

Reassessment of *Trilophodon connexus* Hopwood, 1935 and attributing it to the Choerolophodontidae (Postprint)

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Abstract

Trilophodon connexus Hopwood, 1935 has long been considered a representative species of the Chinese genus *Gomphotherium*. However, due to the unknown morphology of its mandibular symphysis and lower incisors, this attribution remains questionable. A mandible previously assigned to *Gomphotherium* cf. *G. shensiensis* from the Halamagai Formation in the Wulungu River area on the northern margin of the Junggar Basin, Xinjiang, was restudied. This mandible exhibits an elongated, deeply grooved symphysis and lacks lower incisors, thus confirming its attribution to the family Choerolophodontidae. Furthermore, comparison of the holotype of *Trilophodon connexus* with this specimen reveals complete consistency in key features of the cheek teeth, including: highly bunodont morphology, elongated m3 with four lophs, weakly developed “chevron” pattern on the second loph of upper and lower cheek teeth, non-fusion of the mesoconelet and precentral conule on the second loph, and weakly developed or absent enamel folding, accessory denticles in the valleys, and cementum. Therefore, *Trilophodon connexus* is in fact a choerolophodont rather than a gomphothere. In summary, it is tentatively reassigned as “Choerolophodon” *connexus* (Hopwood, 1935). Additionally, these features are relatively similar to those of the North American *Gnathabelodon thorpei*. Moreover, in both *Gnathabelodon* and “Choerolophodon” *connexus*, the typical Choerolophodon features such as a “chevron” pattern on the second loph of cheek teeth, strong enamel folding, accessory denticles in the valleys, and well-developed cementum are weak or absent, while the number of m3 lophs increases, suggesting that *Gnathabelodon* may have originated from the East Asian “Choerolophodon” *connexus*.

Full Text

Preamble

Reassessment of *Trilophodon connexus* Hopwood, 1935 and attributing it to the Choerolophodontidae

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Abstract

Trilophodon connexus Hopwood, 1935 has long been considered a typical species of Gomphotherium in China. However, due to the unknown state of the mandibular symphysis and tusks, there is no definite evidence to assign “*T. connexus*” to Gomphotherium. Here we describe and reevaluate a hemimandible from the Halamagai Formation, Ulungur region, northern Junggar Basin, which was previously identified as Gomphotherium cf. *G. shensiensis*. The mandibular symphysis is deeply troughed and lacks mandibular tusks; therefore, it undoubtedly belongs to the Choerolophodontidae. Further comparison revealed that the cheek tooth morphology is identical to that of the type specimen of *Trilophodon connexus*. The characteristic features include high bunodonty, elongation of the m3 with four lophids, an only weakly chevroned lophid 2, enlargement of the posterior pretrite central conule 2, unfused state of the pretrite mesoconelet 2 (if present) and anterior pretrite central conule 2, as well as the absence of ptychodonty, choerodonty, and cementodonty. Therefore, *T. connexus* Hopwood, 1935 is a choerolophodontid rather than a species of Gomphotherium. Based on the above features, we provisionally refer to it as “Choerolophodon” connexus. “Choerolophodon” connexus is characterized by the following features: weak or absent ptychodonty, choerodonty, and loph chevron (which were all strong in the typical species of Choerolophodon), as well as multiplication of the lophids in the m3, which were similar to that of the North American *Gnathabelodon*. Therefore, *Gnathabelodon* might represent a distinct lineage within the Choerolophodontidae, and may be derived from the East Asian “Choerolophodon” connexus.

Key words Miocene, Gomphotherium, *Gnathabelodon*, *Choerolophodon*, proboscidean

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In several monographs on Chinese fossil proboscideans or mastodonts (Hopwood, 1935; Chow and Chang, 1974; Tobien et al., 1986), *Trilophodon connexus* Hopwood, 1935 (= *Gomphotherium connexum* (Hopwood, 1935)), is always the first

introduced taxon. Therefore, this species was given particular attention by paleontologists working on Chinese proboscideans, and has long been regarded as a representative species of Gomphotherium in China, as this genus was considered the “core” group in mastodonts’ evolution (Tobien, 1973; Tassy, 1985). The type locality is Diaogou, Xining Basin, Qinghai Province, estimating ~16 Ma (Li et al., 2018). The hypodigm includes a left hemimandible bearing the m2 and m3 (holotype), a left M3, and several jaw fragments and isolated cheek teeth. However, in the current view, the lack of diagnostic mandibular symphysis and mandibular tusks makes it problematic to attribute “*T. connexus*” to Gomphotherium. Aside from several broken mandibles and cheek teeth reported by Qiu et al. (1981), no further material from the type locality has been described.

Chen (1988) reported abundant fossil proboscideans from the Ulungur Region, northern Junggar Basin. She described two species of Gomphotherium, Gomphotherium cf. *G. shensiensis*, and Gomphotherium sp. Wang et al. (2015) reviewed this material. They assigned both of these two species to *G. connexus*; however, they did not suspect that “*G. connexus*” indeed belongs to Gomphotherium. Li et al. (2019) first reported *Choerolophodon* sp. from the Ulungur region based on several newly discovered, but rather fragmentary isolated cheek teeth. They also mentioned a mandible photographed by Chen (1988:pl.2, fig. 1 [Figure 1: see original paper], No. IVPP V8567), which she attributed to *G. cf. G. shensiensis*, and considered it as belonging to *Choerolophodon*. Indeed, this mandible possessed a long trough-like mandibular symphysis and lacks mandibular tusks, which are features that clearly diagnose the *Choerolophodontidae*.

However, prior to 2021, none of us knew where this mandible (V8567) was deposited and the original photo is not clear enough to show the details of the morphology of the cheek teeth.

In late 2021, the second author of this paper unexpectedly discovered a long-jawed proboscidean mandible in the basement storage of the IVPP when she was performing her routine work. Although the distal symphysis was broken, it is absolutely the original specimen of IVPP V8567, which Chen (1988) had photographed. This mandible no doubt belongs to the *Choerolophodontidae*. Further comparison of the cheek teeth reveals that V8567 manifests almost identical characters to that of the teeth from the type hemimandibles of “*Gomphotherium connexus* (Hopwood, 1935)”, as well as to the characters of other lower cheek teeth assigned to “*Gomphotherium connexus*” from the Ulungur region. This result led us to carry out the following study: revising *Trilophodon connexus* Hopwood, 1935 and correctly transferring it to the *Choerolophodontidae*.

1.1 Abbreviations

Synonymy abbreviations used in this work follow Matthews (1973): *, the work validates the species; •, the authors agree on the identification at species level (maybe not at generic level); v, the authors have seen the original material of the reference; ?, the allocation of the reference is subject to some doubt; non, the reference actually does not belong to the species under discussion; par, the reference applies only in part to the species under discussion; no sign, the authors were unable to check the validity of the reference.

Institutional abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; FHSU, Fort Hays State University's Sternberg Museum of Natural History, Hays, Kansas, U.S.A.; PMU, Palaeontological Museum, Uppsala, Sweden.

1.2 Materials, terminology, and measurements

The material described in the present work is housed in the IVPP. The comparative material is housed in the IVPP, PMU, and FHSU.

The terminology of the occlusal structure of gomphotheriid molars and mandible follows Wang et al. (2020) (Fig. 1A). Specifically, we used the terms pretrite central conule and pretrite crescentoid for different crown elements, which Osborn (1936) had previously dealt with (he used conule or serration for pretrite central conule and spur or crest for crescentoid, see Osborn, 1936:393). A pretrite crescentoid (green color) is a thick or thin enamel projection that originates from the mesial or distal side of the pretrite main cusp(id) and runs to the base of the loph(id)s (Fig. 1A, green color). The proximal end of a crescentoid merges closely with the attached main cusp(id) without a sulcus between them. Whereas a pretrite central conule (blue color) is a round bulbous cone (Fig. 1A, blue color) or subdivided enamel cones that are either arranged in a line or serrated. It should be noted that the boundary between the crescentoid and central conule might be vague after moderate or deep wear. Pretrite central conules rise directly from the base of the interloph(id) or cingulum(id) with a sulcus that clearly separates the adjacent loph(id).

Cheek tooth measurement protocol follows Tassy (2014) (Fig. 1B, C).

2 Systematics

Order Proboscidea Illiger, 1811 Family Choerolophodontidae Gaziry, 1976
Genus Choerolophodon Schlesinger, 1917 “Choerolophodon” connexus (Hopwood, 1935) (Figs. 2, 3; Tables 1, 2)

v *Trilophodon connexus* Hopwood, 1935, p. 14–19, pl. 5, figs. 1, 2 *v* *Trilophodon connexus* Hopwood Osborn, 1936, p. 702, fig. 662 [Figure 662: see original paper] *v* non *Gomphotherium* cf. *G. connexus* (Hopwood) Zhai, 1961, p. 3, pl. 1, fig. 2 [Figure 2: see original paper] *v* *Gomphotherium connexus* (Hopwood) Chow and

Chang, 1974, p.21, 22, fig. 19 [Figure 19: see original paper] • *Gomphotherium connexus* (Hopwood) Qiu et al., 1981, p. 164, 172, pl. 1, fig. 9 [Figure 9: see original paper] • *Gomphotherium connexum* (Hopwood) Tobien et al., 1986, p. 127-131, figs. 2-6 v par *Gomphotherium* cf. *G. shensiensis* (Chang and Zhai) Chen, 1988, p. 265-268, 274-275, pl. 1, figs. 1-3, pl. 2, figs. 1-3 v *Gomphotherium* sp. Chen, 1988, p. 268, 269, 275, pl. 3, figs. 1, 2 v par *Gomphotherium connexum* (Hopwood) Wang et al., 2015, p. 1075-1080, figs. 2a-g, 3a-i *v *Choerolophodon* sp. Li et al., 2019, p. 5, 6, fig. 4A [Figure 4: see original paper]-F

Diagnosis Cranium and upper tusk unknown; mandibular symphysis greatly elongated, deeply concave (trough-like), and moderately ventrally bent; mandibular tusk absent; cheek teeth highly bunodont with very inflated conelets; both pretrite and posttrite mesoconelet 2 on both upper and lower molars reduced or even absent; loph/lophid 2 not, or at most weakly, chevroned; upper molars possessing a well-developed posterior pretrite central conule 2, which is usually larger than anterior pretrite central conules 2, and tends to be subdivided into two conules; posterior posttrite central conules 2 of upper molars also weakly developed; lower molars possessing a very large posterior pretrite central conule 2; m3, and even M3, showing a tendency of elongation; P3/p3 and P4/p4 present; ptychodonty and choerodonty almost absent; cementodonty weak.

Differential diagnosis Differing from the derived species of the Choerolophodontidae, i.e., *Choerolophodon pentelici*, *C. anatolicus*, *C. corrugatus*, and *C. ngorora* in the weak development or absence of ptychodonty, choerodonty, and cementodonty, in the presence of premolars, in the not chevroned loph/lophid 2; differing from *Afrochoerodon kisumuensis*, *A. zaltenensis*, “*Choerolophodon*” *chioticus*, and “*C.*” *guangheensis*, in the not chevroned loph/lophid 2, and lacking the tendency of fusion of pretrite mesoconelet 2 and anterior central conule 2; differing from *Gnathabelodon thorpei* and *Gn. buckneri* in the larger posterior pretrite central conule 2 in both upper and lower molars; differing from all species of the Choerolophodontidae in the weak development or absence of pretrite and posttrite mesoconelet 2 on both upper and lower molars.

Type specimens Holotype, PMU-M 3469, a left hemimandible with m2 and m3, lacking mandibular symphysis. A cast, IVPP RV35015, were housed in IVPP.

Type locality and horizon Diaogou, Xining City, Qinghai Province. The Diaogou locality situates at the base of the Miocene Guanjiashan Formation, the age was estimated ~16 Ma (Li et al., 2018).

Referred specimens from Diaogou PMU-M 3045 (IVPP RV35D49, a cast), a left M3; PMU-M 3047, a left P4; PMU-M 3049, a left hemimandibles carrying a dentition of p3, dp4, and m1; PMU-M 3046, a right p4; PMU-M 3048, a left m2; IVPP V6019.1, left hemimandible with m2 and m3.

Referred specimens from Ulungur region, northern Junggar Basin

IVPP V8567, a left hemimandible with mandibular symphysis, m2 and m3; V8573, V8574, and V8576, three left M3; V8572, a right M3; V8569, a left dp4; V8575 and V18701, two left m3, V31357, a right m2, V25051, maxillary fragments with M2 and partial M3, V25057, mesial two lophes of M2 or M3, V25058, a fragmented right m3. Except the last one, which is from the very base of Kekemaideng Formation (~14.5 Ma), other specimens are from Halamagai Formation (~16.9–15 Ma) (Wang et al., 2022).

Descriptions Most of the above specimens have been described at least once, in some cases even multi-times (e.g., the holotype) in the previous works (Hopwood, 1935; Chow and Chang, 1974; Chen, 1988, 2021; Tobien et al., 1986; Wang et al., 2015; Li et al., 2019). Here we describe only IVPP V8567 (the critical material which had not been carefully described before) and V31357 (newly discovered).

IVPP V8567 is a left hemimandible with symphysis, bearing the m2 and m3 (Fig. 2A, B, G, K, O, Q), which had previously been photographed by Chen (1988). In the original photo, the symphysis is complete (Fig. 2A), but in the current state, the distal end of the symphysis, especially the left side, is missing (Fig. 2B). The symphysis was broken into two parts at about one third of the proximal, and the two parts could not be completely matched due to the extra loss of the adjacent bone. In dorsal view, the symphysis is very long (longer than the corpus). It is deep and trough-like, and the bony wall is very thin, which is evidently not holding any tusk (Fig. 2Q). The symphysis is slightly transversely expanded distally, and as seen from the original photo, two transversely elongated rough areas are present, with each one aside the mid-axis of the distal end, which possibly represents the remnant of the opening of the tusk alveolus (Fig. 2A). In lateral view, the symphysis is moderately ventrally inflected (close to that of *Gnathabelodon thorpei*) (Fig. 2G), and the anterior mental foramen is very large and tube-like (Fig. 2G), indicating the development of a keratinous structure from the integument of the distal symphysis. In medial view, the proximal end of the symphysis is relatively distant from the cheek tooth row; dorso-ventrally, it is very thin compared to that of the other longirostrine taxa that possess lower tusks (Fig. 2K). The mandibular corpus is strong, and its height at the rostral end is relatively large. However, a large amount of bony structure around the m3 is just missing. Most of the ramus is broken, and a deep vascular impression ventral to the ramus for the facial artery and vein is very pronounced (Fig. 2G, K).

The m2 is deeply worn (Fig. 3A [Figure 3: see original paper]). It is rectangular with three lophids. The lophid 1 is only partially preserved. The dentine of the pretrite and posttrite half lophids 2 are connected to each other due to heavy wear. The lophid 3 is moderately worn. The pretrite half lophid has an anterior and a posterior central conule, which are both large, and the latter is fused with a strong conule that rises directly from the buccal side of the distal cingulid. Another isolated conule also rises from the lingual side of the distal cingulid.

The m3 is erupting from the alveolus and the adjacent bones were removed (Fig.

3A). It is highly bunodont with complete four lophids and a distal cingulid. The pretrite lophid 1 has well developed anterior and posterior central conules. The former is subdivided into two conules and the latter is large, and it links to the main conelet with a strong arm (a short and thick posterior crescentoid). The posttrite half lophid has a large main conelet and a small mesoconelet. The pretrite lophid 2 has a weak anterior central conule, a weak mesoconelet, and a large posterior central conule that rises directly from the interlophid 2. The posttrite lophid 2 has a large main conelet and a very thin flaky mesoconelet. The pretrite and posttrite half lophids are almost not chevroned. The lophid 3 shows very similar morphology to the lophid 2, except that the anterior and posterior pretrite central conules are nearly equivalent, and the posttrite mesoconelet is slightly thicker in the lophid 3. The lophid 4 has a simple trifoliate pretrite half lophid and lacks the posttrite mesoconelet. Only a large conelet rises from the posterior cingulid. Ptychodonty and cementodonty are absent.

IVPP V31357 (Fig. 3C) is a newly discovered specimen from the Dingshanyan locality, Halamagai Formation. It is a deeply worn right m2 and shows a morphology that is very similar to the type m2 (Fig. 3B). The firstly two lophids are deeply worn, with the two half lophids connected to each other. The posterior posttrite central conules 1 and 2 are large. The lophid 3 is simple, with a large posterior posttrite central conule directly rising from the distal cingulid. The pretrite and posttrite mesoconelets are weak. A small amount of cementum is deposited in the interlophids.

3 Comparison and discussion

The primary difference between the Choerolophodontidae and other longirostre elephantiforms is that the former possesses a trough-like mandibular symphysis and lacks mandibular tusks (Tassy, 1983; Konidaris et al., 2016; Li et al., 2019). Therefore, IVPP V8567, the hemimandible from Halamagai Formation, Junggar Basin, is without a doubt a choerolophodontid. The following is concerned with the comparison of V8567 and the type mandible PMU-M 3469.

PMU-M 3469 is also a left hemimandible (Fig. 2C, F, J, N). However, it is missing the vast majority of the symphysis, except for the most proximal part. In comparing the proximal end of the mandibular symphysis with the Halamagai mandible, IVPP V8567 (Fig. 2A, B, G, K, O, Q), and with a “true” Gomphotherium, V22781 (Fig. 2E, I, M), it can be seen that both PMU-M 3469 (type) and V8567 have a very dorso-ventrally thin proximal extremity of the mandibular symphysis (Fig. 2J, K, thin dis. sym.) that is a relatively far distance from the cheek teeth row (Fig. 2B, C, J, K), which suggests that the mandibular symphysis is very weak and could not hold a tusk. However, in the mandible of Gomphotherium tassyi, which has a pair of strong mandibular tusk, the symphyseal proximal extremity is dorso-ventrally thick and close to the cheek teeth row (Fig. 2E, M, thick dis. sym.). Tobien et al. (1986) mentioned that “an alveolus of incisor” is present in the type cast, and they even

argued that the tusks have been weakened in “*G. connexum*” . However, we did not agree with this because an alveolus cannot be inserted so deeply (as to reach the very base of the proximal end of symphysis), and it is not positioned so dorsally and laterally (tusk alveolus should be very close to the mid-axis). What they mentioned is in fact the mandibular channel that links to the anterior mental foramen (Fig. 2N, mc). In choerolophodontids, the anterior mental foramen (and the following mandibular channel) is very thick and tube-like.

The cheek teeth of the two specimens are in a very similar ontogenetic stage, which facilitates the comparison (Fig. 3A, B). It is unnecessary to compare the deeply worn m2, and only the diagnostic characters of the m3 will be discussed. The m3s of both specimens are highly bunodont. They are relatively narrow, and they are composed of four lophids and a distal cingulid. The lophid 2 (the most characterized part of a cheek tooth) of both m3s are almost not chevroned and only show a slight mesial shifting of the pretrite mesoconelet, which is rather weak. The posttrite mesoconelet is almost absent in the m3 of both specimens. The posterior pretrite central conule 2 rises directly from the interlophid without a link (posterior crescentoid) to the main conelet. The anterior pretrite central conule 2 is small. In the lophid 1 of both m3s, the posterior pretrite central conule is very large, links to the main conelet with a thick posterior crescentoid, and the anterior pretrite central conule is subdivided into two isolated conules that link to the mesial cingulid. The pretrite mesoconelet is moderately developed and the posttrite mesoconelet is either weak (Halamagai m3) or absent (type m3).

Finally, choerodonty, ptychodonty, and cementodonty are absent in both m3s, and they are even similar in size (Table 1). Therefore, both m3s are identical in critical characters, and these characters are also the diagnostic characters of the species “*connexum*” . Finally, the Halamagai mandible seems to be slightly more derived than the type mandible in the more ventrally inflected symphysis, and in the earlier eruption of the m2. Except for these minor differences, these two mandibles can be attributed into the same species “*connexum*” but belong to the Choerolophodontidae rather than to Gomphotherium.

Additionally, Wang et al. (2015) also provided strong evidence that the upper molars from the type locality and from the Halamagai Formation belong to the same species, “*connexum*” , and we will not repeat this comparison (Fig. 3E, F). Hereby we transfer them to the Choerolophodontidae altogether. Moreover, we also attribute Choerolophodon sp. from the Ulungur region reported by Li et al. (2019) to the species “*connexum*” .

It should be noted that the hypodigm of *Trilophodon connexus* Hopwood, 1935 includes several premolars, i.e., PMU-M 3047 (a P4), and PMU-M 3049 (left juvenile hemimandibles bearing a p3) (Tobien et al., 1986:figs. 3, 4). Although Tassy (1983) previously mentioned that premolars are yet unknown in the Choerolophodontidae, it is no surprise that premolars were still developed in a relatively primitive evolutionary stage of this family. Wang and Deng (2011) reported P4s in Choerolophodon guangheensis, and Wang et al. (2023) found a

P3 in *C. guangheensis*. Here, even a p3 was found in “connexus” (a p4 should be also present) despite the fact that this premolar is very small and very easily shed.

The next step is to determine to which genus *Trilophodon connexus* Hopwood, 1935 should be attributed within the Choerolophodontidae. Unfortunately, a common agreement on the generic taxonomy of the Choerolophodontidae has not yet been reached. Before 2001, *Choerolophodon* was the only included genus. Pickford (2001) established *Afrochoerodon* based on *Choerolophodon kisumensis* (Macinnes, 1942), *C. zaltanensis* Gaziry, 1987, *C. ngorora* (Maglio, 1974), and *C. chioticus* Tobien, 1980. In the recent studies, *Afrochoerodon* was considered the paraphyletic ancestral group of *Choerolophodon* (Shoshani and Tassy, 2005), and Konidaris et al. (2016) reattributed all the species into *Choerolophodon*. However, in some of the other existing literature (Sanders and Miller, 2002; Sanders et al., 2010), *Afrochoerodon kisumuensis* was still used, and *C. palaeindicus* was sometimes attributed to *Afrochoerodon*. Li et al. (2019) attributed North American *Gnathabelodon* to the Choerolophodontidae. In this case, which group was *Gnathabelodon* derived from remains an interesting issue.

There is no doubt that the mandible of *Gnathabelodon thorpei* (FHSU VP18) (Barbour and Sternberg, 1935) (Fig. 2D, H, L, P), as well as that of *Gn. buckneri* (Sellards, 1940), resemble all the known Early and Middle Miocene choerolophodontid mandibles, including the mandible of *Choerolophodon chioticus* and the Halamagai mandible (IVPP V8567), except the much larger size of *Gn. thorpei*. Here, we will further compare the cheek tooth morphology. The lower m3 of *Gn. thorpei* and *Gn. buckneri* possesses four lophids with a distal cingulid (Fig. 3D). The pretrite half lophid 2 is situated at the normal position seen in most gomphotheres, and the pretrite mesoconelet 2 is not fused with the corresponding anterior central conule. These characters were all seen in “connexus”. However, in some derived species of *Choerolophodon*, including the type species *Choerolophodon pentelici*, *C. ngorora*, and *Afrochoerodon kisumensis*, the pretrite half lophid 2 of the lower molars shifts to a very buccal position, and the pretrite mesoconelet 2 and anterior central conule 2 are fused.

The upper M3 of *Gn. thorpei* possesses four lophids (Fig. 3G). The loph 2 is almost not chevroned, the pretrite mesoconelet 2 and anterior central conule 2 are clearly individualized (without any tendency for fusion), and the posterior pretrite central conule 2 is large (a synapomorphy of *Gnathabelodon* within the Choerolophodontidae). These characters also resemble those of “connexus”. In *Choerolophodon pentelici*, *C. ngorora*, *C. corrugatus*, and *Afrochoerodon kisumensis*, the loph 2 is strongly chevroned, the pretrite mesoconelet 2 and anterior central conule 2 are fused, and the posterior pretrite central conule 2 is weak (possibly even absent). Furthermore, choerodonty, ptychodonty, and cementodonty are all not pronounced in the molars of *Gn. thorpei*, which is also close to what is observed in “connexus”. After all, loph/lophid 2 chevroning, choerodonty, ptychodonty, and cementodonty were previously considered to be the typical characters of choerolophodontids (Tassy, 1983; Konidaris et al.,

2016). However, this observation may not be suitable for all choerolophodontid members.

Gnathabelodon might represent a distinct lineage in the very initial evolution of loph/lophid 2 chevrons, choerodonty, ptychodonty, and cementodonty, but shows a tendency for the enlargement of the posterior pretrite central conule 2, as well as m3 elongation. Therefore, the morphology of “connexus” is closer to that of *Gnathabelodon thorpei* than to that of species of *Choerolophodon* and *Afrochoerodon*. However, before a comprehensive phylogenetic study and a complete revision of all choerolophodontid species have been done, we provisionally assign “connexus” into the type genus *Choerolophodon*, with quotation marks, i.e., “*Choerolophodon*” *connexus* (Konidaris et al. (2016) also attributed all species into *Choerolophodon*). Nevertheless, “C.” *connexus* provides a missing link between the Old-World choerolophodontids with the New-World enigmatic proboscidean *Gnathabelodon*.

4 Conclusion

In the present article, we transfer *Trilophodon connexus* Hopwood, 1935 to “*Choerolophodon*” *connexus*. Lacking a comprehensive amending of the Choerolophodontidae, this attribution is somewhat provisional. However, we have identified the possible origin of North American *Gnathabelodon thorpei*, which has long been considered an enigmatic taxon. “*Trilophodon connexus* Hopwood, 1935” has been considered a representative Gomphotherium in China because of its highly bunodont cheek tooth morphology. The reevaluation of the mandible from the Halamagai Formation of the Ulungur region compels us to remove it from Gomphotherium. Our empirical studies in Chinese gomphotheres reveal that “true Gomphotherium” is relatively rare in China, especially for such a highly bunodont taxa. As *G. spectabilis* was synonymized with *Platybelodon grangeri* (Amebelodontidae) (Tobien et al., 1986); and *G. wimani* should be revised as *Protanancus wimani* (Amebelodontidae) (Wang, 2021; Wang et al., 2023); Furthermore, *G. connexum* is transferred to “*Choerolophodon*” *connexus* (Choerolophodontidae). It is confirmed that Gomphotherium from China includes the following species: *G. cooperi* from the Tongxin region (Li et al., 2022), *G. inopinatum* from Linxia Basin (Wang, 2014), *G. tassyi* from Linxia Basin and the Zhongning region (Wang et al., 2017), and *G. steinheimense* from the Ulungur region (Wu et al., 2018). Nevertheless, in the Early and Middle Miocene of China, Gomphotherium is relatively rare, and members of the Choerolophodontidae and Amebelodontidae are the dominant groups in gomphotheres.

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