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Article

A Possible Euhelopodid from the Jehol Biota, Liaoning of China

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Abstract: Our paper conducted a re-examine of the Sauropod individuals PMoL from the Jehol Biota, Lower Cretaceous, Liaoning of China, including partial vertebrae and appendicula. First, we re-exam the osteology of the PMoL. Next, we used TNT 1.5 and PAUP 4.0 software and the newest matrix of the Titanosauriformes to analyze the phylogenetic position of the PMoL, the result revealed that PMoL was reconsidered in the Euhelopodid. Then, the comparison in the PMoL and other Titanosauriformes in the Jehol Biota was conducted. Finally, we conducted a paleobiogeographic analysis to infer the origination of the Euhelopodidae and considered that the origin region of the Euhelopodidae is Asia.

Keywords: dinosaur; Sauropod; Euhelopodidae; Titanosauriformes; Titanosauria

1. Introduction

Titanosauriformes flourished in South America and Asia during the Cretaceous period [1]. In Asia, most taxa were excavated in China, until at the end of 2024, 32 taxa were recorded in China [2]. However, in the Jehol Biota, a famous biota for the Non-avian feathered Theropod dinosaur located in northeastern China of the Early Cretaceous [3], only three taxa of Titanosauriformes were recorded: *Dongbeititan dongi*, *Liaoningotitan sinensis* and *Ruixinia zhangii* [4,5,6].

The individual PMoL (PMoL: Paleontological Museum of Liaoning) is a Sauropod dinosaur individual that preserved partial cervical and dorsal vertebrae, scapula, ulna, and tibia. The individual was excavated in the Xiaobeigou Village, Beipiao City, Chaoyang City of Liaoning Province, China, close to the fossil point of the *Liaoningotitan sinensis* holotype [5]. However, this individual has been ignored for a long time, even some of its elements were wrongly classified as *Liaoningotitan*. To explore the Sauropod dinosaur in the Jehol Biota, we conducted total osteological research and phylogenetic analysis on the PMoL. We used The matrix in the TNT 1.5 and PAUP 4.0 software from *Beeston et al., 2024*, the newest matrix about the Titanosauriformes.

2. Materials and Methods

Systematic Paleontology

Saurischia [8]

Sauropodomorpha [9]

Sauropoda [10]

Titanosauriformes [11]

Somphospondyli [12]

Titanosauria [13]

Euhelopodidae [14]

Locality and horizon

The fossil point is in the Xiaobeigou Village, Shangyuan Town, Beipiao City, Chaoyang City, Liaoning Province, China (Figure 1). Yixian Formation, Aptian, Lower Cretaceous.

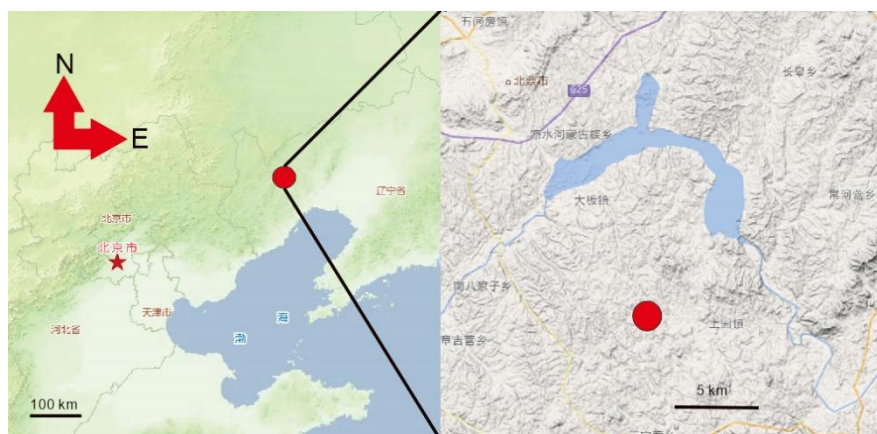


Figure 1. Geographic of PMoL. Locality of PMoL (red point) in Xiaobeigou Village, Shanyuan Town, Beipiao City, Chaoyang City, Liaoning Province, Map copyright: <https://map.tianditu.gov.cn/>.

3. Results

3.1. Description

3.1.1. Cervical Vertebrae

Five interrelated middle cervical vertebrae and one hindmost cervical vertebra are preserved. All middle cervical vertebrae are flat, presumably flattened by the rock bed. All neural arches and neural spines are incomplete. The height of the neural spines is increased progressively. The diapophyses are triangular and extend laterally. The diapophysis is elongated more than half the length of the centrum. Only the last three cervical ribs are well preserved and are double-head type. The cervical ribs are elongated. A lateral pneumatic fossa/foramen extends almost to the posterior end of the centrum, leaving only a thin strip of bone. Posteriormost cervical and anteriormost dorsal neural spines. The spinoprezygapophyseal lamina is broken. The location of the cervical rib is on a level that is similar to that in the centrum. The lateral surface of the cervical rib developed a bulge. The location of the cervical ribs is aligned to the centrum. The angle between spinodiapophyseal lamina and the arch is acute. The dorsoventral height divided by the posterior centrum height of the hindmost cervical vertebra is greater than 1.0. The hindmost cervical vertebra developed a long neural arch.

3.1.2. Dorsal Vertebrae

Four foremost dorsal vertebrae are preserved, but only two vertebrae were preserved well (B1 and B2), and the orientation of the dorsal vertebrae is inverted with the hindmost cervical vertebra. The neural spine is not bifurcated and vertical to the centrum. The centrum is opisthocoele. In B1, the neural spine is vertical to the vertebra. The diapophysis extends dorsoposteriorly. The parapophysis is extending dorsoanteriorly. The anterior centrodiaepophyseal lamina, posterior centrodiaepophyseal lamina, and posterior centroparapophyseal lamina consist of a K form. The pleurocoel is divided by a short plate.

In B2, the diapophysis and parapophysis are vertical to the centrum. A shallow and long pneumatic (pleurocoel) foramen is on the dorsal vertebra's lateral side. The type of the dorsal rib is plate-like.

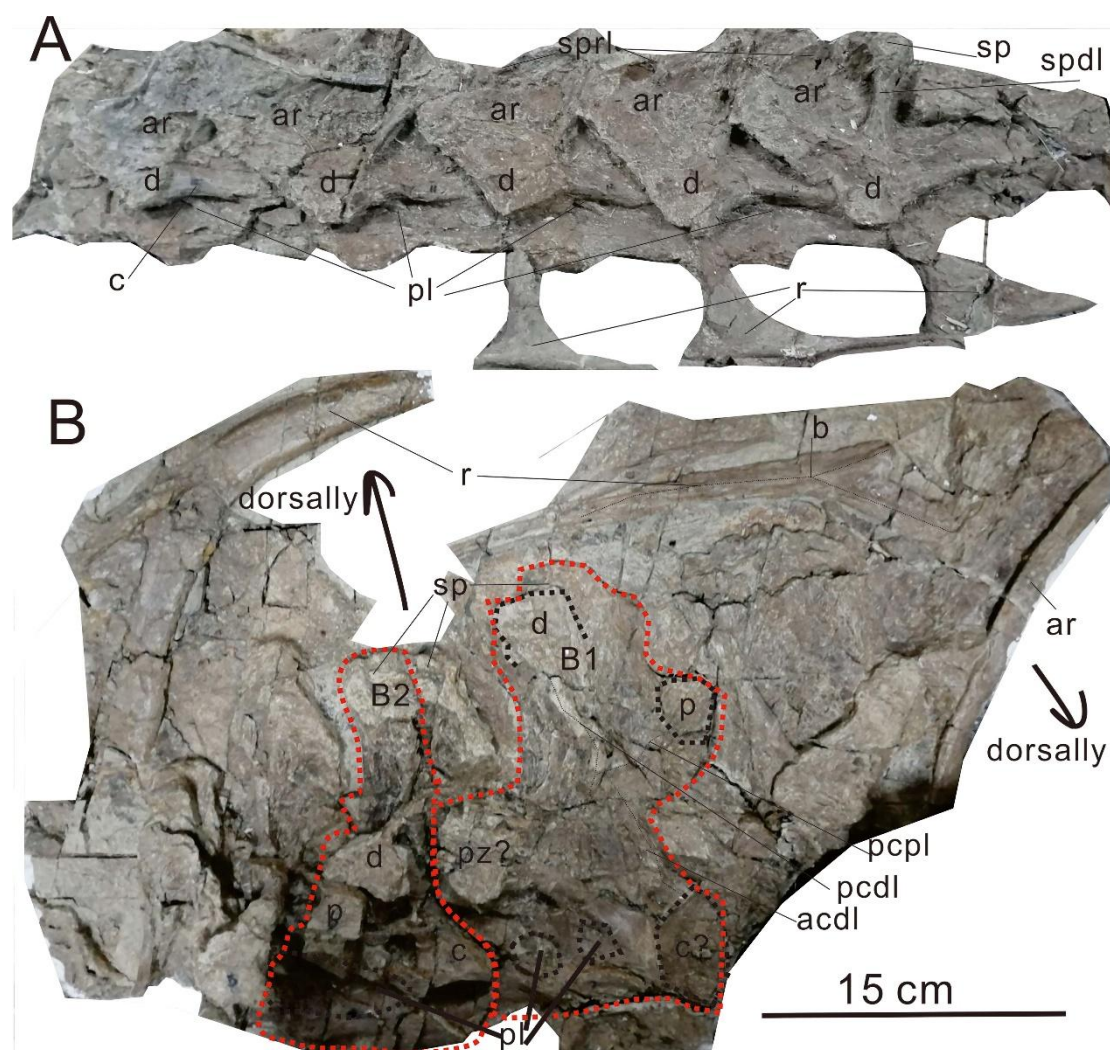


Figure 2. Vertebrae of PMoL. Scale bar: 15 cm. A: middle cervical vertebrae in left view; B: posterior vertebra and anterior dorsal vertebrae in right view. Abbreviations: acdl, anterior centrodiapophyseal lamina; ar, arch; b, bulge; c, centrum; d, diapophysis; p, parapophysis; pcdl, posterior centrodiapophyseal lamina; pcpl, posterior centroparapophyseal lamina; pl, pleurocoel; r, rib; sp, spine; spd, spinodiapophyseal lamina; sprl, spinoprezygophyseal lamina.

3.1.3. Scapula

Only one right scapula and partial coracoid are preserved and the medially of all individuals are covered by gypsum, therefore, only the laterally of the scapula and the coracoid are visible. The scapula is 100 cm in length. The dorsal side is thick, and the ventral side is thin. The proximal end of the scapula is medially curved, similar to that in *Somphospondyli*. The ratio of the maximum dorsoventral height to the minimum dorsoventral height of the scapular blade is 1.7, less than that in the *Daxiatitan binglingi* and *Jiangshanosaurus lixianensis* but greater than that in the *Yongjinglong datangi* and *Patagotitan mayorum* [15,16,17,18,]. The orientation of the scapula blade long-axis concerning coracoid articulation is 72°. The scapular glenoid face is medially, dissimilar from the *Jiangshanosaurus* and *Liaoningotitan* [16]. An anteroposteriorly concave region posterior to the scapular glenoid, followed by a flattened area. The scapula has a lateral ridge in the middle of the shaft and extends to the anterior and posterior, similar to that of *Jiangshanosaurus lixianensis* and *Patagotitan mayorum* [16,18], and speculated to be the attachment point of the subcoracoscapularis muscle. The ratio of the overall length of the scapula to its narrowest dorsoventral length is 6.13, less than that in the *Daxiatitan binglingi* [15]. The acromion process is not preserved. The posterior margin of the acromial plate is flat. The acromial ridge is developed but broken. The angle between the acromion posterior region and the scapular shaft long axis is 32°. The dorsal margin of the acromion

is broken, therefore we cannot estimate whether there is an acromion corner or not. The scapula developed no subtriangular process in the anteroventral corner of the scapular blade, which is the tuberosity (located in the anterior ventral side of the scapula blade, also called the attachment point of the triceps brachii muscle), dissimilar to that in *Yongjinglong datangi* and *Daxiatitan binglingi* [17,15]. The scapular suture is vertical to the coracoid almost. The thickest area of the shaft is located in the 1/3 area of the blade. The dorsoventral height of the distal end is greater than the dorsoventral height of the proximal end of the blade. The distal end extends to the dorsoposterior and posterior side, with an attachment point of the teres major muscle (tm) located on the laterally distal end of the scapula.

3.1.4. Ulna

The right ulna is preserved, triradiate (Figure 3), 45 cm long, and only the posterior side is visible. The width of the proximal end is 18 cm, and the width of the distal end is 14 cm.

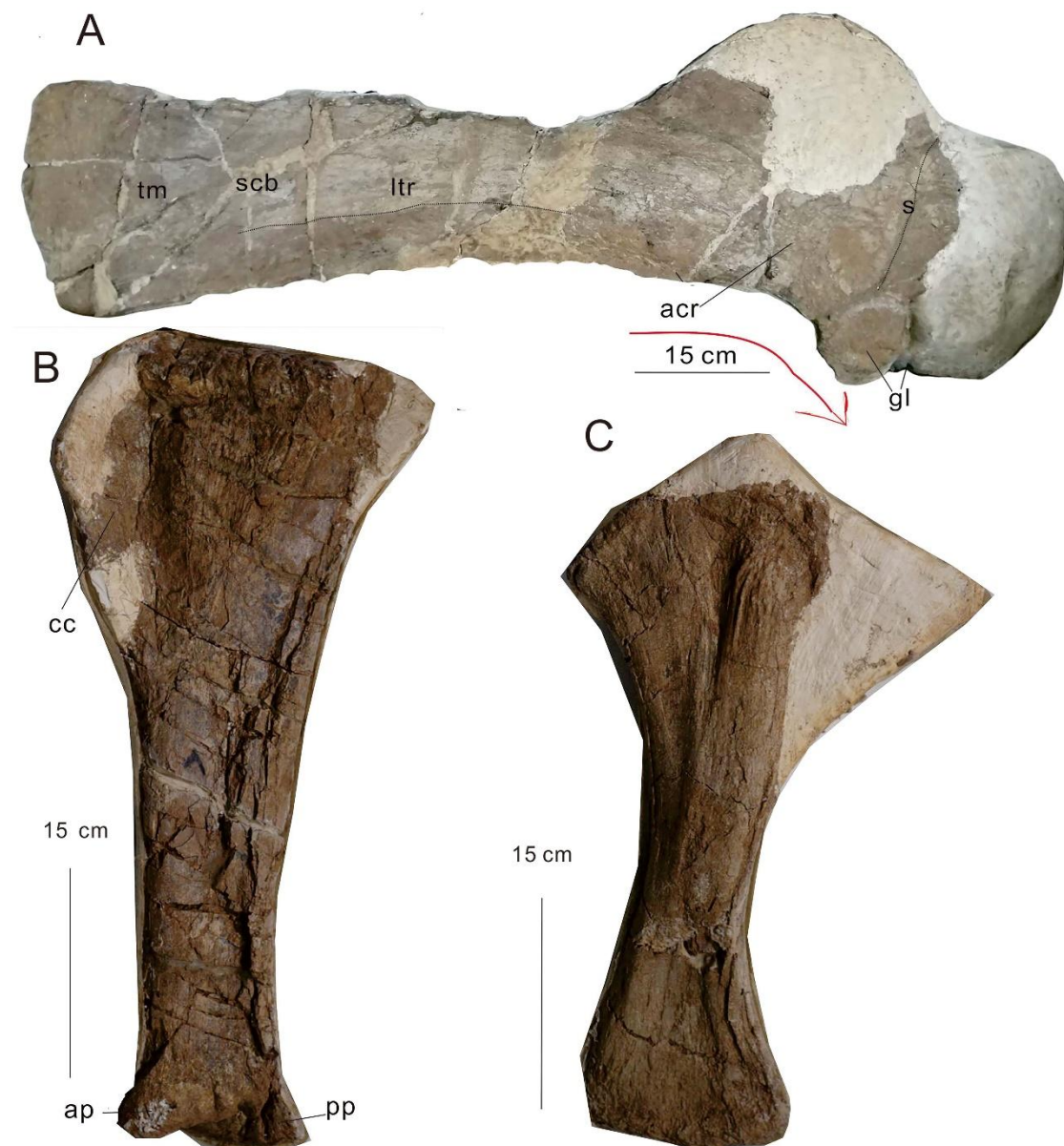


Figure 3. Appendicular elements of PMoL. Scale bar: 15 cm. A: Scapula in lateral view. B: Tibia in anterior view. C: Ulna in medial view. Abbreviations: acr acromial ridge; ap: anterior process; cc: cnemial crest; gl: glenoid lip; ltr, lateral ridge; pp: posterior process; scb, scapular blade; tm, the attachment point of the teres major muscle.

3.1.5. Tibia

The proximal end extends lateromedially. The cnemial crest is well-developed and extends anterolaterally to the 1/3 position of the shaft. The crest length is 30% of the width of the tibial proximal end. The lateral margin of the cnemial crest in the anterior view is subtriangular, forming a point. The fibular articular surface is flat. The length of the proximal end/middle position is 2.04. The narrowest position of the tibia is located at the distal end. The distal end extends to both anteriorly and posteriorly and the length is 50% of the length of the proximal end. The second cnemial crest is absent, similar to that in Euhelopodidae [7]. The proximal lateral face with a double ridge extending distally from the lateral projection of the proximal articular area and posterolateral fossa posterior to the double ridge, containing a lower tuberosity and an upper deep pit is absent. The location of the anterior process is higher than that of the posterior process. The appendicula is shown in Figure 3.

3.2. Phylogenetic Analysis

Our analysis used the matrix modified from [19] in TNT 1.5 software and PAUP 4.0 [20] for the phylogenetic analysis, in which the matrix includes 131 taxa (OTUs) and 560 characteristics. We added PMoL and *Liaoningotitan* into the matrix. Extended implied weighting (EIW) analyses were used with the following settings: max.trees was set to 10,000; tree bisection and reconnection (TBR) was used; new technology search was selected; random addition sequences were changed from 1 to 1,000 addseqs; sect search, ratchet, drift, and tree fusing were all used; set K=9, similar in the previous analysis [16,19]. All other options were set to default. The results show 3 strict consensus trees, a tree length of 2,840, a CI of 0.208, and a RI of 0.584. Standard bootstrap with the number of replicates changed from 100 to 5,000. The final result identifies that *Liaoningotitan* is a member of the Euhelopodidae, and PMoL is a member of the Euhelopodidae too, as shown in Figure 4.

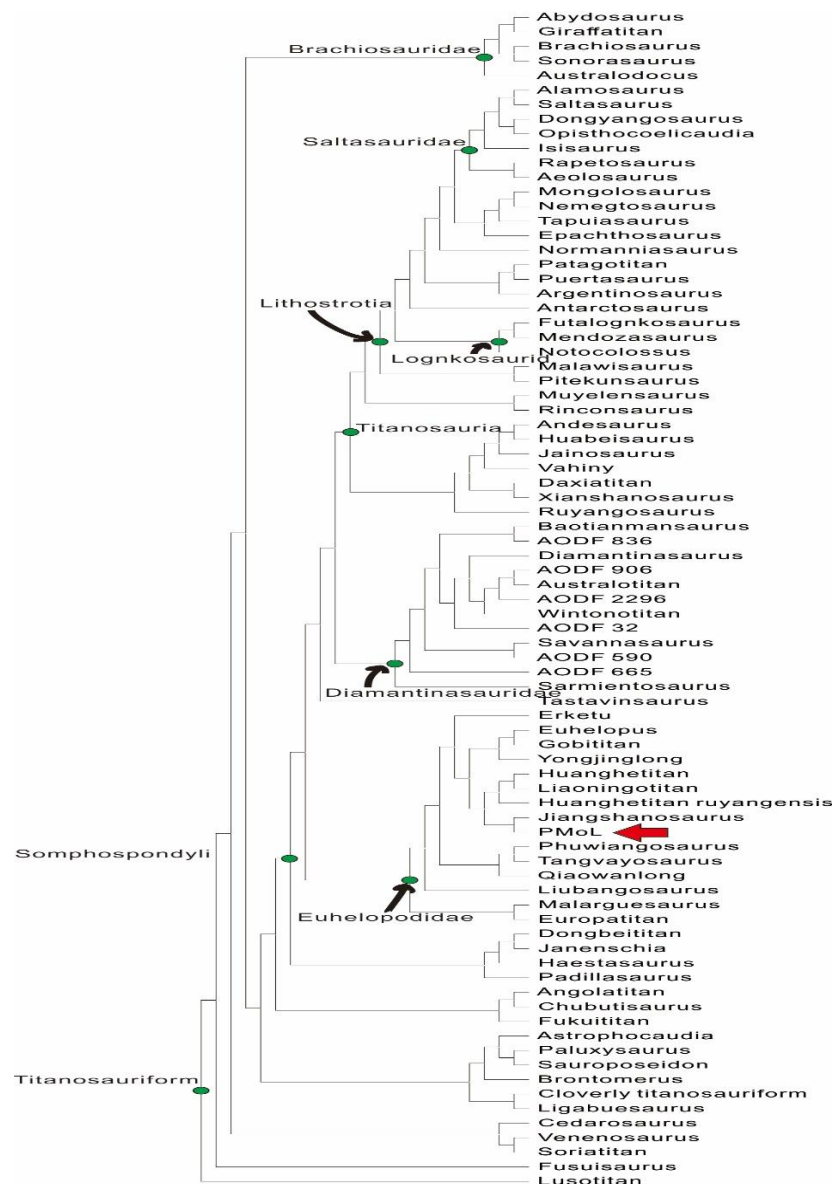


Figure 4. Phylogenetic analysis of strict consensus tree of PMoL (red arrow). Matrix from [19].

4. Discussion

4.1. The phylogenetic Position of the Titanosauriformes in China

In the result of our analysis, Titanosauriformes in China reflected a high degree of diversity. *Fusuissaurus* was reconsidered in the Basal Titanosauriform, similar to that of the initial analysis [21]. *Liubangosaurus* was reconsidered as a Non-Neosauropod taxon and a Lithostrotian in the previous analyses and as a Euhelopodid in our analysis [23,7]. *Qiaowanlong* was classified as a Brachiosaurid in the initial analysis too [22]. The *Dongbeititan* is considered a Basal-Somphospondylan. *Liaoningotitan*, *Yongjinglong*, *Jiangshanosaurus*, *Qiaowanlong*, *Liubangosaurus*, *Euhelopus*, *Gobititan*, two *Huanghetitan* taxa, and PMoL are reconsidered Euhelopodidae. *Daxiatitan*, *Ruyangosaurus*, *Xianshanosaurus*, *Huabeisaurus*, *Dongyangosaurus* and *Mongolosaurus* are Titanosaurian. In which, *Dongyangosaurus* and *Mongolosaurus* are reconsidered as Lithostrotian.

4.2. Euhelopodid in the Jehol Biota

At the end of 2024, three Sauropod taxa were named in the Jehol Biota: *Dongbeititan dongi*, *Liaoningotitan sinensis*, and *Ruixinia zhangii*, all taxa were considered as the Euhelopodid exclude *Dongbeititan* (this paper; [6]). In addition, some fragmentary individuals reveal the Euhelopodid existence in the Jehol Biota, such as teeth [24], indicating that the Jehol Biota is an important habitat of Euhelopodid dinosaurs. PMoL increased the diversity of the Euhelopodid in the Jehol Biota. PMoL is different from other Sauropods from the Jehol Biota in the following positions: 1. The location of the cervical ribs is aligned to the centrum, dissimilar to that of the *Liaoningotitan* and *Ruixinia*. 2. The ratio of the length of the proximal end to the middle position of the PMoL is 2.04, greater than that of the *Dongbeititan* (1.89) and less than that of the *Liaoningotitan* (2.7) and *Ruixinia* (2.58) [4, 6], support that the PMoL is an independent taxon that different to others.

4.3. The Paleobiogeographic Reconstruction of Euhelopodidae

This study utilized the R package BioGeoBears [25] to reconstruct the ancestral distribution of Titanosauriformes in Asia. The BioGeoBears was used to add a time axis to the tree, root length =2 Ma (Million years). FAD (First Appearance Date) and LAD (Last Appearance Date/Extinct Date) of taxa were referred to the Paleobiology Database (<https://www.paleobiodb.org/>) and previous research [1], the geological period information refers to the 2020 version of the International Commission on Stratigraphy Chronostratigraphic Chart. BioGeoBears supports DEC, DEC + J, DIVA, DIVA + J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, and BAYAREALIKE + J models to analyze the ancestral distribution of creatures. These models allow different vicariance to occur on nodes. In the analysis, we put the potential ancestral distribution into geographical areas A – C and allow each ancestor to occupy up each two geographical areas (such as AB, AC, etc). By comparing all models, we chose model BAYAREALIKE for our analysis, the result of reconstruction is seen in Figure 5, and the model test result is seen in Figure 6. The disk represents the proportion of the possibility of originating from somewhere.

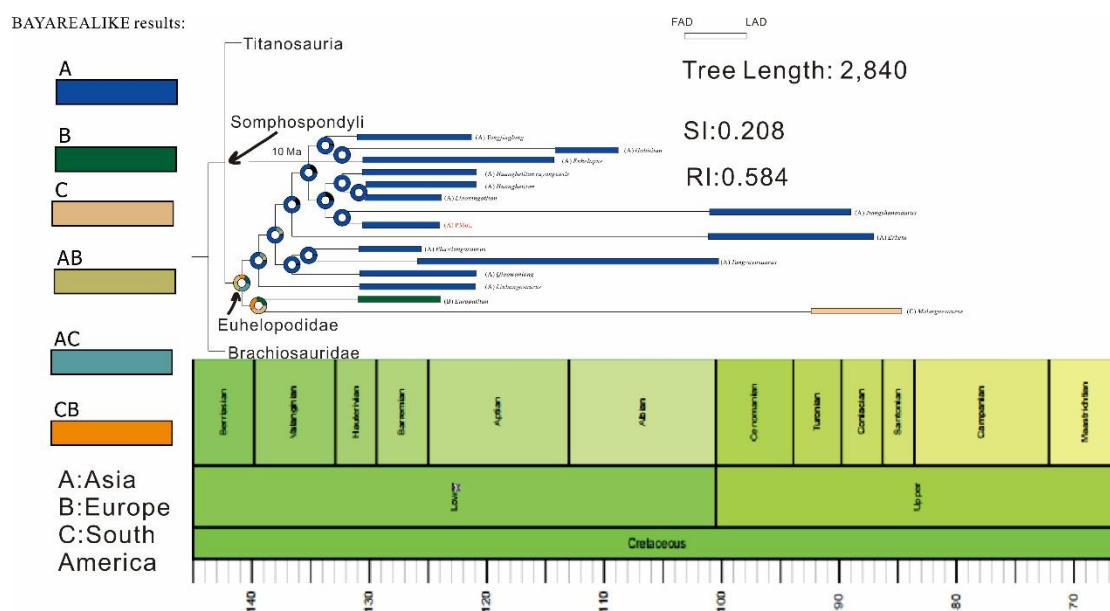


Figure 5. The paleobiogeographic reconstruction of Euhelopodidae (including PMoL and *Liaoningotitan*).

```

#Results of Model Test#
LnL      numparams d      e      j      AICc      AICc_wt
DEC      -220.3      2      0.0089      0.3      0      444.81.2e-10
DEC+J    -197.7      3      1.0e-12      0.3      0.055      401.7      0.28
DIVALIKE -210.2      2      0.011      1.06      0      424.53.1e-06
DIVALIKE+ -197.4      3      0.0029      1.22      0.035      400.9      0.4
BAYAREALIF -218.5      2      0.0099      0.38      0      441.17.5e-10
BAYAREALIF -197.6      3      0.0009      0.47      0.046      401.4      0.32
# Use the highest AICc_wt to select the best model
=====
alt      null      LnLalt      LnLnull      DFalt      DFnull      DF      Dstatisticpval      test      tail      AIC1      AIC2      AICwt1      AICwt2      AICweight      AICweight_ratio_model2
DEC+J    DEC      -197.7      -220.3      3      2      1      45.171.8e-11      chi-square one-tailed      401.5      444.7      1.4.2e-10      2.37e+09      4.2e-10
DIVALIKE+ DIVALIKE -197.4      -210.2      3      2      1      25.684.0e-07      chi-square one-tailed      400.7      424.4      1.7.2e-06      138391.7.2e-06
BAYAREALIF BAYAREALIF -197.6      -218.5      3      2      1      41.831.0e-10      chi-square one-tailed      401.2      441      1.2.2e-09      4.45e+08      2.2e-09
# The p-value of the LRT (Likelihood Ratio Test) tells you whether or not you can reject
# the null hypothesis that without J and +J confer equal likelihoods on the data.

```

Figure 6. Model test results of the paleobiogeographic reconstruction of Euhelopodidae (including PMoL and *Liaoningotitan*).

Our result revealed The Euhelopodidae originated from Asia but is not an endemic taxon in Asia. The Euhelopodidae consists of a gigantic monophyletic group. The group has a spread distribution range including Asia, Europe, and South America, but excluding North America, Africa, and Australia. In our reconstruction, the Euhelopodid origin is estimated in the Berriasian, which is compatible with the earliest Euhelopodid known-*Euhelopus zdanskyi*. The MRCA (the most common ancestor) of European and South American taxa possibly emigrated out from Asia by land bridge in the Early Cretaceous, the origination of them is estimated to generally correspond to the Asia and Europe separated by a massive transgression in the Early Cretaceous.

Most taxa remain in Asia. Asian Euhelopodid is divided into two Monophyletic groups and reveals an obvious regional distribution difference between North and South. All taxa in the upper blade are found in northern Asia excluding *Jiangshanosaurus*. All taxa in the lower blade are found in southern Asia excluding *Qiaowanlong*, indicating that a massive spread event appeared in the Asia of the Early Cretaceous, it is also speculated that it is also related to the geographical isolation caused by transgression or other geological phenomenon, we prospect the geological and paleontological evidence excavated in the future.

5. Conclusions

Our paper researched and analyzed an incomplete Sauropod individual PMoL from the Yixian Formation of the Jehol Biota and considered the PMoL as a possible Euhelopodid, and considered that the origin region of the Euhelopodidae in Asia by the paleobiogeographic reconstruction. However, we also considered that the Euhelopodidae is not an endemic taxon in Asia, they may also be distributed in Europe and South America. This viewpoint may have rewritten the evolutionary history of the Euhelopodidae. However, we should also note that the poor preservation of the individual and fossil record has limited our ability to conduct further research on it. Therefore, we look forward to seeing more complete Sauropod dinosaur fossils excavated in the future to solve these problems.

Supplementary Materials: The supplementary materials 'FileS2.tnt.txt' can be found and used at <https://figshare.com/account/items/28517621/edit>.

Author Contributions: All works were conducted by only one author Mr Shan bingqing. Paleontological Museum of Liaoning, Shenyang Normal University supplied fossil individual.

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Conflicts of Interest: The author declares no conflict of interest.

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