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EDITED BY

Chenyang Cai,
Nanjing Institute of Geology and Paleontology
(CAS), China

REVIEWED BY

Damien Becker,
JURASSICA Museum,
Switzerland
David Marjanović,
Museum of Natural History Berlin (MfN),
Germany

*CORRESPONDENCE

Deng Tao
✉ dengtao@ivpp.ac.cn

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Reconstructing the phylogeny of the hornless rhinoceros Aceratheriinae

Xiao-Kang Lu^{1,2}, Tao Deng^{3,4,5*} and Luca Pandolfi⁶

¹Human Anatomy and Histology Department, Henan University of Chinese Medicine, Zhengzhou, China, ²State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (CAS), Nanjing, China, ³Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (CAS), Beijing, China, ⁴CAS Center for Excellence in Life and Palaeoenvironment, Beijing, China, ⁵University of Chinese Academy of Sciences, Beijing, China, ⁶Dipartimento di Scienze della Terra, Università di Firenze, Firenze, Italy

This study presents the first phylogenetic analysis focused on the subfamily Aceratheriinae to date, with 392 characters (361 parsimony-informative characters) coded from 50 taxa at the species level. We added 80 newly defined and 33 revised characteristics to an existing matrix, covering features of the skull, teeth, and postcranial bones. Based on the results of ordered and unordered analyses, combined with a diagnosis in accordance with traditional morphological taxonomy, we revised the diagnosis of Aceratheriinae and reconstructed the phylogeny of Aceratheriinae. The tribe Teleoceratini, as well as the tribe Aceratheriini, was reclassified within Aceratheriinae; however, the traditionally established contents of each tribe were changed somewhat. Aceratheriinae underwent evolutionary adaptation several times during the early stages of its evolution, and several genera are herein reconstructed as early-diverging taxa, such as *Floridaceras*, *Chilotheridium*, and *Plesiaceratherium*. *Turkanatherium* and *Protaceratherium* are excluded from Aceratheriinae in this study. We suggest another two subclades of Aceratheriinae, containing *Hoploaceratherium* and *Aprotodon*, respectively. Aceratheriini and Teleoceratini are redefined as two highly specialized groups of Aceratheriinae.

KEYWORDS

Rhinocerotidae, Aceratheriinae, Aceratheriini, Teleoceratini, morphology, phylogeny

Introduction

Aceratheres are an extinct group of rhinocerotids widespread throughout Eurasia, North America, and Africa during the Neogene and characterized by the absence of nasal and/or frontal horns. The first hornless genus *Aceratherium*, from the Late Miocene, was recorded by Kaup (1832) in Eppelsheim, Germany. Based on this record, Dollo (1885) established the subfamily Aceratheriinae as a member of the family Rhinocerotidae, which has another two subfamilies, Rhinocerotinae and Elasmotheriinae (Prothero et al., 1989; Heissig, 1999; Antoine, 2002). Osborn (1900) recognized the subfamily Aceratheriinae and included some Oligocene and Miocene European species within it, giving the following diagnosis: “dolichocephalic with long, narrow nasals; smooth or with rudimentary horns at sides of the tips; frontals finally developing horns; large cutting teeth; relatively persistent tetradactyl manus; long-limbed” (Osborn, 1900, p. 240). Osborn (1900) included the following species within Aceratheriinae: “*Aceratherium*” *filholi*, “*A.*” *lemanense*, “*A.*” *platyodon*, “*A.*” *blanfordi*, “*A.*” *tetradactylum*, *A. incisivum*. Heissig (1973) included within Aceratheriinae the tribe Teleoceratini Hay, 1902,

which contains the brachypotheres *Teleoceras* Hatcher, 1894, *Brachypotherium* Roger, 1904, *Aprotodon* Forster-Cooper, 1915, *Diaceratherium* Dietrich, 1931, and the tribe Aceratherini Dollo, 1885, which includes the genera *Aceratherium* Kaup, 1832, *Plesiaceratherium* Young, 1935, *Chilotherium* Ringström, 1924, and *Aphelops* Cope, 1873. In 1989, Heissig included within Aceratherini the genera *Mesaceratherium* Heissig, 1969, *Alicornops* Ginsburg & Guérin, 1979, *Aceratherium* Kaup, 1832, *Plesiaceratherium* Young, 1935, *Hoploaceratherium* Ginsburg & Heissig, 1989, *Aphelops* Cope, 1873, *Peraceras* Cope, 1880, *Chilotheridium* Hooijer, 1971, *Turkanatherium* Deraniyagala, 1951, *Chilotherium* Ringström, 1924, *Subchilotherium* Heissig, 1972, and *Acerorhinus* Kretzoi, 1942.

In the many years since being established, over 90 species have been referred to Aceratheriinae. However, according to Prothero (2005), this taxon has been used as a taxonomic wastebasket for all hornless rhinoceroses. Not every hornless rhinoceros can be classified as Aceratheriinae, which is advanced and even includes rhinoceroses with a small nasal horn. Other features that characterize Aceratheriinae include a deep nasal notch, reduced upper incisor I1, considerably large lower incisor i2, brachycephalic skull, tetradactyl manus, and shortened and massive metapodials (Heissig, 1989; Cerdeño, 1995).

The content of Aceratheriinae has been in dispute for a long time. Pavlow (1892) united *Aphelops*, *Teleoceras*, and *Brachypotherium*, but assigned *Aceratherium* to the subfamily Rhinocerotinae. Scott and Osborn (1898) recognized the close relationship between *Peraceras* and *Aphelops*. Heissig (1973, 1999) was the first to include the tribe Teleoceratini in Aceratheriinae. Prothero et al. (1986) and Prothero et al. (1989) suggested that only the members of Aceratheriini could be recognized as Aceratheriinae; thus, the tribe Teleoceratini should be a member of Rhinocerotinae. Using 72 characters coded from 43 rhinocerotid taxa, Cerdeño (1995) found that Teleoceratini was more closely related to Aceratheriini than the other groups within Rhinocerotidae.

In order to explore the phylogeny of the elasmotheres, Antoine (2002) expanded the matrix to 282 characters. Deng (2008) used this matrix to discuss the taxonomic identity of new elasmotheres. However, this combination of characters could not resolve the phylogeny of the aceratheres (Antoine et al., 2003, 2010), despite the addition of several features by Lu (2013).

Aceratheriinae (Aceratheriini or Aceratheriina) represents a monophyletic group within the subfamily Rhinocerotinae according to Antoine (2002), Antoine et al. (2003, 2010), Becker et al. (2013). The aceratheres were classified as the subfamily Aceratheriinae by Prothero (2005) and also by Heissig (2012), who considered this group the sister to the Rhinocerotinae and Elasmotheriinae clade. The latest phylogenetic analysis of Rhinocerotidae found the traditional contents of Aceratheriinae, Rhinocerotinae, and Elasmotheriinae to form polyphyletic groups with confusing relationships (Lu et al., 2016).

This study aims to produce a new inclusive phylogenetic analysis of Aceratheriinae, for both taxa and characters, partly including previously defined characters. We also aim to reappraise the phylogenetic definition of Aceratheriinae and discuss the taxonomic positions of several genera. In order to provide a comprehensive suggestion, the following discussion is not only based on the results of the present cladistic analysis but also on the traditional ways of morphological comparison.

Materials and methods

The characters in the present matrix were mainly from the works by Antoine (2002) and Lu (2013). After an extensive examination of the morphology of the members of Rhinocerotidae, we added 80 newly defined characters, and revised 33 previously used characters, covering features of the skull, teeth, and postcranial bones. These were directly from the unpublished doctoral dissertation of one author (Lu, 2014). In total, 392 characters were used in this analysis, 93 characters of the skull, 168 of the teeth, and 131 of the postcranium (Supplementary materials 1, 2).

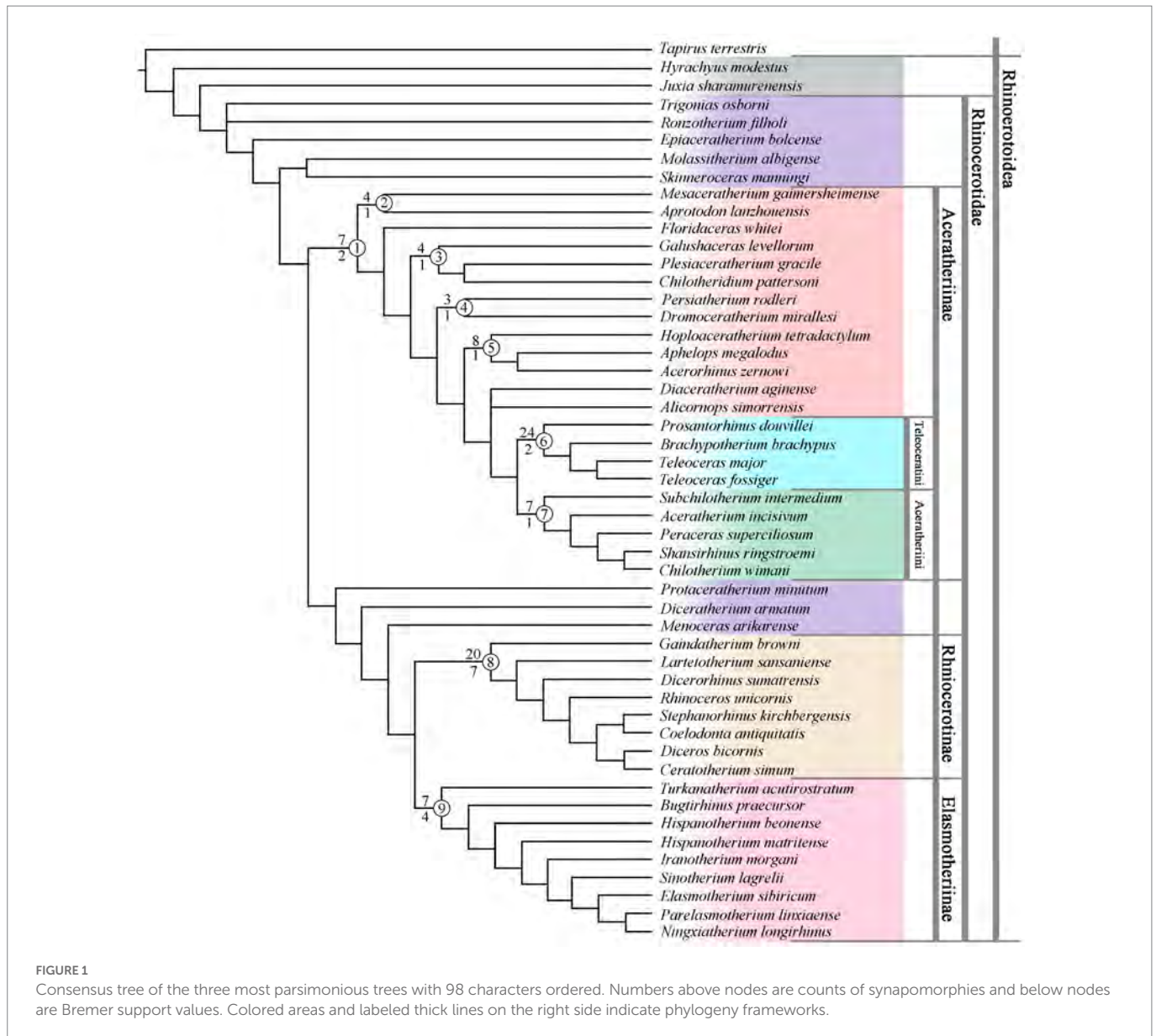
In this matrix, some characters were potentially continuous, such as the widening of the mandibular symphysis. As many authors have pointed out that such characters should be ordered (Slowinski, 1993; Wiens, 2001; Grand et al., 2013; Rineau et al., 2015, 2018; briefly reviewed in Marjanović and Laurin, 2019), we designed 98 characters as ordered: 6, 9, 14–16, 18, 35, 43–46, 50, 52–53, 58–61, 63, 69, 77, 79–80, 82, 84, 89, 91, 95–98, 108, 114–117, 119–120, 124–125, 127, 129, 133, 148, 153, 155–156, 161–162, 166–169, 171, 173–176, 184–187, 191, 196, 198, 211, 213–214, 216, 220–221, 223–227, 233–234, 253, 258, 260, 279, 293, 308, 312, 314, 318–319, 323, 331–332, 348, 357, 368, 370, 372–373, and 384. However, we also performed another analysis, treating all characters as unordered. Finally, we will present and discuss the results generated from these different assumptions.

Because there is no consensus on the phylogeny of Aceratheriinae, the present analysis incorporated all the genera once referred to as Aceratheriini and Teleoceratini, with 25 taxa, and other genera of rhinocerotoids, with 24 taxa, which provided a larger basis for reconstructing a reliable topology. The outgroup is *Tapirus terrestris*. All the taxa in this analysis were at the species level, represented mainly by the type species of each genus. *Teleoceras* is known for its graviportal limbs, but the relevant materials are at present not accessible for the type species *Teleoceras major*, so we further included the most characterized species, *Teleoceras fossiger*. The type species of *Aprotodon* is only known from a crushed skull and tooth fragments; thus, we chose the Chinese species *Aprotodon lanzhouensis*, the phylogenetically informative parts of whose body are well known, particularly the lower incisor i2. For the same reasons, we included two taxa of *Hispanotherium*. The character scoring relied on direct observation or data from the literature (Supplementary material 3).

The parsimony analyses were performed using TNT version 1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016), with 1,000 replicates, tree bisection-reconnection (TBR) branch swapping, and 100 trees saved per replicate. All characters were equally weighted. The Bremer support values were calculated in TNT by running a traditional search on the most parsimonious tree, with 1,000 replications and TBR branch swapping.

Results

We present the results generated by the ordered and unordered analyses, based on which we discuss the diagnosis and definition of Aceratheriinae in the following section. By ordering or not ordering certain characters in our dataset, we received two results with little difference. With all characters unordered, the maximum parsimony analysis resulted in one tree with 1,825 steps (CI=0.28, RI=0.51; Figure 1). When 98 characters were treated as ordered, with 361



parsimony-informative characters, three most parsimonious trees were generated, and the consensus tree had 2,018 steps (CI = 0.25, RI = 0.54; Figure 2). The Bremer support values were low for the clades of interest under both assumptions. This is likely due to the high proportion of missing data and homoplastic characters, which could increase the instability in the suboptimal trees, thereby causing the clades to collapse.

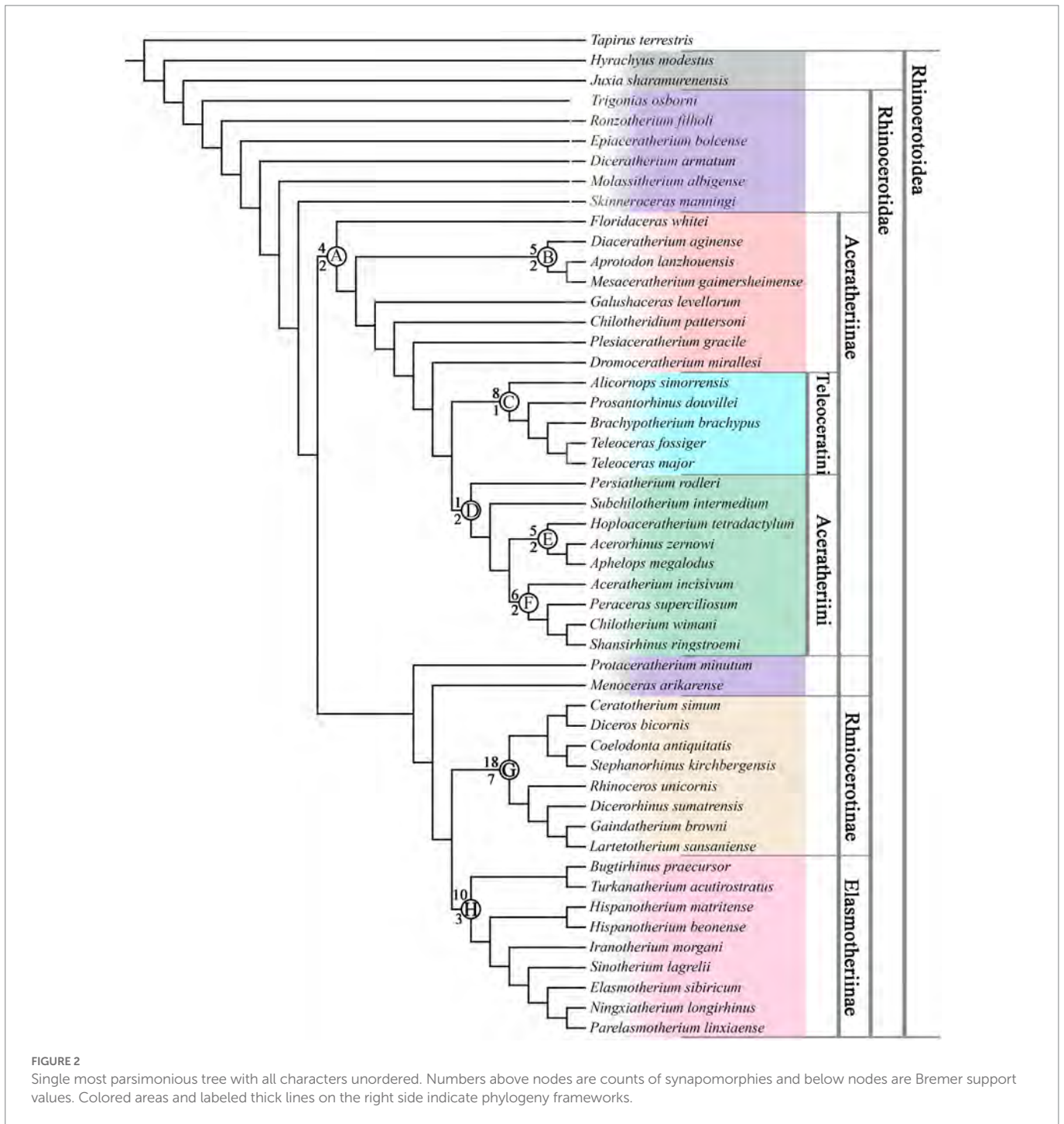
Both reconstructed trees were roughly consistent with the widely recognized contents of Rhinocerotinae (Figure 1, node 8, Char. 6¹⁻⁰, 15⁰⁻¹, 17⁰⁻¹, 67⁰⁻¹, 107⁰⁻¹, 123⁰⁻¹, 164³⁻⁰, 174¹⁻⁰, 196¹²⁻⁰, and 213³⁻²; Figure 2, node G, Char. 6⁰⁻², 15⁰⁻¹, 17⁰⁻¹, 61⁰⁻², 67⁰⁻¹, 124⁰⁻¹, 164³⁻⁰, 174¹⁻⁰, 196²⁻⁰, 240⁰⁻¹, 242⁰⁻¹, 265⁰⁻¹, 301¹⁻⁰, 308¹⁻², 330¹⁻², 331¹⁻², 380⁰⁻¹, and 388¹⁻⁰) and Elasmotheriinae (Figure 1, node 9, Char. 14¹⁻⁰, 38⁰⁻¹, 39⁰⁻¹, 42⁰⁻¹, 133¹⁻⁰, 148²⁻¹, and 153²⁻¹; Figure 2, node H, Char. 38⁰⁻¹, 39⁰⁻¹, 99¹⁻², 142²⁻³, 149⁰⁻¹, 153²⁻¹, 158²⁻³, 175⁰⁻³, 202⁰⁻², and 366⁰⁻¹; Cerdeño, 1995; Antoine, 2002; Antoine et al., 2010).

Nearly all taxa that were previously referred to as the tribe Aceratheriini or the tribe Teleoceratini were clustered as a large clade (Figure 1, node 1, Char. 31⁰⁻¹, 89⁰⁻¹, 107⁰⁻¹, 108⁰⁻¹, 175²⁻³, 176⁰⁻¹, and

201⁰⁻¹; Figure 2, node A, Char. 107⁰⁻¹, 109⁰⁻¹, 118⁰⁻¹, and 156⁰⁻¹). It was unexpected that *Protaceratherium* was excluded from the clade of Aceratheriinae. Furthermore, *Turkanatherium* was found to be a member of Elasmotheriinae, similar to the results by Geraads and Zouhri (2021).

However, the results of the present analysis did not fully support the previously suggested content of Aceratheriini in detail, and likewise for Teleoceratini (Heissig, 1989; Prothero and Schoch, 1989; Cerdeño, 1995). With 98 characters ordered, *Plesiaceratherium*, *Chilotheridium*, and *Galushaceras* were united as one group, supported by four synapomorphies (Figure 1, node 3, Char. 8⁰⁻¹, 16¹⁻², 68⁰⁻¹, and 77¹⁻⁰). *Dromoceratherium* and *Persiatherium* were an independent pair of sister groups (Figure 1, node 4, 149⁰⁻¹, 154¹⁻², and 168⁰⁻²).

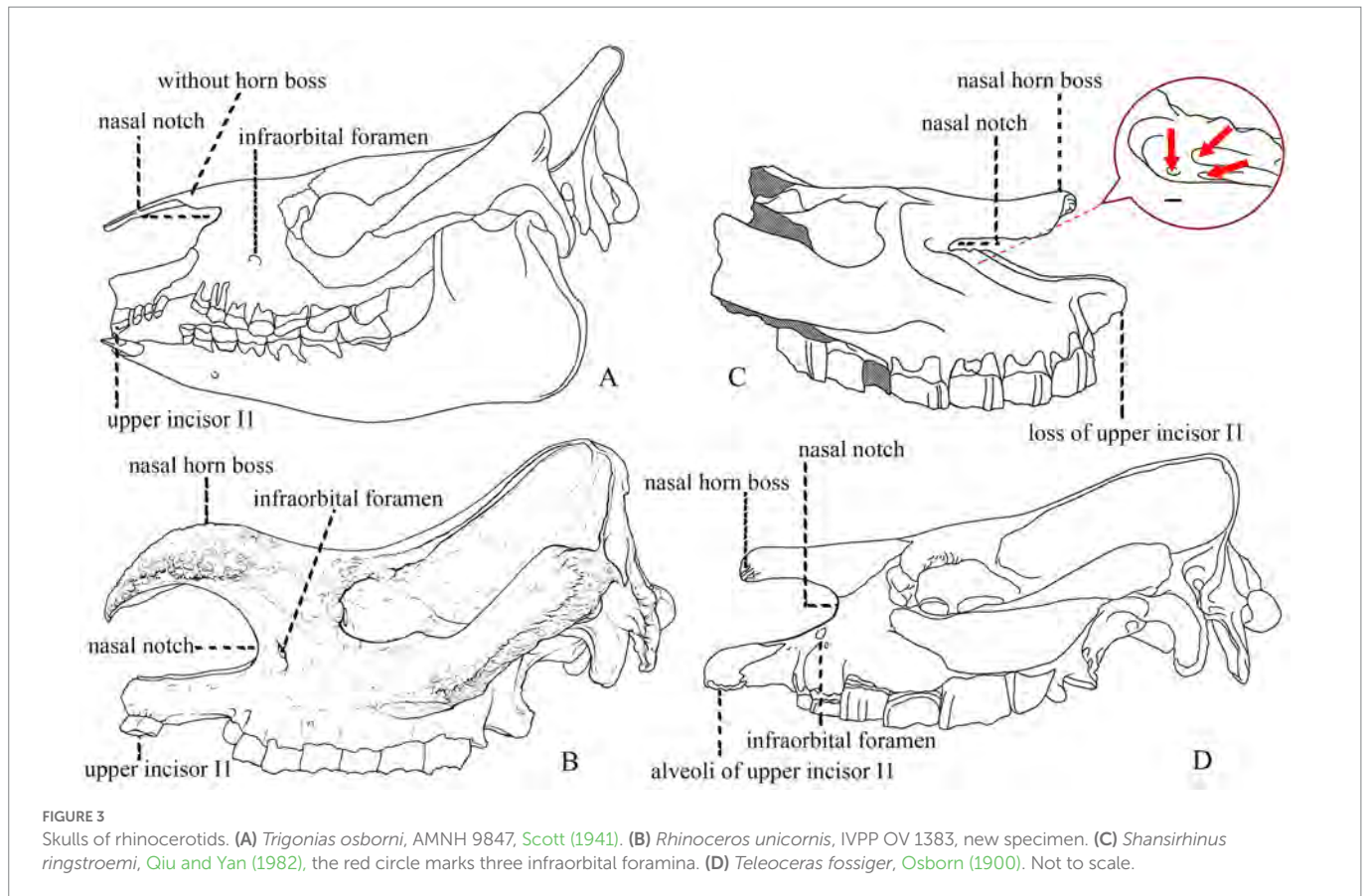
On the other hand, when all characters were unordered, the content of Aceratheriinae was slightly different from above. *Floridaceras*, *Galushaceras*, *Chilotheridium*, *Plesiaceratherium*, and *Dromoceratherium* were placed as early diverged single-genus clades in Aceratheriinae. There was a clade clustering *Diaceratherium*, *Mesaceratherium*, and *Aprotodon*, consistent with their mosaic characters: less advanced upper



premolars, greatly specialized incisors (I1 and i2), and symphysis (Deng, 2013; Figure 2, node B, Char. 32¹⁻⁰, 59⁰⁻¹, 98¹⁻², 156¹⁻³, and 217⁰⁻¹). In the alternative result, only *Mesaceratherium* and *Aprotodon* were clustered, supported by similarities such as the incisors (Figure 1, node 2, Char. 80¹⁻², 82⁰⁻¹, 108¹⁻², and 223⁰⁻¹).

Two subclades were slightly different in the two trees (Figures 1, 2). Five genera previously referred to as Aceratheriini, namely *Aceratherium*, *Peraceras*, *Chilotherium*, *Shansirhinus*, and *Subchilotherium*, were clustered as a clade among the most advanced group of Aceratheriinae (Figure 1, node 7, Char. 3⁰⁻¹, 25⁰⁻¹, 96⁰⁻¹, 110⁰⁻¹, 119⁰⁻¹, 259⁰⁻¹, and 361⁰⁻¹). However, with all characters unordered, *Subchilotherium* was placed as a single-genus clade and the first four genera were united (Figure 2, node

F, Char. 56⁰⁻¹, 61⁰⁻¹, 69¹⁻², 161⁰⁻³, 341⁰⁻¹, and 347¹⁻⁰). Under this assumption, three genera, *Brachypotherium*, *Prosantorhinus*, and *Teleoceras*, were retained within Teleoceratini. *Alicornops*, which has long been referred to as Aceratheriini (Prothero et al., 1986; Cerdeño, 1995), was placed as a sister group to the clade merging these three genera of Teleoceratini (Figure 2, node C, Char. 83⁰⁻¹, 155²⁻¹, 213¹⁻², 315¹⁻⁰, 348⁰⁻¹, 357¹⁻², 361¹⁻⁰, and 391¹⁻⁰). On the other hand, with 98 characters ordered, these three genera were also united (Figure 1, node 6, 5¹⁻³, 8⁰⁻¹, 43¹⁻², 68⁰⁻¹, 99¹⁻⁰, 117⁰⁻¹, 124⁰⁻¹, 167¹⁻⁰, 206⁰⁻¹, 258⁰⁻¹, 279¹⁻², 293⁰⁻², 296⁰⁻¹, 300⁰⁻¹, 301¹⁻⁰, 329⁰⁻¹, 330¹⁻², 331²⁻³, 334⁰⁻¹, 357¹⁻², 364⁰⁻¹, 369⁰⁻¹, 389⁰⁻¹, and 392⁰⁻¹), and *Alicornops* was present as a sister group of this clade.



There was one stable subclade with three genera in the results of both analyses, *Hoploaceratherium*, *Aphelops*, and *Acerorhinus* (Figure 1, node 5, Char. 3⁰⁻¹, 25⁰⁻¹, 96⁰⁻¹, 122⁰⁻¹, 184⁰⁻¹, 213²⁻³, and 294⁰⁻¹; Figure 2, node E, Char. 34¹⁻⁰, 122⁰⁻¹, 127²⁻¹, 299¹⁻⁰, and 361¹⁻⁰). With all characters unordered, this subclade was united with the subclade of *Aceratherium*, forming a pair of sister groups. Two single-genus clades, namely *Persiaceratherium* and *Subchilotherium*, showed a close relationship with them (Figure 2, node D, Char. 161¹⁻⁰).

Discussion

Diagnosis of Aceratheriinae

Our phylogenetic analyses provide characters supporting the Aceratheriinae node; those would be used as diagnostic features, but there are only four or seven characters, far from enough to provide a distinct outline of aceratheres. On the other hand, some features that have long been considered as diagnostic of Aceratheriini or Teleoceratini were not found as synapomorphies, such as features concerning the tusk i2, the brachycephalic skull, and the graviportal limbs. These features demonstrate a series of gradually changing tendencies and should be considered when reamending the diagnosis.

The clear starting point when studying the characteristics of hornless rhinoceroses is the horn. A small horn and the enlarged upper incisors I1 were two crucial characteristics that Prothero et al. (1986) used to include Teleoceratini in Rhinocerotinae rather than Aceratheriinae. However, among members once classified as Aceratheriini, at least four genera developed a small nasal horn, namely

Chilotheridium, *Hoploaceratherium*, *Peraceras*, and *Shansirhinus*. In Teleoceratini, the presence of a nasal horn has interspecific variation in *Diaceratherium* and *Brachypotherium* (Répelin, 1917; Heissig, 1999, 2017; Figure 3). Nasal horns developed in different lineages of rhinocerotids several times.

Another notable structure lies in the rostral end of the skull and involves two aspects, namely the retracted nasal notch and the specialized incisors, both of which are closely related to feeding behavior (Prothero et al., 1986; Heissig, 1989, 1999; Cerdeño, 1995). The enlarged lower incisor (i2) is a typical feature differentiating rhinocerotids from other rhinocerotoids and was maximized in the evolution of Aceratheriini and Teleoceratini, exemplified by *Aceratherium*, *Chilotherium*, and *Teleoceras* (Ringström, 1924; Deng, 2001; Prothero, 2005; Figure 3). However, adaptations of the upper incisor I1 diverged in the two tribes; most taxa retained the upper incisor I1 (Figure 2, node B, Char. 98), while in the advanced members, I1 was lost (Figure 1, node 5 and 7, Char. 96), and the enlarged lower incisor i2 subsequently lost the occlusal surface on the internal edge and developed a labially upturning occlusal surface (Figure 1, node 1, Char. 107; Figure 2, node A, Char. 107, 109), such as in *Chilotherium* (Deng, 2001; Lu, 2013; Figure 4).

Another feature in the rostral area is the retracted nasal notch, even to the level of M1, which evolved gradually and occurred in nearly all rhinocerotids (Prothero et al., 1986; Heissig, 1989; Cerdeño, 1995; Antoine, 2002; Prothero, 2005). Its consistent appearance in the members of Aceratheriini and Teleoceratini could be evaluated by its position relative to the infraorbital foramen: the position of the infraorbital foramen moved from the posterior to the nasal notch to below it. In the primitive rhinocerotids from the Eocene *Hyrachyus* and

Trigonias to the extant *Rhinoceros*, the nasal notch is shallow, and the infraorbital foramen is behind the notch and above the level of P2–P4 (Gregory and Cook, 1928; Prothero, 2005). However, in the Oligocene *Aprotodon*, the nasal notch was moderately retracted, at P3, and the infraorbital foramen moved to below its posterior end. By the Late Miocene, this foramen had increased to three openings in *Shansirhinus* and *Teleoceras* but remained below the ventral edge of the nasal notch (Figure 3; Qiu and Yan, 1982; Qiu and Xie, 1997; Deng, 2005; Prothero, 2005; Lihoreau et al., 2009).

The broadening and shortening tendencies of the skull occurred exclusively in Aceratheriini and Teleoceratini and have important systematic value (Heissig, 1989; Cerdeño, 1995). However, both are gradually changing characteristics, with a long history of evolution; their maximum degree only occurred in very advanced taxa. Based on the maximum length/maximum width ratio, several genera had a brachycephalic skull, namely *Peraceras*, *Teleoceras*, *Brachypotherium*, and *Prosantorhinus* (Prothero, 2005; Heissig, 2017). In this analysis, the skull outline was found to be one of the synapomorphies uniting Teleoceratini (Figure 1, node 6, Char. 43). The graviportal limbs were exemplified in several aspects, and we have added new features to discern, such as the length ratio between the dorsal and lateral sides of the magnum (Char. 312), the length/width ratio of the third metacarpal (Char. 330, 331), and the outline of the unciform (Char. 317; Figure 5). The brachycephalic skull, accompanied by graviportal limb, occurred in *Peraceras*, *Teleoceras*, and *Prosantorhinus* (Figure 1, node 6, Char. 330, 331, 357; Prothero, 2005; Heissig, 2017). Both characters are related to a short and massive body and are notable aspects of the appearance of Aceratheriini and Teleoceratini.

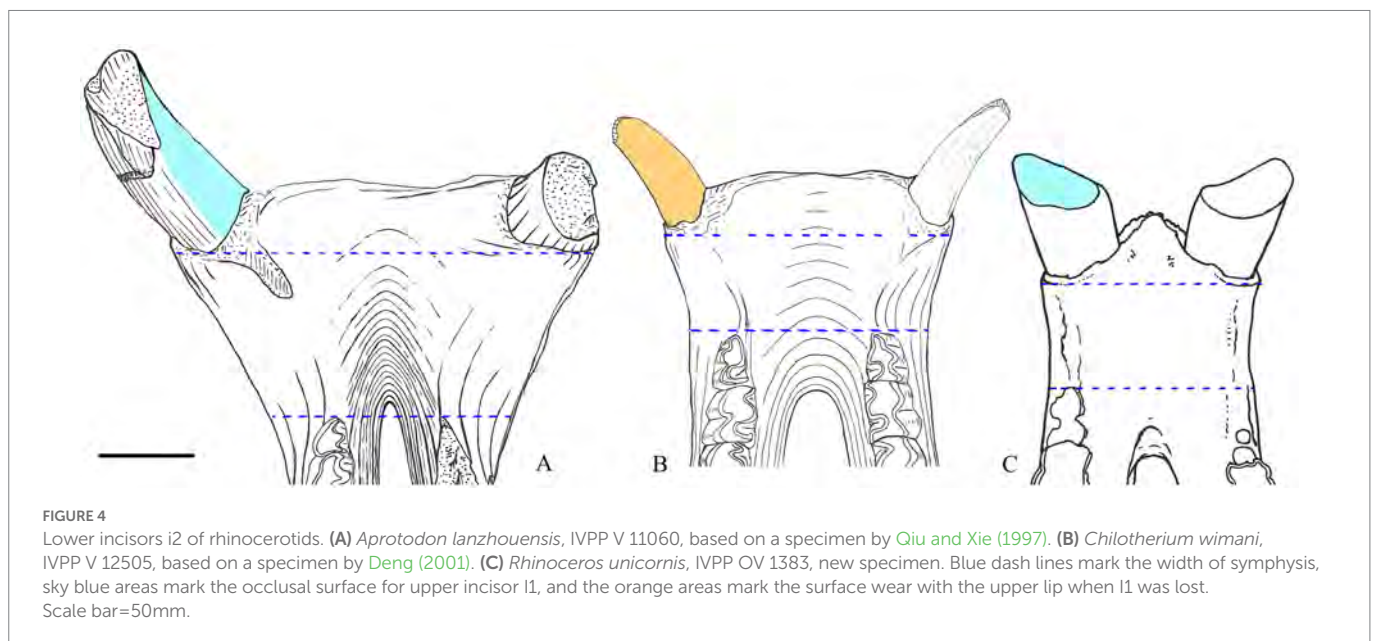
In addition to the graviportal tendency of the limbs, Aceratheriini and Teleoceratini demonstrate another diagnostic character regarding the postcranial bones: the primitive members maintained a functional fifth metacarpal (Heissig, 1989, 1999; Prothero, 2005). The functional fifth metacarpal was inherited from the primitive ancestor of the Rhinocerotidae, and has been reduced to a small sesamoid-like bone in the advanced members of Aceratheriini and Teleoceratini (Figure 1, node 6, Char. 334; Figure 4; Ringström, 1924; Deng, 2002).

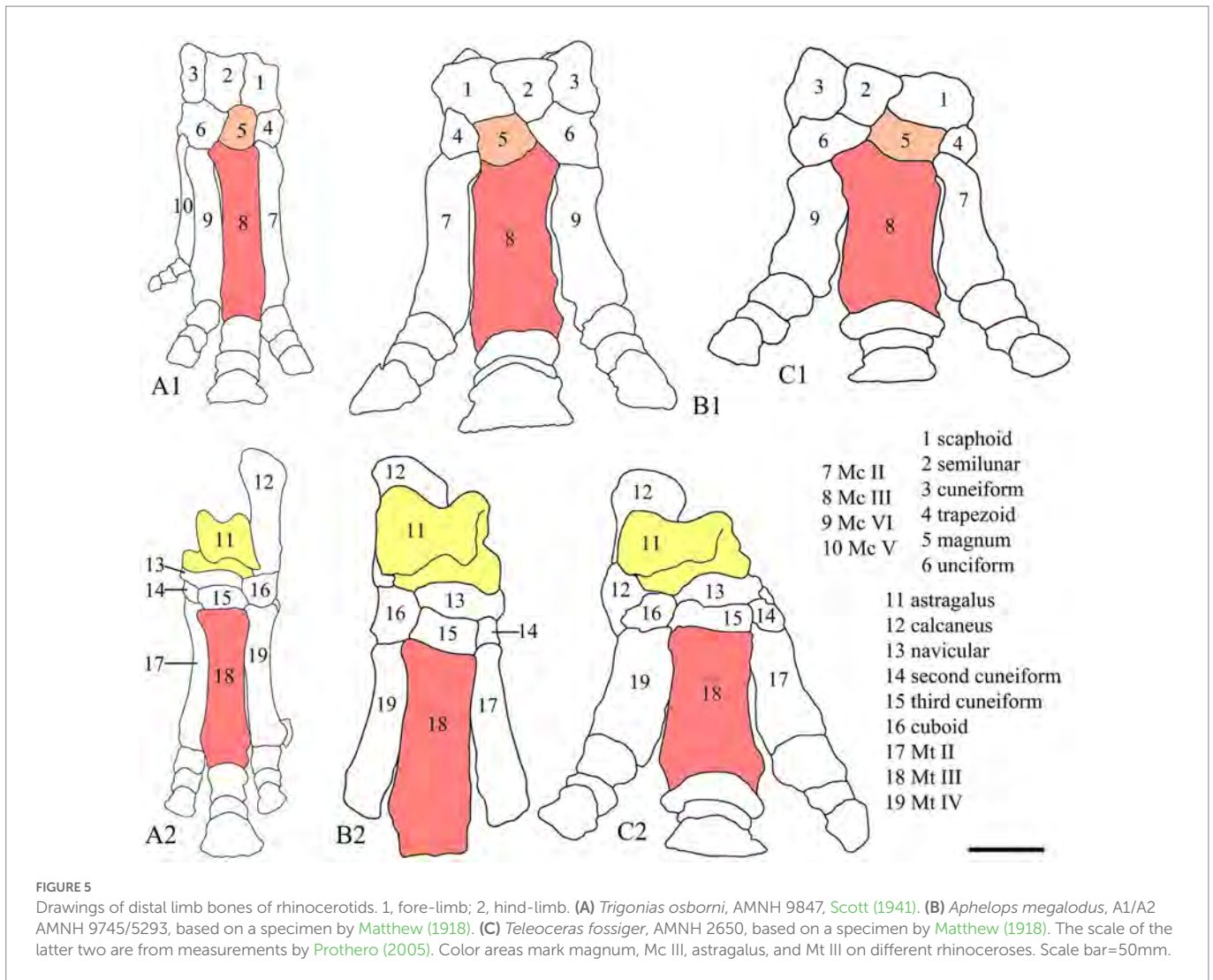
Traditionally, cheek teeth are an important diagnosis of Aceratheriini or Teleoceratini: deep constriction of both lingual cusps of the upper cheek teeth (Figure 1, node 1, Char. 175; Figure 2, node A, Char. 156) with a maximum degree that is just slightly weaker than that of elasmotheres; and the continuous lingual cingulum of the upper premolars, which was inherited from a primitive ancestor (Heissig, 1989, 1999; Figure 5). The former could complicate the occlusal pattern of the cheek teeth, and the latter would reinforce the lingual enamel wall of significantly worn teeth. Both features are quite useful for determining the taxonomic identity of fossil material of aceratheres.

Phylogeny of Aceratheriinae

The present two analyses found that Aceratheriini and Teleoceratini were closely related and united as Aceratheriinae, consistent with the results of Heissig (1989, 1999) and Cerdeño (1995). Here, we used the node-based definition of Aceratheriinae as the last common ancestor of *Aceratherium*, *Teleoceras*, and *Aprotodon* and all of its descendants. On the other hand, Elasmotheriinae and Rhinocerotinae showed a closer relationship relative to Aceratheriinae. This result is partly consistent with Cerdeño's work (1995), in which Aceratheriinae formed a clade, and Elasmotheriinae and Rhinocerotinae were united but each did not form their monophyly, respectively. Antoine and his colleagues established the subfamily Elasmotheriinae but placed aceratheres and rhinoceroses together as a paraphyletic group (Antoine, 2002; Antoine et al., 2003, 2010). In this study, Elasmotheriinae and Rhinocerotinae were united as sister groups, supported by many characters (Supplementary material 4). These synapomorphies revealed that, compared to aceratheres, elasmotheres and rhinoceroses were more advanced in their skull, particularly the large nasal and frontal horns, and in their cheek teeth, such as the hypsodont crown of elasmotheres and the much higher crown, widened crest, and strong ectoloph (mesostyle and metacone rib) of rhinoceroses, but less advanced in their limb bones, preserving the tetradactyl manus and slender or strong limb.

Among the 25 taxa previously referred to as Aceratheriinae, *Turkanatherium* was excluded from this group and recovered as





Elasmotheriinae. Deraniyagala (1951) described and established *Turkanatherium* based on materials from the middle Miocene of Moruorot, Kenya, while, Arambourg (1959) and Hooijer (1966) referred to this taxon as *Aceratherium* without further discussion. However, Geraads (2010) re-identified it as *Turkanatherium* based on the differences between *Turkanatherium acutirostratum* and *Aceratherium incisivum*, and attributed it to the subtribe Aceratheriina. The position of *T. acutirostratum* was recently reported within Elasmotheriinae by Geraads et al. (2016), who, however, suggested that their results should be interpreted cautiously. Furthermore, four features of this genus differed from Aceratheriinae; the nasal notch was shallow at the level of P2, and the infraorbital foramen was behind the nasal notch; the upper premolars had a metacone rib on the ectoloph and had lost the lingual cingulum. *Turkanatherium* maintained a notably primitive structure of the upper premolars; the metaloph had yet to be fully formed. Evidently, *Turkanatherium* was not an acerathere, so we tentatively followed the result of the analysis and assigned it as a basal elasmothere.

Protaceratherium was represented only by the type species *P. minutum*, found in the early Miocene of Western Europe, and had long been considered a member of Aceratheriinae (Cerdeño, 1995; Heissig, 1999). This genus had a pair of enlarged lower incisors i2, long and narrow nasal bones, and primitive cheek teeth Roman, 1912.

Antoine (2002) and Becker et al. (2013) have suggested that it was close to the group of Aceratheriinae and Rhinocerotinae. In this analysis, its position was within Rhinocerotinae.

Teleoceratini: This tribe was established based on the genus *Teleoceras* from the Late Miocene in North America, previously with five widely recognized genera, *Aprotodon*, *Diaceratherium*, *Brachypotherium*, *Teleoceras*, and *Prosantorhinus* (Heissig, 1989, 1999; Prothero and Schoch, 1989; Prothero, 2005). However, the present analysis, which sampled all genera of Aceratheriini and Teleoceratini, questioned previous taxonomic opinions and reconstructed a different clade that included *Brachypotherium*, *Teleoceras*, and *Prosantorhinus*, but excluded *Aprotodon* and *Diaceratherium*; both the latter, together with *Mesaceratherium*, were recovered as an early-diverging clade of Aceratheriinae.

Aprotodon from the late Oligocene in Asia has long been recognized as an early member of Teleoceratini: the skull has a slender outline, the parietal crests fuse and form the sagittal crest, and the upper premolar has yet to be fully molarized (Forster-Cooper, 1915; Borissiak, 1954). In Cerdeño's (1995) analysis, it was recovered as the most basal Rhinocerotinae. The description of the new materials of *Aprotodon* from China, Qiu and Xie (1997) likewise suggested it should be an early-diverging lineage of Rhinocerotidae. *Mesaceratherium* from the late Oligocene of Eurasia has long been

considered the earliest genus of Aceratheriini, with less molarized premolars (Heissig, 1969). Antoine et al. (2010) placed it as a *sensu lato* acerathere, and in the newest paper this genus and some other Paleogene rhinoceroses were placed as an early clade of Rhinocerotinae (Tissier et al., 2020). Given its enlarged upper and lower incisors, like *Aprotodon*, we suggested *Mesaceratherium* should be an acerathere, consistent with the present analyses.

Diaceratherium from the late Oligocene to the early Miocene was widely distributed around the old world (Heissig, 1999; Becker et al., 2009; Lu et al., 2021). It was a large-sized rhinoceros, with a small nasal horn, dolichocephalic skull, large upper and lower incisors, and long and robust distal limb bones (Lu et al., 2021). This genus has long been considered an early ancestor of some advanced teleoceratini genera. Sizov et al. (2022) tried to classify all species of *Diaceratherium* except the type species to *Brachydiceratherium*, indicating a complicated relationship of this genus, and put *D. tomerdingense* in the basal position of Teleoceratini. Together with the discussion of the relationship between *Diaceratherium* and *Prosantorhinus* by Heissig (2017), the taxonomic and phylogenetic relationships are debatable and complex. The present analyses suggested that *Diaceratherium* was a single-genus clade of Aceratheriinae, with the position unstable. Consequently, meanwhile, the diagnosis of Teleoceratini no longer primarily depended on features of the nasal horn and the upper incisors; the skull outline and metapodial proportions were more significant, as discussed in the above section.

Alicornops has long been referred to as Aceratheriini (Prothero et al., 1986; Cerdeño, 1995). This genus from the middle Miocene was a moderately specialized genus, with a medium-sized skull and moderately specialized cheek teeth (Cerdeño and Sánchez, 2000; Deng, 2004). Heissig (1999, 2012) once considered *Alicornops* a subgenus of *Aceratherium*. This referral is confusing because the latter had lost the upper incisors I1 and its limb bones were slender. In addition to the synapomorphies at node C, *Alicornops* showed a robust distal limb bone, similar to that of Teleoceratini. The lateral and medial sides of the diaphysis of the third metacarpal were irregular, so the width of the diaphysis was similar from the proximal to distal portions—there was no narrowest position. *Alicornops* was distinct from *Aceratherium* and *Chilotherium*, because, in the latter two, the narrowest position of the diaphysis was at the proximal extremity (Hünemann, 1989; Cerdeño and Sánchez, 2000; Deng, 2002). The outlines of the astragalus in *Alicornops* were more flattened than *Chilotherium*, which was the most advanced member of Aceratheriini (Ringström, 1924; Deng, 2002). We tentatively consider *Alicornops* a single-genus clade with an unstable phylogenetic position.

Aceratheriini: The results of the present analyses do not support the previously established contents of Aceratheriini and Aceratheriinae (Heissig, 1989; Prothero and Schoch, 1989; Cerdeño, 1995). *Turkanatherium* and *Mesaceratherium* have been mentioned above. Three subclades were consistently reconstructed in both trees, but two were unstable (Figures 1, 2).

In the clade of *Hoploaceratherium*, *Acerorhinus*, and *Aphelops* (Figure 1, node 5; Figure 2, node E), the relationship between the former two has been noted in previous studies because of their longer nasal bones (Heissig, 1989). Additionally, among the synapomorphies supporting this clade, the most significant was a uniquely derived feature, the expansion of the lingual cusps of the upper cheek teeth (Char. 122). The constriction of the lingual cusps was an efficient way to complicate the occlusal pattern of the cheek teeth and was present

in nearly all lineages of rhinocerotids, excluding the members of Rhinocerotini that expanded the lingual cusps while losing the constriction. The combination of both characters in *Acerorhinus* was first noted by Deng (2000): the expanded and rounded lingual cusps in the upper cheek teeth and the shallow constriction in the upper molars; however, the antecrochet remains present, although with a narrow outline (Figure 6). This synapomorphy, found only in these three genera, powerfully demonstrates a closer evolutionary relationship.

Another subclade of Aceratheriinae clustered five Late Miocene genera: *Subchilotherium*, *Aceratherium*, *Peraceras*, *Chilotherium*, and *Shansirhinus* (Figure 1, node 7). The most obvious synapomorphy of these five genera was related to the specialization of the rostral end of the skull: the premaxillae were slender, the upper incisor I1 were fully reduced, and the occlusal face of i2 directed outward. Furthermore, when all characters were unordered, and consequently *Subchilotherium* was excluded from this clade, the most obvious feature shared by these four genera related to the skull outline: the occipital crest was wide (Char. 56), and the parietal crest was not fused (Char. 61).

Persiatherium from Maraghen, Iran, was exemplified by a crushed skull with the cheek tooth row. For this rhinoceros from the Late Miocene, the most outstanding feature was the presence of the lingual cingulum on the upper molars. Reduction of the cingulum was a common tendency widely occurring among contents of rhinocerotids since the Oligocene (Heissig, 1989). *Dromoceratherium* had limited materials, consisting of fragments of upper and lower teeth, and limbs (Deraniyagala, 1951). As for now, no exclusive similarity was found between these two genera, and we did not expect them to form a clade.

Chilotheridium from the early Miocene in Africa was also an early-diverging genus, which is consistent with its mosaic morphology: dolichocephalic skull, slender limb bones, complicated cheek teeth, and a horned nasal bone at the subterminal position (Hooijer, 1971; Geraads, 2010). *Plesiaceratherium* was a well-known acerathere from the early Miocene of China, and its differences from *Chilotheridium* are many, such as the nasal horn (Yan and Heissig, 1986; Lu et al., 2016). It was also true for *Galushaceras*. This subclade and the subclade of *Persiatherium* and *Dromoceratherium* were not consistently present in the two analyses using different assumptions; their relationships were unstable and reconstructed as single-genus clades (Figures 1, 2).

When discussing the phylogeny of Aceratheriinae, Heissig (1973, 1989), Prothero et al. (1986), and Cerdeño (1995) did not distinguish its content from that of the tribe Aceratheriini. It is not reasonable and possible to perfectly refer each taxon of Aceratheriinae to either Aceratheriini or Teleoceratini. Here, some taxa were tentatively recovered as a set of single-genus clades. With 98 characters ordered, the subclade of *Hoploaceratherium* was placed outside Aceratheriini, indicating the possibility of a new tribe, as well as a subclade of *Aprotodon*. Tribes Aceratheriini and Teleoceratini were restricted to include taxa that were more specialized compared to a set of basal clades.

Conclusion

1. According to the results of the phylogenetic analyses of the newly established matrix, Aceratheriinae is defined as the last common ancestor of *Aceratherium*, *Teleoceras*, and *Aprotodon* and all of its descendants (node-based).

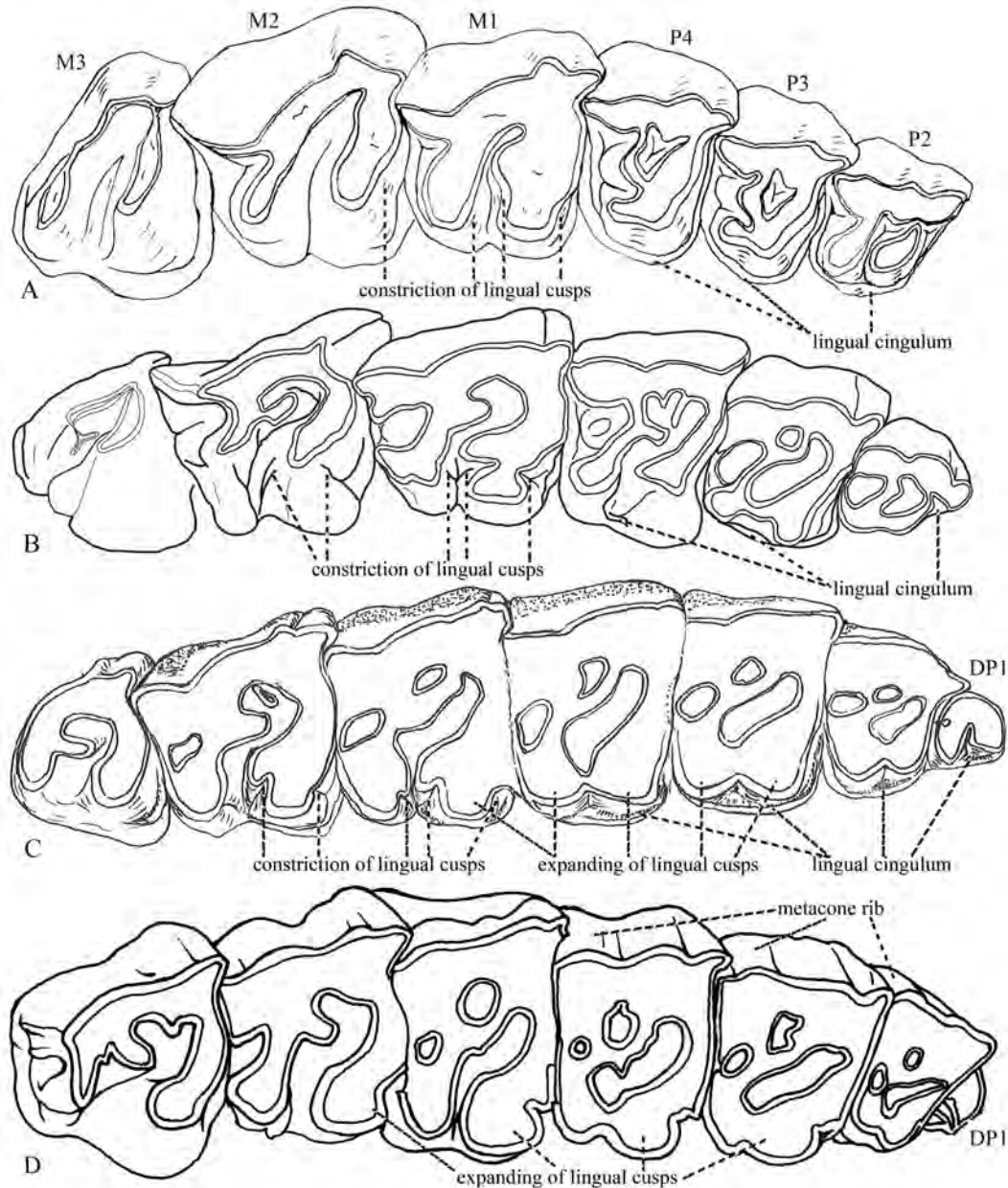


FIGURE 6

Upper cheek teeth of rhinocerotids. (A) *Trigonias osborni*, DMNH 414, based on a specimen by Gregory and Cook (1928). (B) *Teleoceras fossiger*, Osborn (1904), Figure 21. (C) *Acerorhinus hezhengensis*, HMV 0639, new specimen. (D) *Rhinoceros unicornis*, IVPP OV 1383, new specimen. Not to scale.

- The diagnosis of Aceratheriinae is revised as follows. It was of medium-large size, tended to evolve a brachycephalic skull, and the presence of a nasal horn varied. It had a deep nasal notch, to the level of P3–M1, with an infraorbital foramen below the nasal notch. It exhibited an enlarged or lost upper incisor I1, the lower incisor i2 was tusk-like, even extremely enlarged. It had moderately specialized cheek teeth: the labial cingula of the upper and lower cheek teeth were reduced with residuals, but the lingual cingulum of the upper premolars was always unreduced; the lingual cusps of the upper cheek teeth could be constricted, or sometimes also expanded. It had a functional fifth metacarpal and the limbs had a tendency toward graviportality, their distal parts were always massive and flattened.
- Aceratheriini and Teleoceratini are sister-groups. Teleoceratini includes *Prosantorhinus*, *Brachypotherium*, and *Teleoceras*. Aceratheriini includes *Subchilotherium*, *Aceratherium*, *Peraceras*, *Chilotherium*, and *Shansirhinus*. On the other hand, *Floridaceras*, *Plesiaceratherium*, *Chilotheridium*, *Galushaceras*, *Dromoceratherium*, *Persiaceratherium*, *Diaceratherium*, and *Alicornops* are tentatively considered single-genus clades.
- In addition, we suggest another two subclades of Aceratheriinae. One consists of two genera from the late Oligocene to the early Miocene, *Aprotodon* and *Mesaceratherium*. Another unites three genera from the middle to Late Miocene, *Hoploaceratherium*, *Acerorhinus*, and *Aphelops*.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

Ethics statement

Ethical review and approval was not required for the animal study because there has no animal experiment.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1005126/full#supplementary-material>

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