This molar was figured in
5 Hussain *et al.* (1978: 100, Plate 6, fig. 9), and recognized as an “aberrant specimen” among
6 the dental material attributed to “*Saykanomys*” *sondaari* (i.e., *Birbalomys sondaari sensu*
7 [Kumar et al., 1997](#)).
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15 **Figure 7.** Strict consensus tree of the cladistic phylogenetic analyses ([Fig. 2](#)), transposed onto
16 a chronostratigraphical context. The solid bars of different lengths indicate the stratigraphic
17 occurrences (or extensions) of the ctenohystrican taxa sampled. Note the numerous Eocene
18 gaps (long branches = phylogenetically implied ghost lineages) in the Asian and African
19 fossil records of hystricognathous rodents. The rectangular area with a gradient of grey (left to
20 right) indicates the temporal window for which the fossil record of hystricognathous rodents
21 is virtually non-existent in Asia and Africa. The black star indicates the unique tooth from the
22 middle Eocene of Pakistan, which could illustrate one of the oldest/earliest representatives of
23 the Hystricognathi clade. Taxon names (and stratigraphic extensions) are coloured according
24 to their continental geographic location.
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35 **Figure 8.** Allcompat consensus tree of the Bayesian tip-dating analysis ([Fig. 4](#)). The
36 rectangular area with a gradient of grey (left to right) indicates the temporal window for
37 which the fossil record of hystricognathous rodents is virtually non-existent in Asia and
38 Africa. Taxon names are coloured according to their continental geographic location.
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45 **Figure 9.** Tentative hypothetical scenarios of hystricognathous rodent dispersals between
46 Asia, Africa and South America during the Eocene, based on the results of the cladistic
47 analyses. The color-coded and highly simplified phylogenetic tree derives from the strict
48 consensus topology of the parsimony analyses ([Fig. 2](#)), and it is superimposed on a simplified
49 late middle Eocene global palaeogeographic reconstruction (simplified after a
50 palaeogeographic map of R. Blakey). These three scenarios (A-C) illustrate the evolutionary
51 and biogeographic patterns discussed in the text. The Asian clades are depicted in blue, the
52 African ones are in red, and the South American ones are in green. **A**, African clades are
53 patchy nested within the paraphyletic Asian radiation, implying then multiple (a least three)
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3 unidirectional dispersals to Africa from Asia; **B**, African clades are patchy nested within the
4 paraphyletic Asian radiation, implying in this case at least two colonisations of Africa from
5 Asia, and one dispersal return event to Asia from Africa (considering here an African taxon
6 colonizing Asia); **C**, African clades form a monophyletic group, nested within the
7 paraphyletic Asian radiation, thereby implying only one dispersal event to Africa from Asia
8 of the common ancestor of the African taxa. In this context, the Asian clades nested within the
9 monophyletic African radiation indicate at least two dispersal return events to Asia of African
10 taxa. For each scenario, we provide a color-coded non-simplified tree as Supplemental
11 Material online ([Appendix S8A-C](#)). Bal, baluchimyines (-ids); Bug, bugtimyids; Cav, stem
12 caviomorphs; Chp, chapattimyids; Coc, cocomyids; Dia, dianomyids; Gau, gaudeamurids;
13 Gob, gobiomyids; Met, metaphiomyines (-ids); Phc, phiocricetomyines (-ids); Phi,
14 phiomyids; Pro, protophiomyines (-ids); Taq, tamquammyids; Yuo, yuomyids.
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27 **Figure 10.** Tentative hypothetical scenarios of hystricognathous rodent dispersals between
28 Asia, Africa and South America during the Eocene, based on the results of the Bayesian
29 analyses (standard and tip-dating). The color-coded and highly simplified phylogenetic trees
30 derive from the Allcompat consensus trees of the standard Bayesian (A-B; [Fig. 3](#)) and
31 Bayesian tip-dating (C-D; [Fig. 4](#)) analyses, and they are superimposed on a simplified late
32 middle Eocene global palaeogeographic reconstruction (simplified after a palaeogeographic
33 map of R. Blakey). For each scenario, we provide a color-coded non-simplified tree as
34 Supplemental Material online ([Appendix S8D-G](#)). **A** and **C**: African clades are patchy nested
35 within the paraphyletic Asian radiation, implying then multiple (a least three) unidirectional
36 dispersals to Africa from Asia; **B** and **D**, African clades form a monophyletic group, nested
37 within the paraphyletic Asian radiation, thereby implying only one dispersal event to Africa
38 from Asia of the common ancestor of the African taxa (+ some Asian). In this context, the
39 Asian clades nested within the monophyletic African radiation indicate at least two dispersal
40 return events to Asia of African taxa. Bal, baluchimyines (-ids); Bug, bugtimyids; Cav, stem
41 caviomorphs; Chp, chapattimyids; Coc, cocomyids; Dia, dianomyids; Gau, gaudeamurids;
42 Gob, gobiomyids; Met, metaphiomyines (-ids); Phc, phiocricetomyines (-ids); Phi,
43 phiomyids; Pro, protophiomyines (-ids); Taq, tamquammyids; Yuo, yuomyids.
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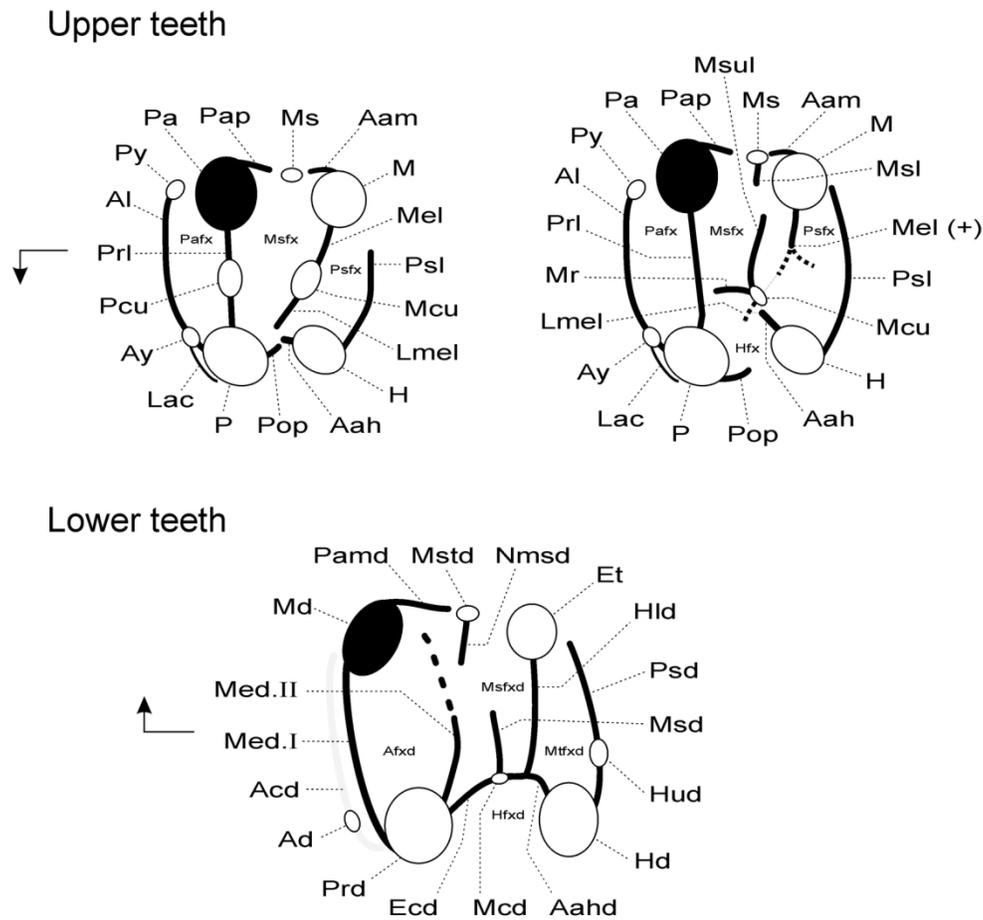


Figure 1. Dental terminology (updated and modified after Marivaux et al., 2004, 2014a, 2017a; Boivin & Marivaux, 2018). Abbreviations for upper teeth: Aah, anterior arm of the hypocone; Aam, anterior arm of the metacone; Al, anteroloph (or anteroconingulum); Ay, anterostyle; H, hypocone; Hfx, hypoflexus; Lac, lingual anteroconingulum; Lmel, lingual metaloph (= enterocrest); M, metacone; Mcu, metaconule; Mel, buccal metaloph; Mel (+), buccal metaloph and its possible lingual connections (+); Msfx, mesoflexus; Ms, mesostyle; Msl, Mesoloph; Msul, mesolophule; Mr, mure; P, protocone; Pa, paracone; Pafx, paraflexus; Pap, posterior arm of the paracone; Pcu, protoconule; Pop, posterior outgrowth of the protocone (Pop + longitudinal Aah = endoloph); Prl, protoloph; Psfx, posteroflexus; Psl, posteroloph; Py, parastyle. Abbreviations for lower teeth: Aahd, anterior arm of hypoconid; Acd, anteroconingulid; Ad, anteroconid, Afxd, anteroflexid (= paraflexid); Ecd, ectolophid (Ecd mesial + Ecd distal); Et, entoconid; Hd, hypoconid; Hfxd, hypoflexid; Hld, hypolophid (= entolophid); Hud, hypoconulid; Mcd, mesoconid; Md, metaconid; Med. I, metalophulid I (= ancestral paralophid); Med. II, metalophulid II (= protolophid or long posterior arm of the protoconid); Msd, mesolophid; Msfxd, mesoflexid; Mstd, mesostylid; Mfxd, metaflexid; Nmsd, neo-mesolophid; Pamd, posterior arm of the metaconid; Prd, protoconid; Psd, posterolophid. Arrowheads point mesiolingually to indicate the orientation of the teeth on the jaws (mesiolingual).

142x136mm (300 x 300 DPI)

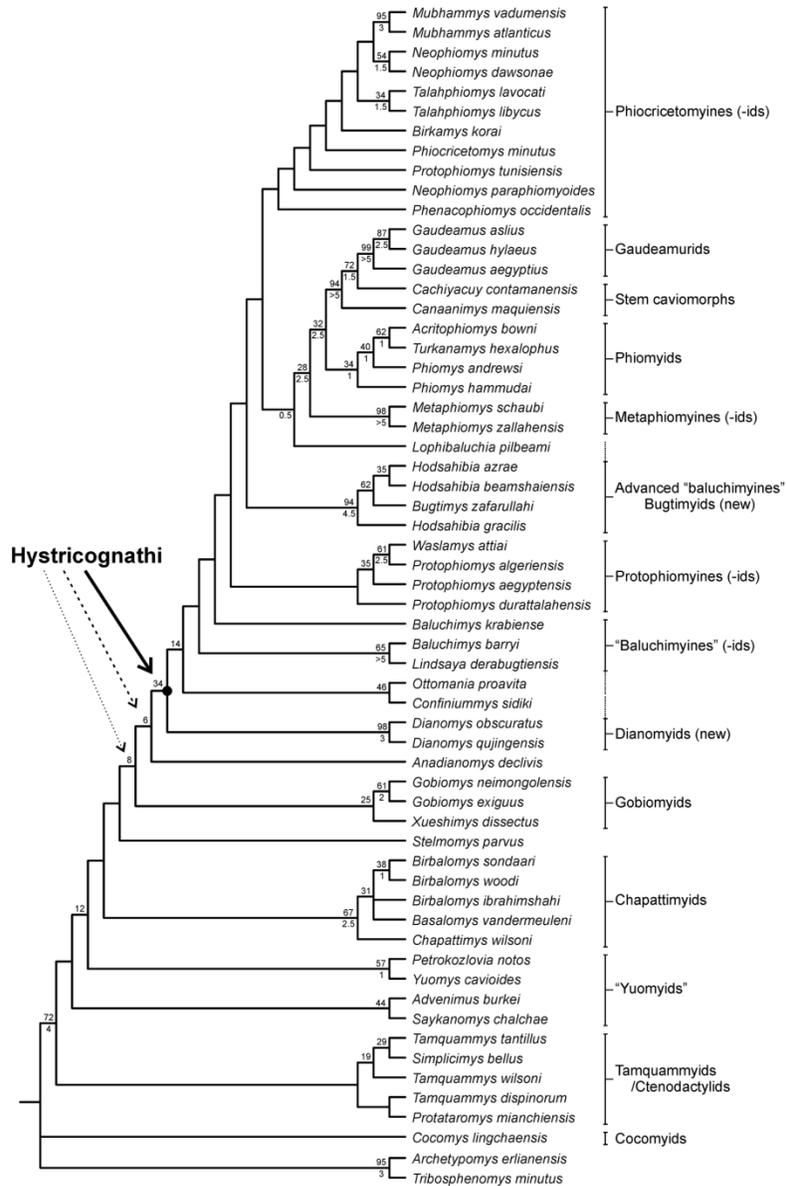


Figure 2. Results of the cladistic phylogenetic analyses. Strict consensus tree of two equally most parsimonious trees of 1042.46 steps each (CI= 0.373; RI= 0.637). Bootstrap (BP) and Bremer (B) values are indicated by the numbers labelled above and under internal branches, respectively (BP > 15; B ≥ 0.5). The solid line arrow indicates the Hystricognathi clade (including taxa formerly considered as such, plus *Dianomys* as proposed and discussed here). The dashed arrows indicate the possibilities of taxonomic enlargements regarding the basal content of the Hystricognathi clade (considering *Anadianomys* and gobiomyids; but see discussion in the main text). Quotation marks mean paraphyletic taxonomic unit.

153x232mm (300 x 300 DPI)

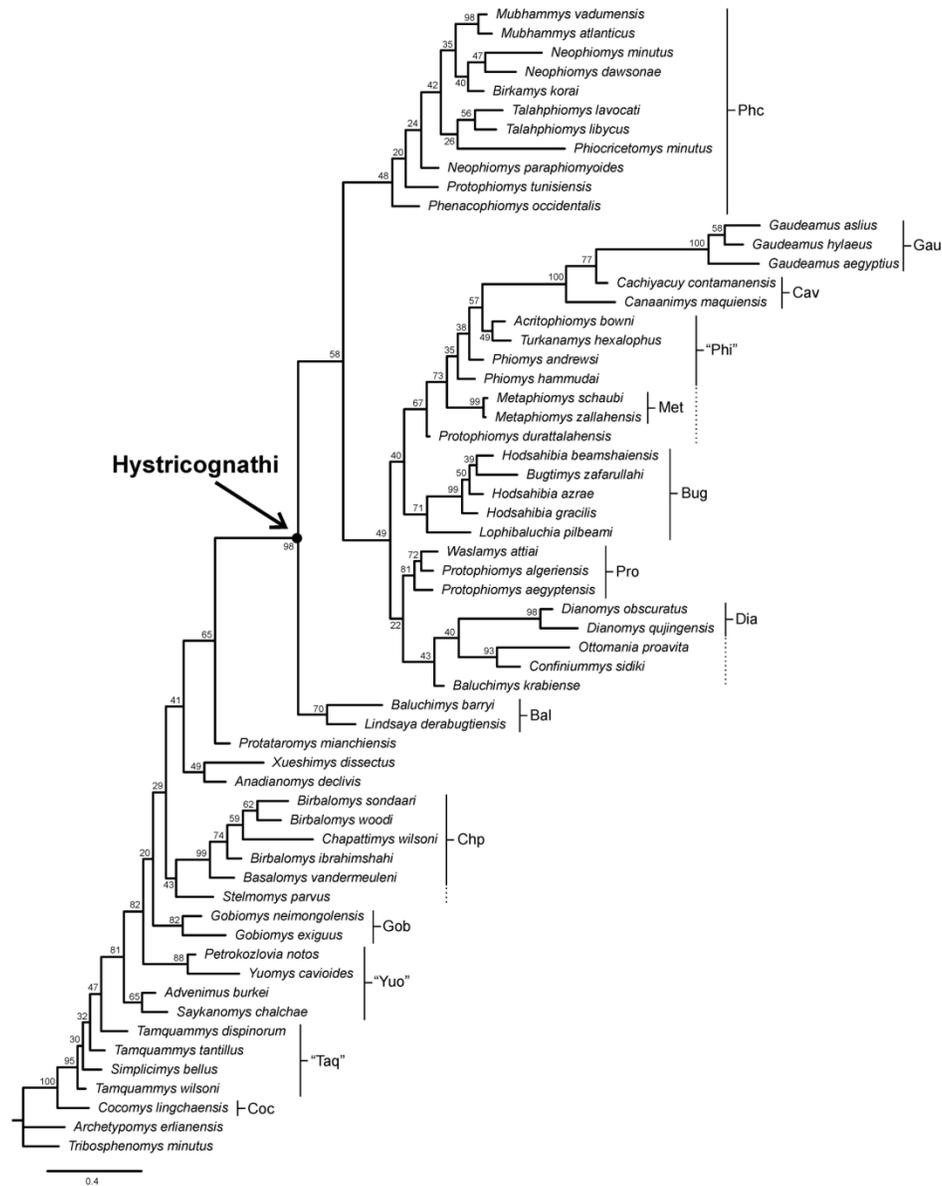


Figure 3. Results of the Bayesian phylogenetic analysis. Allcompat consensus tree (majority-rule plus compatible groups) of 25,000 post-burn-in trees retained by the Bayesian analysis. Numbers at nodes represent posterior probabilities (PP; in percent). The solid line arrow indicates the Hystricognathi clade (including taxa formerly considered as such, plus *Dianomys*, which is nested here within the Hystricognathi clade). Bal, baluchimyines (-ids); Bug, bugtimyids; Cav, stem caviomorphs; Chp, chapattimyids; Coc, cocomyids; Dia, dianomyids; Gau, gaudeamurids; Gob, gobiomyids; Met, metaphiomyines (-ids); Phc, phiocricetomyines (-ids); Phi, phiomyids; Pro, protophiomyines (-ids); Taq, tamquammyids; Yuo, yuomyids. Quotation marks mean paraphyletic taxonomic unit.

166x211mm (300 x 300 DPI)

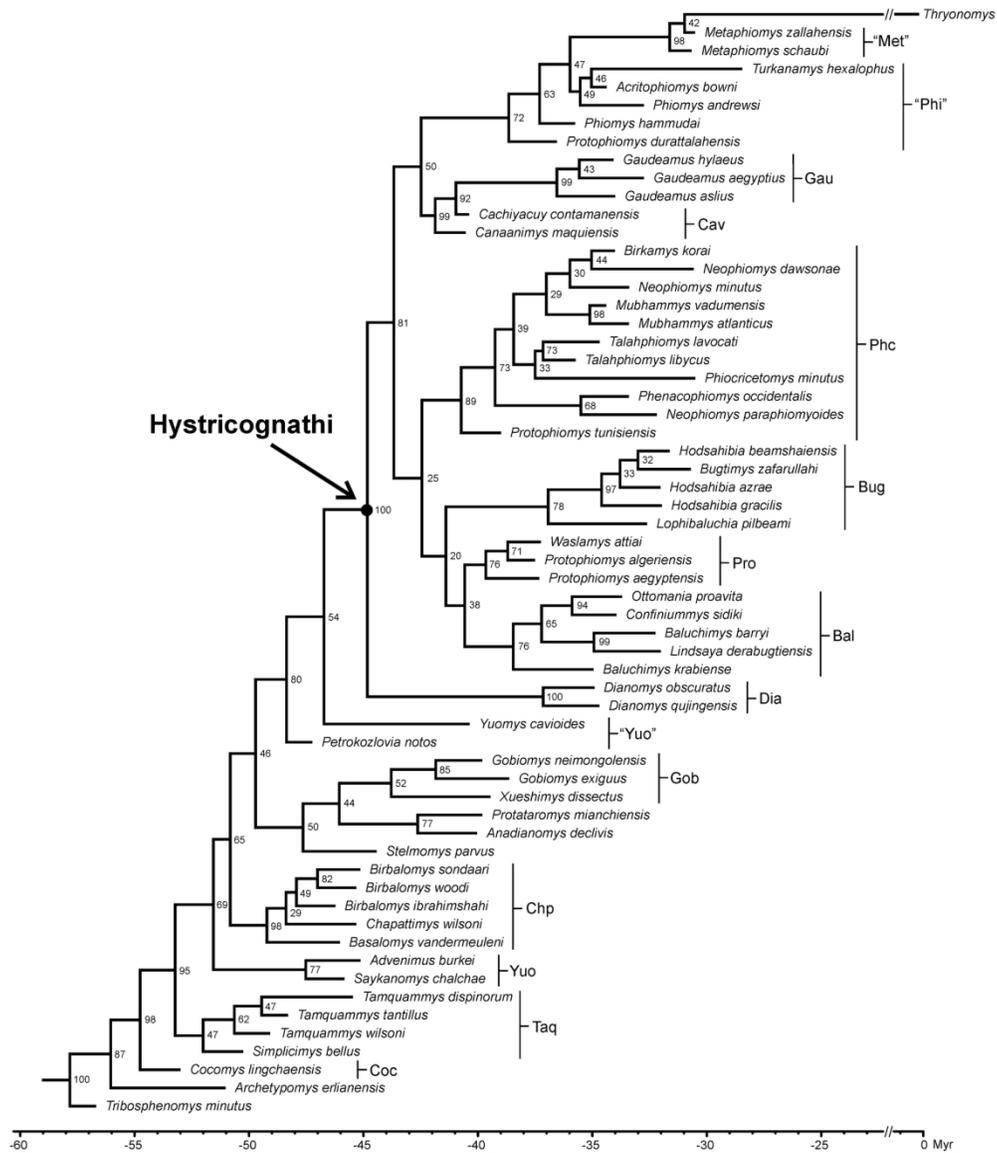


Figure 4. Results of the Bayesian phylogenetic tip-dating analysis with the fossilized birth-death prior. Allcompat consensus tree (majority-rule plus compatible groups) of 50,000 post-burn-in trees retained by the tip-dating analysis. Numbers at nodes represent posterior probabilities (PP; in percent). The solid line arrow indicates the Hystricognathi clade (including taxa formerly considered as such, plus *Dianomys* as proposed and discussed here). Bal, baluchimyines (-ids); Bug, bugtimyids; Cav, stem caviomorphs; Chp, chapattimyids; Coc, cocomyids; Dia, dianomyids; Gau, gaudeamurids; Gob, gobiomyids; Met, metaphiomysines (-ids); Phi, phiomyids; Pro, protophiomysines (-ids); Taq, tamquammyids; Yuo, yuomyids. Quotation marks mean paraphyletic taxonomic unit.

159x185mm (300 x 300 DPI)

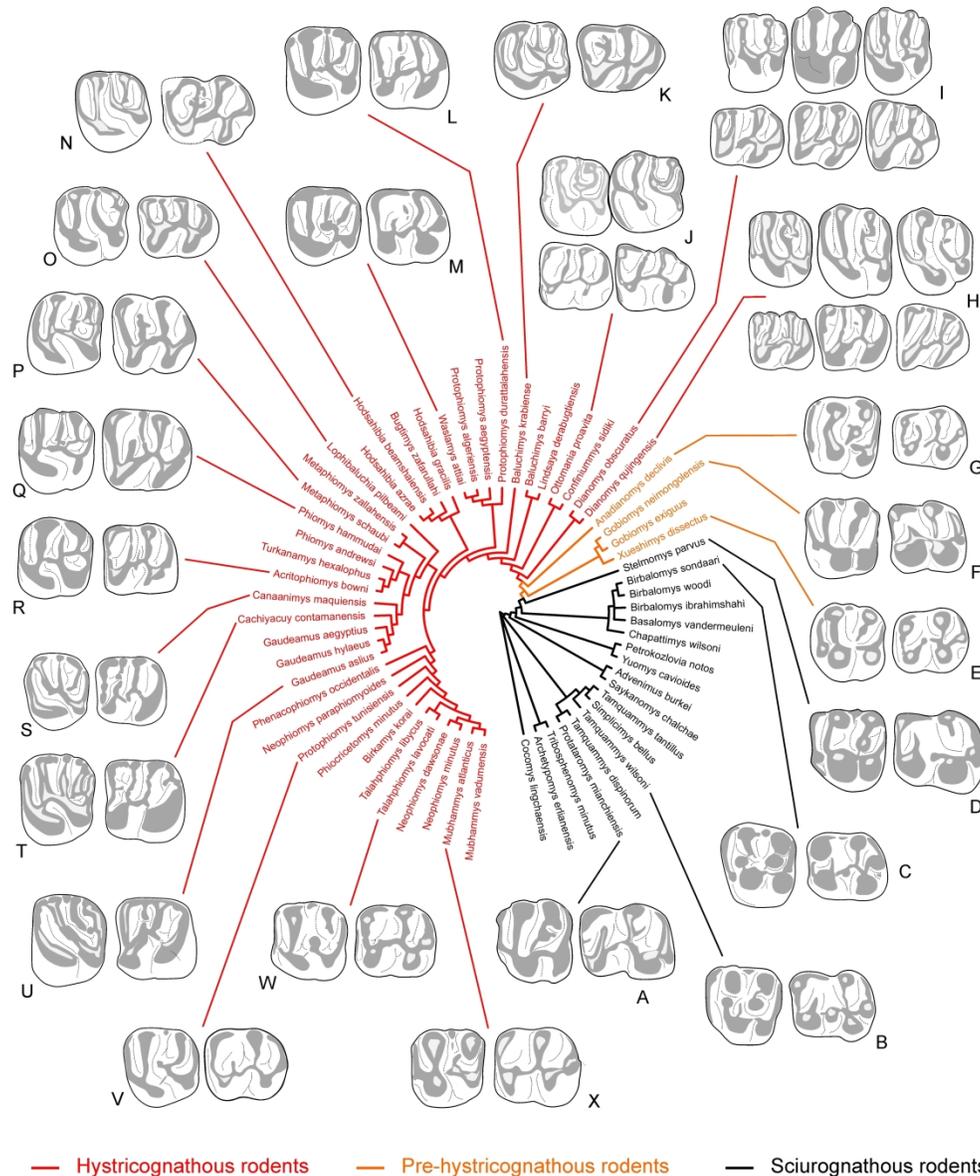


Figure 5. Phylogeny and dental patterns. The circular tree corresponds to the strict consensus tree topology of the cladistic analyses (Fig. 2). The computerized schematic line drawings of upper and lower teeth illustrate the dental patterns of selected tenohystrican taxa of the main subclades. All the line drawings illustrate left upper and lower molars (some drawings were reversed from the corresponding original fossil specimens), and primarily represent M2 and m2, respectively. The upper molars (and the lower molars associated) are scaled to have equal buccolingual width. For some taxa recognized here as members of the Hystricognathi clade (e.g., *Dianomys* and *Ottomania*), we have illustrated additional upper and lower specimens (*Dianomys obscuratus* and *D. qujingensis*: M1-3 and m1-3; *Ottomania proavita*).

171x206mm (600 x 600 DPI)

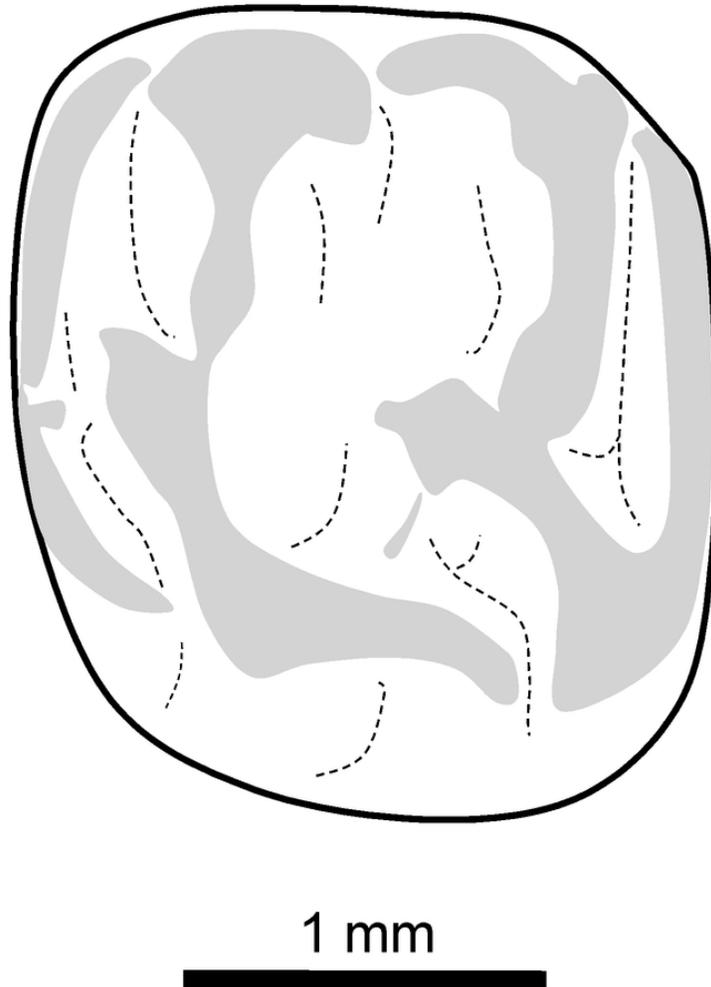


Figure 6. Schematic line drawing of the unique upper molar (M2) documenting a taxon from the middle Eocene of Pakistan (Kala Chitta Range, Punjab). This molar was figured in Hussain et al. (1978: 100, Plate 6, fig. 9), and recognized as an "aberrant specimen" among the dental material attributed to "Saykanomys" sondaari (i.e., *Birbalomys sondaari* sensu Kumar et al., 1997).

76x84mm (300 x 300 DPI)

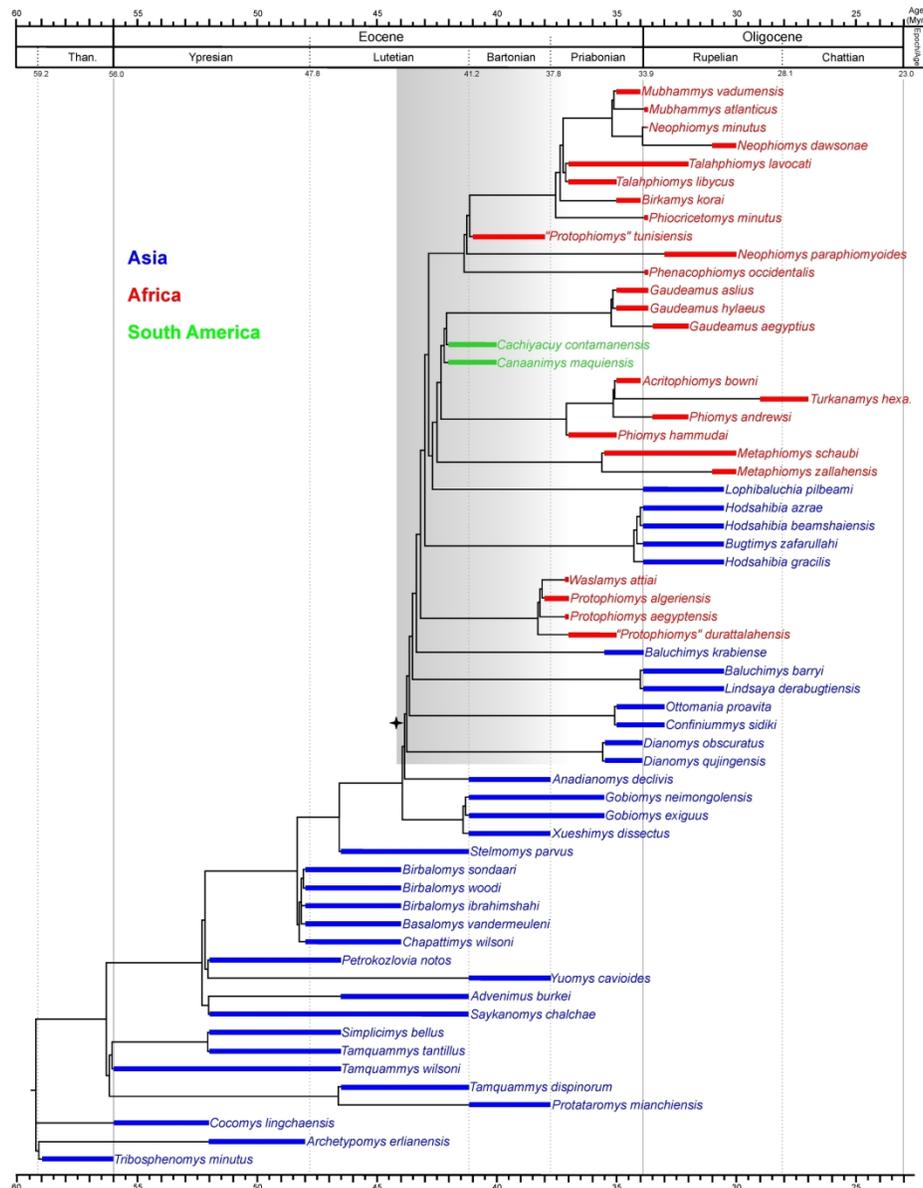


Figure 7. Strict consensus tree of the cladistic phylogenetic analyses (Fig. 2), transposed onto a chronostratigraphical context. The solid bars of different lengths indicate the stratigraphic occurrences (or extensions) of the ctenohystrican taxa sampled. Note the numerous Eocene gaps (long branches = phylogenetically implied ghost lineages) in the Asian and African fossil records of hystricognathous rodents. The rectangular area with a gradient of grey (left to right) indicates the temporal window for which the fossil record of hystricognathous rodents is virtually non-existent in Asia and Africa. The black star indicates the unique tooth from the middle Eocene of Pakistan, which could illustrate one of the oldest/earliest representatives of the Hystricognathi clade. Taxon names (and stratigraphic extensions) are coloured according to their continental geographic location.

189x244mm (300 x 300 DPI)

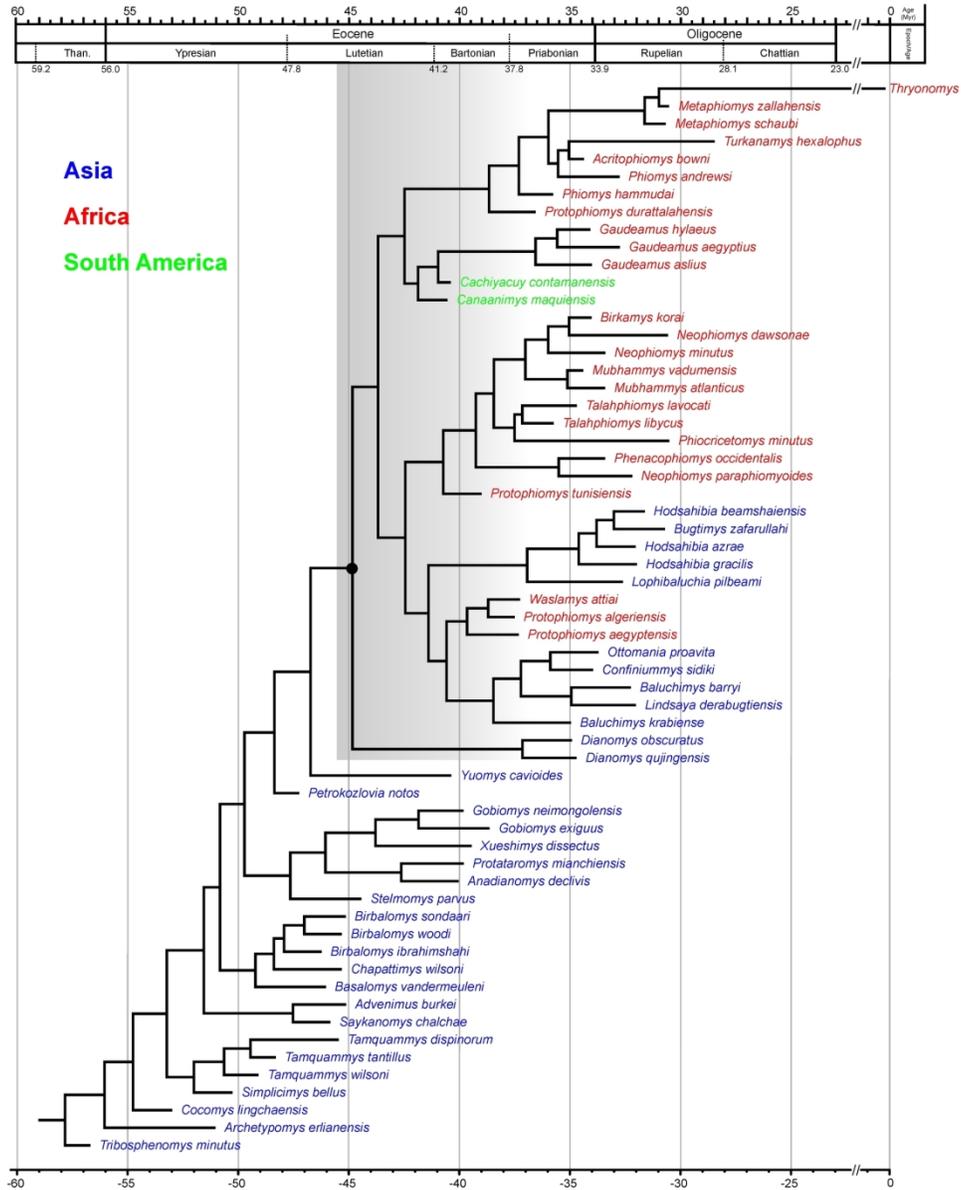


Figure 8. Allcompat consensus tree of the Bayesian tip-dating analysis (Fig. 4). The rectangular area with a gradient of grey (left to right) indicates the temporal window for which the fossil record of hystricognathous rodents is virtually non-existent in Asia and Africa. Taxon names are coloured according to their continental geographic location.

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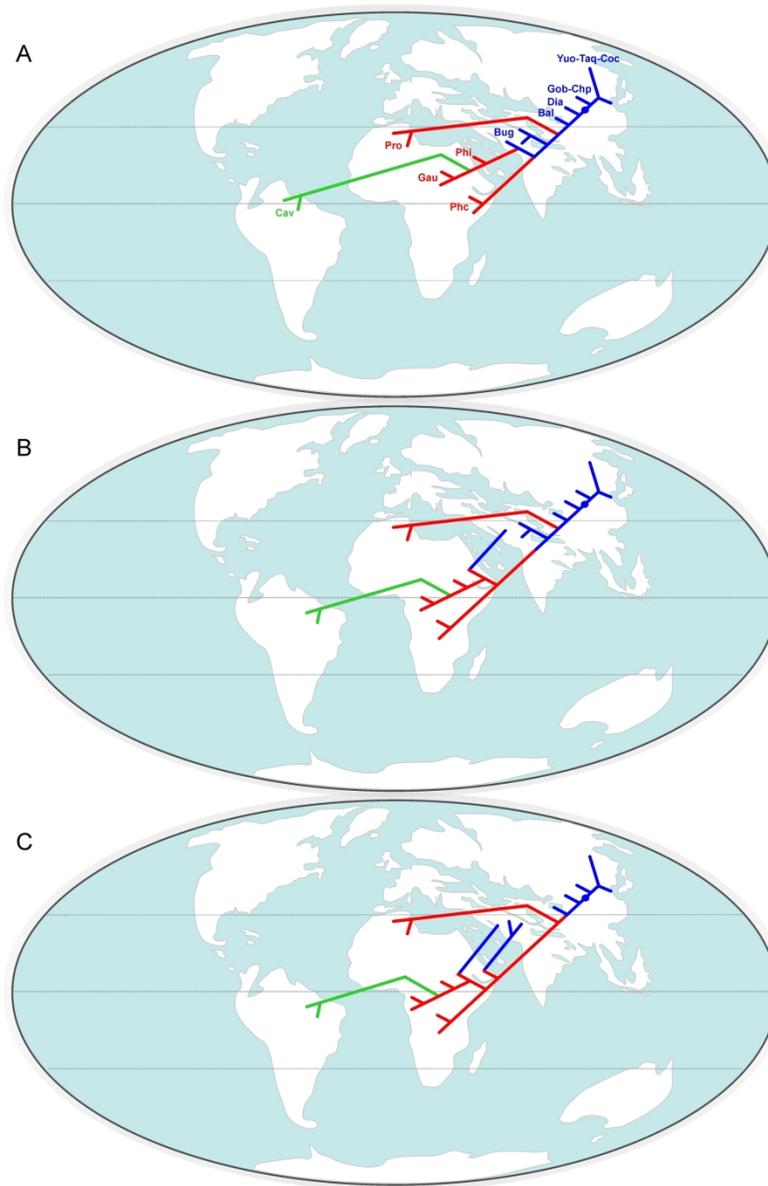


Figure 9. Tentative hypothetical scenarios of hystricognathous rodent dispersals between Asia, Africa and South America during the Eocene, based on the results of the cladistic analyses. The color-coded and highly simplified phylogenetic tree derives from the strict consensus topology of the parsimony analyses (Fig. 2), and it is superimposed on a simplified late middle Eocene global palaeogeographic reconstruction (simplified after a palaeogeographic map of R. Blakey). These three scenarios (A-C) illustrate the evolutionary and biogeographic patterns discussed in the text. The Asian clades are depicted in blue, the African ones are in red, and the South American ones are in green. A, African clades are patchy nested within the paraphyletic Asian radiation, implying then multiple (a least three) but unidirectional dispersals to Africa from Asia; B, African clades are patchy nested within the paraphyletic Asian radiation, implying in this case at least two colonisations of Africa from Asia, and one dispersal return event to Asia from Africa (considering here an African taxa colonizing Asia); C, African clades form a monophyletic group, nested within the paraphyletic Asian radiation, thereby implying only one dispersal event to Africa from Asia of the common ancestor of the African taxa. In this context, the Asian clades nested within the monophyletic African radiation indicate at least two dispersal return events to Asia of African taxa. For each scenario, we provide a color-coded non-

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3 simplified tree as Supplemental Material online (Appendix S8A-C). Bal, baluchimyines (-ids); Bug,
4 bugtomyids; Cav, stem caviomorphs; Chp, chapattomyids; Coc, cocomyids; Dia, dianomyids; Gau,
5 gaudeamurids; Gob, gobiomyids; Met, metaphiomyines (-ids); Phc, phiocricetomyines (-ids); Phi,
6 phiomyids; Pro, protophiomyines (-ids); Taq, tamquammyids; Yuo, yuomyids.

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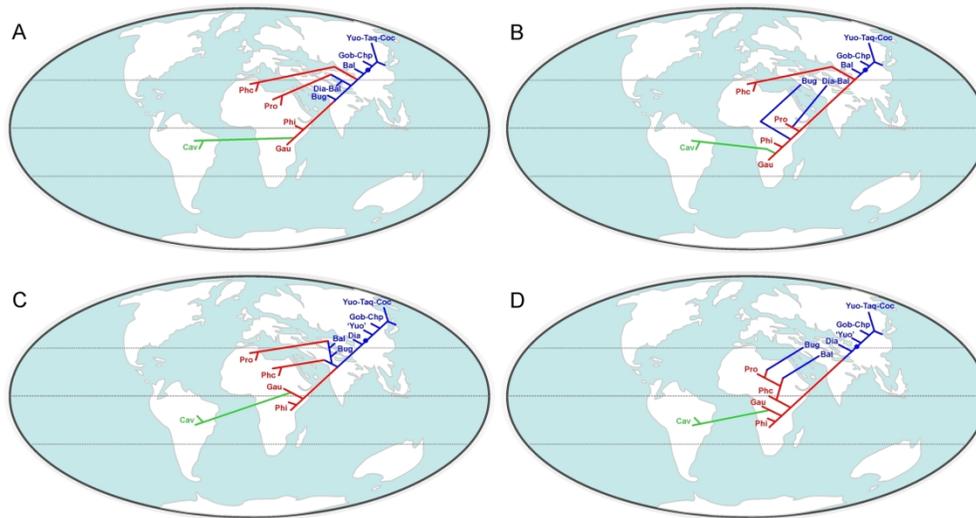


Figure 10. Tentative hypothetical scenarios of hystricognathous rodent dispersals between Asia, Africa and South America during the Eocene, based on the results of the Bayesian analyses (standard and tip-dating). The color-coded and highly simplified phylogenetic trees derive from the Allcompat consensus trees of the standard Bayesian (A-B; Fig. 3) and Bayesian tip-dating (C-D; Fig. 4) analyses, and they are superimposed on a simplified late middle Eocene global palaeogeographic reconstruction (simplified after a palaeogeographic map of R. Blakey). For each scenario, we provide a color-coded non-simplified tree as Supplemental Material online (Appendix S8D-G). A and C: African clades are patchy nested within the paraphyletic Asian radiation, implying then multiple (a least three) but unidirectional dispersals to Africa from Asia; B and D, African clades form a monophyletic group, nested within the paraphyletic Asian radiation, thereby implying only one dispersal event to Africa from Asia of the common ancestor of the African taxa (+ some Asian). In this context, the Asian clades nested within the monophyletic African radiation indicate at least two dispersal return events to Asia of African taxa. Bal, baluchimyines (-ids); Bug, bugtomyids; Cav, stem caviomorphs; Chp, chapattomyids; Coc, cocomyids; Dia, dianomyids; Gau, gaudeamurids; Gob, gobiomyids; Met, metaphomyines (-ids); Phc, phiocricetomyines (-ids); Phi, phiomyids; Pro, protophomyines (-ids); Taq, tamquammyids; Yuo, yuomyids.

198x105mm (300 x 300 DPI)