



## Full length article

# Revisiting of the Paleocene orthopteran insect *Hylophalangopsis chinensis* Lin and Huang, 2006 in northern Tibet



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## ABSTRACT

In the Dazhuoma stratigraphic section near the Gangni Township, Amdo County, northern Tibet, China, the Paleocene-lower Eocene Niubao Formation yields plenty of well-preserved microfossils and insects. A restudy of *Hylophalangopsis chinensis* Lin and Huang, 2006, an orthopteran insect from this formation, indicates that it should be attributed to Zeuneropterinae of Stenopelmatoidea instead of Prophalangopsidae of Hagloidea in the original study. Some characters preserved in this species are herein considered transitional between Aboilinae (Prophalangopsidae) and Stenopelmatoidea, supporting the deduction that a close relationship exists between Stenopelmatoidea and Aboilinae. The close relationship of *Hylophalangopsis* with the other zeuneropterines in Canada and Scotland indicates a middle-late Paleocene age for the lower Niubao Formation, supported by some previous studies, and further suggests a warm and humid climate in the Dazhuoma area in the middle-late Paleocene, supported by some important evidence.

## 1. Introduction

The Dazhuoma stratigraphic section is located along a gulley near Dazhuoma, Gangni Township, Amdo County, northern Tibet, China, in which the 1986 m thick Niubao Formation is in fault contact with the overlying and underlying Jurassic deposits (Cai and Fu, 2003) (Fig. 1). The formation is subdivided into three members and composed of darkish purple, greenish grey mudstone, silty mudstone, purplish red thin bedded siltstone, and greyish white and greenish grey muddy gypsolyte and gypsolyte. Plenty of charophytes, sporopollen, ostracods and insects have been found from the second member of the formation, indicating a Paleocene-early Eocene age for the Niubao Formation (Cai and Fu, 2003; Li and Zhang, 2005; Peng and Yang, 2005; Wang et al., 2005) (Fig. 1B). A preliminary study shows that at least 20 species attributed to 18 genera and 12 families are recorded from the insect assemblage (Zhao et al., 2001; Cai and Fu, 2003; Lin and Huang, 2006; Szwedo et al., 2013, 2015), of which only an orthopteran was described as *Hylophalangopsis chinensis* Lin and Huang, 2006 attributed to Prophalangopsidae (Lin and Huang, 2006) and two hemipterans as *Priscoflata subvexa* Szwedo, Stroiński and Lin, 2013 and *Gesaris gnapo* Szwedo, Stroiński and Lin, 2015 assigned to Flatidae and Lophopidae, respectively (Szwedo et al., 2013, 2015). The deposits yielding the insect

assemblage are considered to be Paleocene in age (Lin and Huang, 2006; Szwedo et al., 2013).

Reexamination of the holotype of *H. chinensis* Lin and Huang, 2006 indicates that this species cannot be assigned to Prophalangopsidae but to a subfamily within Stenopelmatoidea. Here we re-describe this species, based on which we discuss its systematic position and palaeoclimatic significance.

## 2. Material and methods

The specimen restudied here was collected from the lower part of the second member of Paleocene-lower Eocene Niubao Formation in the Dazhuoma stratigraphic section, northern Tibet. The fossil is preserved as a compression on the surface of the grey mudstone.

There is no consensus on the interpretation of wing-venation nomenclature of Orthoptera, here we follow the wing-venation nomenclature proposed and amended by Béthoux and Nel (2001, 2002). The venational terms used by Zeuner (1939) and Sharov (1968, 1971), and amended by Gorochov (1986, 1995) are listed here following their corresponding ones by Béthoux and Nel (2001, 2002) in parentheses if any differences are present between the two terminologies. The wing-vein abbreviations used are: ScA (C) = Costa; ScP (Sc) = Subcosta;

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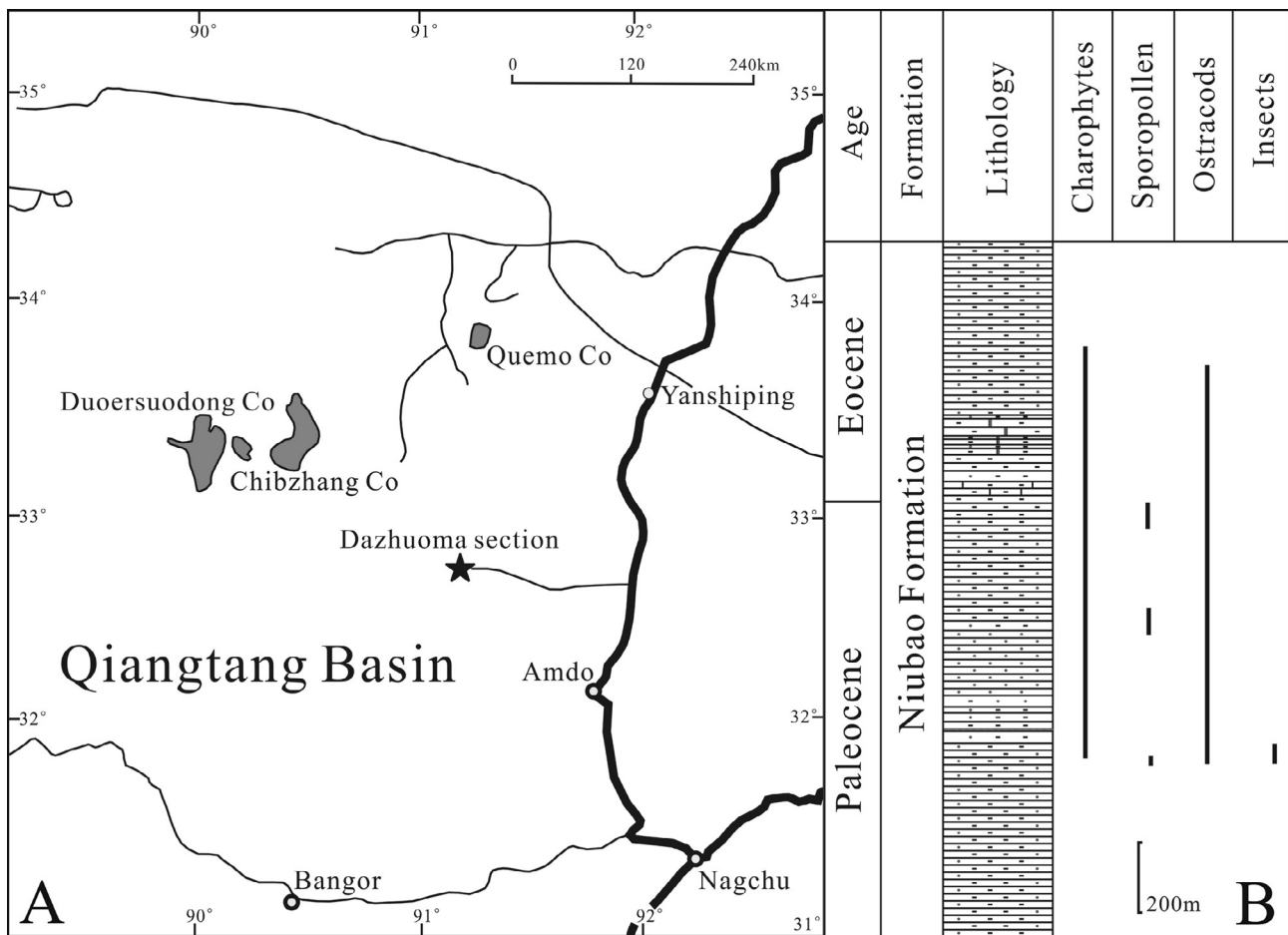


Fig. 1. Geographic and stratigraphic details of strata yielding the orthopteran *Hylophalangopsis chinensis* Lin and Huang, 2006. (A) Map showing the location of the Dazhuoma stratigraphic section; (B) Stratigraphic column showing the lithology of the Niubao Formation and the position of fossils collected in the Dazhuoma stratigraphic section (revised from Cai and Fu, 2003; Li and Zhang, 2005; Peng and Yang, 2005; Wang et al., 2005).

RA = Radius anterior; RP (RS) = Radius posterior; M (MA) = Media; MA (MA1) = Media anterior; MP (MA2) = Media posterior; CuA (MP) = Cubitus anterior; CuPa (CuA) = first cubitus posterior; CuPac (CuA1) = anterior branch of the first cubitus posterior; CuPa $\beta$  (CuA2) = posterior branch of the first cubitus posterior; CuPb (CuP) = second cubitus posterior; A = analis; and 1A = first anal vein.

The specimen was examined dry using a Nikon SMZ1000 stereomicroscope. The photographs were prepared using a NIKON D800 digital camera, and the line drawing was readjusted on the photographs using image-editing softwares (CorelDraw X5 and Adobe Photoshop CS6). The specimen is deposited at the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

### 3. Systematic palaeontology

Order ORTHOPTERA [Olivier, 1789](#)

Superfamily Stenopelmatoidea [Burmeister, 1838](#)

Family Stenopelmatidae [Burmeister, 1838](#)

Subfamily Zeuneropterinae [Kevan and Wighton, 1983](#)

Genus: *Hylophalangopsis* [Lin and Huang, 2006](#)

*Type species. Hylophalangopsis chinensis* [Lin and Huang, 2006](#)

*Holotype.* Incomplete male forewing, part (NIGP135799) and counterpart (NIGP135815); part with posterior area partly lost, counterpart with posterior margin and apical half missing ([Fig. 2](#)).

*Type horizon and locality.* Second member of the Niubao Formation, Paleocene; Dazhuoma area, Gangni Township, Amdo County, northern Tibet, China.

*Revised diagnosis.* Male forewing only. Area between ScA and

anterior margin subtriangular; ScP long and distinct, reaching anterior margin; stem R oblique anteriorly and subparallel to ScP; longitudinal venation still looking parallel; CuPb sigmoidal without stridulatory apparatus.

*Description.* Forewing incomplete with posterior area partly lost, long and narrow. Preserved length about 35 mm, width about 9.5 mm; ratio of length to maximal width about 3.7. Area between ScA and anterior margin elongate and subtriangular, with at least 9 veinlets. ScA long and slightly sigmoidal, reaching anterior margin at wing mid-length. ScP long and distinct, reaching anterior margin at about basal 4/5ths forewing length, and giving off 7 or more distinct and oblique branches, of which at least 2 end in stem ScA; crossveins irregularly distributed between some branches of ScP. Stem R oblique upwards and subparallel to ScP; crossveins between ScP and R almost straight. RA and RP diverging at about basal 2/3rds forewing length; RA pectinately 3-branched; RP with at least 2 branches; crossveins between branches of RA and RP simple. M + CuA diverging at about basal 1/4th wing length; stem M long, twice as long as stem CuA, bifurcating into MA and MP at 14 mm distad of wing base; both MA and MP very long, simple, and slightly arched; areas between R and MA, and between MA and MP with crossveins almost straight and simple, and regularly spaced. Stem CuA sigmoidal, and fusing with CuPac $\alpha$  at 11 mm distad of forewing base. CuPac $\alpha$  diverging from CuPa at 6 mm distad of forewing base; CuA coalescing with CuPac $\alpha$  at 5 mm distad of origin of CuPa $\beta$ , forming a short fused interval (2 mm) and then dividing into 2 simple branches; areas between these branches with crossveins straight; crossveins between CuPac $\alpha$  and CuPa $\beta$  slightly curved. CuPb and 1A slightly curved, and additional 4 anal veins distinguishable. Branches of CuA + CuPac,

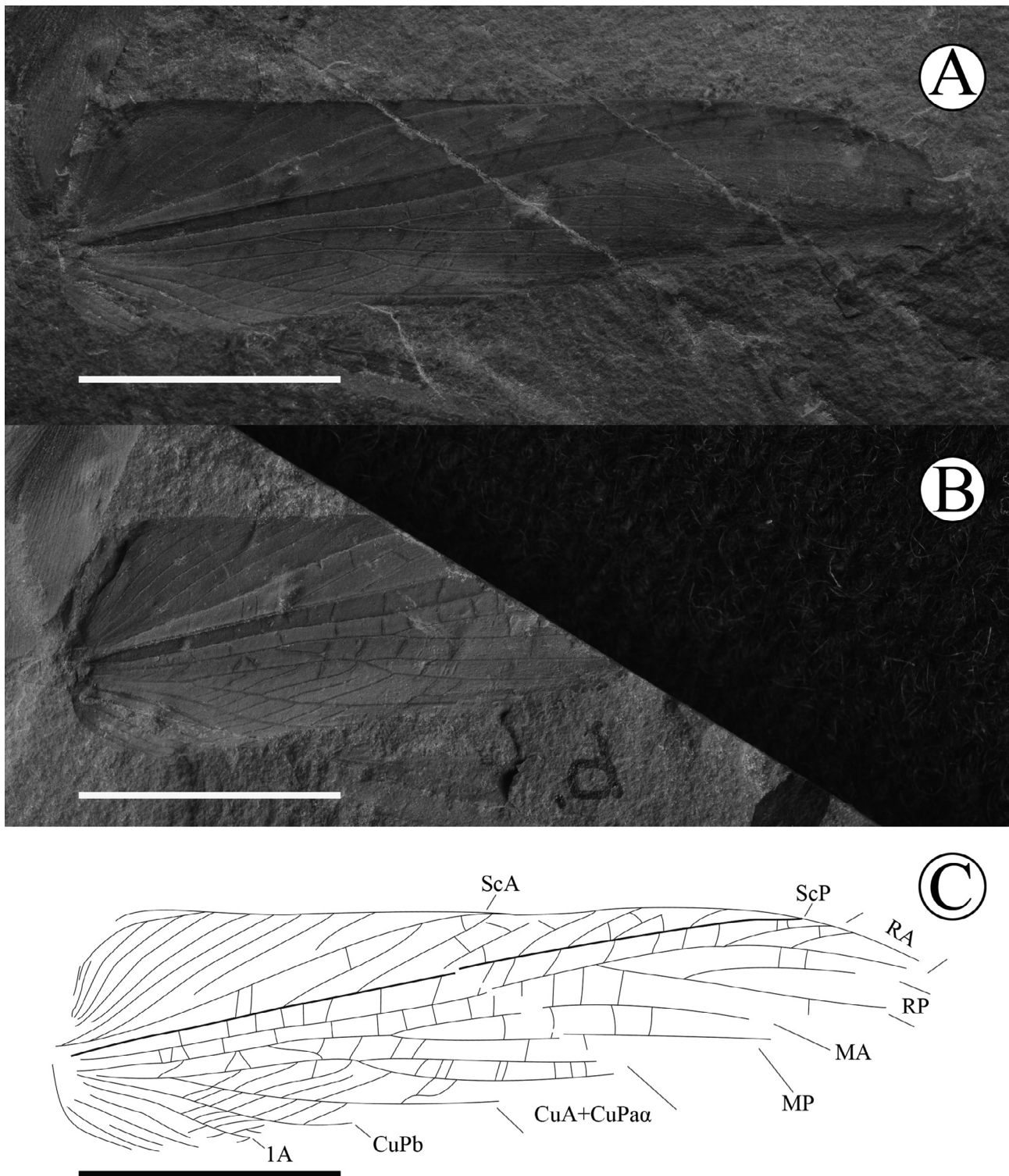


Fig. 2. *Hylophalangopsis chinensis* Lin and Huang, 2006, holotype. (A) counterpart (NIGP135799), (B) part (NIGP135815), (C) reconstruction based on both part and counterpart. Scale bars represent 10 mm.

CuPa $\beta$ , CuPb and 1A subparallel.

#### 4. Discussion

Stenopelmatoidea were thought to be closely related to the subfamily Aboilinae of Prophalangopsidae, Hagloidea (Gorochov, 2001) and are divided into three families: Anostomatidae, Gryllacrididae

and Stenopelmatidae (Song et al., 2015). Cooloolidae were ever placed in Stenopelmatoidea (Zhang, 2011) and are now considered to be actually aberrant Anostomatidae (Song et al., 2015).

The genus *Hylophalangopsis* was previously assigned to Prophalangopsidae, and considered to represent a new genus based on the stridulatory specializations and to differ from all known prophalangopsid genera in the length/width ratio, the precostal area, and the



R vein (Lin and Huang, 2006). These differences, however, suggest that this genus cannot be attributed to Prophalangopsidae. Our observation of the holotype of *H. chinensis* shows that the forewing longitudinal venation is more or less parallel, veins CuPb and 1A probably end in the distal half of the wing (as suggested by their position and direction in the poorly preserved posterior area of the forewing), the stridulatory apparatus is absent, branches of vein ScP are crossed by vein ScA, and the two subparallel branches of CuA + CuPα are developed and probably end in the distal wing. These are all the diagnostic characters of the Stenopelmatoidea (Gorochov, 2001). On the other hand, *Hylophalangopsis* is similar to Prophalangopsidae in having a subtriangular precostal field (between vein ScA and the anterior margin) with some radial veinlets, and ScA reaching the anterior margin subparallel to vein R. These similarities are considered herein as evidence supporting a close relationship between Stenopelmatoidea and Prophalangopsidae as suggested by Gorochov (2001). The gender of this specimen is attributed to a male suggested by the sigmoidal CuPb vein, the same opinion taken by Lin and Huang (2006). However, the slightly curved CuPb vein is greatly different from that of the male Aboilinae of Prophalangopsidae which is clearly curved (more or less Z-shaped), and furthermore lacks the sound teeth. All these suggest that *H. chinensis* has lost the tegminal stridulatory apparatus, also a diagnostic character of Stenopelmatoidea. The above discussions indicate that *H. chinensis* should not be assigned to Prophalangopsidae but to Stenopelmatoidea.

Almost all stenopelmatooids are living species except the subfamily Zeuneropterinae which includes two Paleocene genera, *Zeuroptera* Sharov, 1962 and *Albertoilus* Kevan and Wighton, 1981 (Gorochov, 1988; Zhang, 2011). The preserved characters in *H. chinensis* are quite different from those in the extant stenopelmatooid representatives but similar to those in *Zeuroptera*: the forewing narrow and long; some branches of vein ScP ending on vein ScA; veins MA and MP nearly straight; the longitudinal venation more or less parallel; and veins CuPb and 1A probably ending in the distal half of the forewing. These similarities indicate that *Hylophalangopsis* should be assigned to the subfamily Zeuneropterinae. Gorochov (1988) provisionally included *Albertoilus* in Zeuneropterinae. The monotypic genus *Albertoilus*, with *Albertoilus cervirufi* Kevan and Wighton, 1981 as its type species, was erected based on an orthopteran hindwing from the Paleocene Paskapoo Formation of Alberta, Canada and originally assigned to Prophalangopsidae (Kevan and Wighton, 1981). Later a female forewing from the same horizon and locality as above was attributed to this species (Kevan and Wighton, 1983). This genus really shares the following characters with *Zeuroptera*: the longitudinal venation more or less parallel; veins CuPb and 1A probably ending in the distal half of the forewing; vein CuA short; and the area between veins CuA + CuPα and CuPβ broad. So it is reasonable to assign this genus to Zeuneropterinae. *Hylophalangopsis* is different from *Zeuroptera* in having less branches of veins RA, RP and CuA + CuPα, a sigmoidal CuA vein, a longer CuPα vein and a narrower area between veins CuA + CuPα and CuPβ in the forewing; and from *Albertoilus* in having a much narrower area between veins CuA + CuPα and CuPβ, and between veins M + CuA and CuPa, a sigmoidal CuA vein and fewer branches of CuA + CuPα.

The systematic position of Zeuneropterinae, however, is questionable within Stenopelmatoidea. Sharov (1968) placed it in Gryllacrididae but Gorochov (2001, 2003) assigned it to Anostomatidae. Very recently, Cigliano et al. (2017) considered it to be a subfamily of Stenopelmatidae. It is difficult to determine its position before more well-preserved material has been found and studied. Nevertheless, it is undoubted that the Zeuneropterinae are the most ancient and primitive group of all known Stenopelmatoidea (Gorochov, 2001), and probably a basal group in Stenopelmatoidea. Here we follow Cigliano et al. (2017) and tentatively assign the subfamily to Stenopelmatidae.

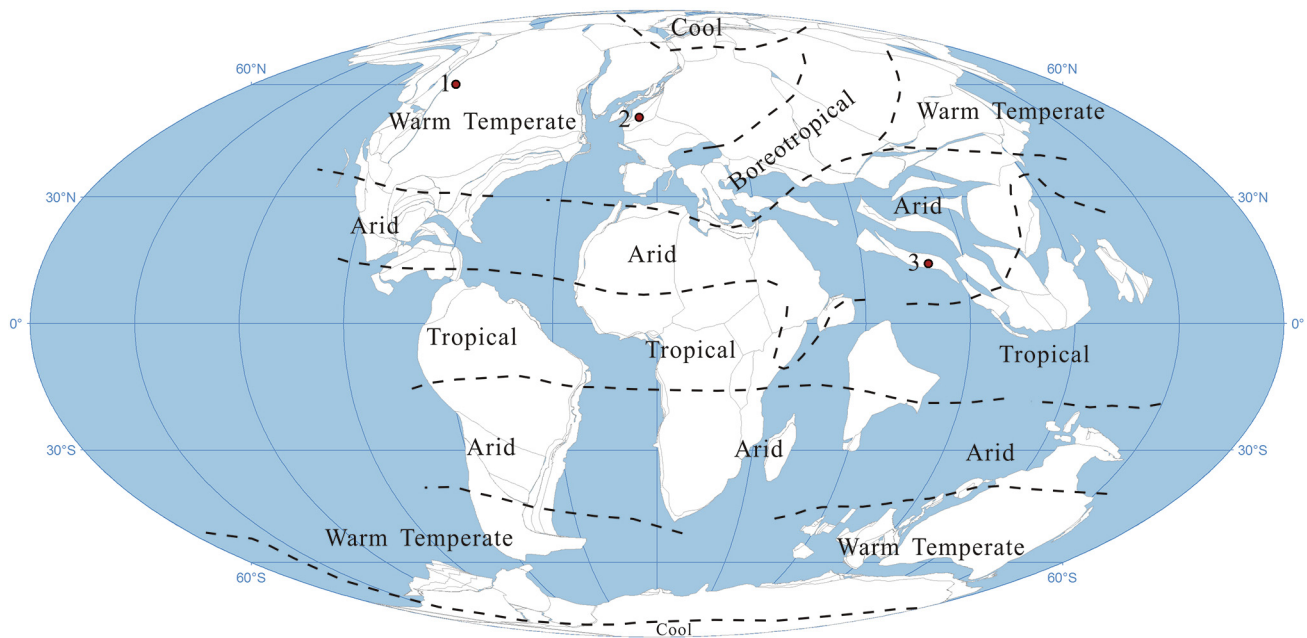
## 5. Palaeoclimatic implications

Up to now, three species in three genera have been assigned to the subfamily Zeuneropterinae. *Zeuroptera scotica* (Zeuner, 1939) Sharov, 1962 was found in the interbasaltic beds in Mull, Ardtun Head, Scotland (Zeuner, 1939; Frederick, 1941; Sharov, 1962) which have an age of probably 60.5–57.5 Ma (Jolley et al., 2002), middle-late Paleocene (Cohen et al., 2013). *A. cervirufi* was reported in the Paskapoo Formation near Red Deer in Alberta, western Canada (Kevan and Wighton, 1981, 1983). The formation is middle-late Paleocene in age based on detailed palynostratigraphic, mammal biostratigraphic, radiostopic and magnetostratigraphic studies (Hamblin, 2004). The similarities of *Hylophalangopsis* to *Zeuroptera* and *Albertoilus* suggest that the lower Niubao Formation is probably middle-late Paleocene in age, which is supported by some previous studies (Lin and Huang, 2006; Szwedo et al., 2013, 2015).

It is considered that the pole to equatorial temperature gradient was low in the Paleocene, which means that the warm temperate belt spread out over high latitudes (Boucot et al., 2013). The Paleocene palaeogeographic map shows that both *Z. scotica* and *A. cervirufi* lived in the warm temperate zone but *H. chinensis* existed in the arid zone in the Northern Hemisphere (Fig. 3). However, palaeobotanical data suggest the region yielding *H. chinensis* was located in the tropical zone with a wet equatorial climate in the Paleocene (Akhmetiev, 2004), and the palynological assemblages collected from the Dazhuoma stratigraphic section indicate a warm and moist subtropical climate (Li and Zhang, 2005). Furthermore, the hemipteran species *Gesaris gnapo* Szwedo, Stroiński and Lin, 2015 preserved together with *H. chinensis* is a representative of Lophopidae, a family of planthoppers present today in tropical and subtropical zones of the Old World (Szwedo et al., 2015), which also supports *H. chinensis* living in a warm and wet climate. A mesothermal humid climate was inferred from the flora of the Ravenscrag Formation in southeastern Alberta-southwestern Saskatchewan, which can be correlated to the Paskapoo Formation (Hamblin, 2004). This as well as coals in the upper Paskapoo Formation indicates a similar climate in Alberta when the Paskapoo Formation was deposited (Hamblin, 2004). The interbasaltic beds in Scotland not only contain insects but also a lot of plants (Frederick, 1941; King, 2016). Palaeoclimate estimates derived from the fossil angiosperm leaves indicate that the climate of the Allt Mor locality on Skye in western Scotland at the age of  $60.16 \pm 0.45$  Ma had a mean annual temperature (MAT) of  $-5^{\circ}\text{C}$  to  $9^{\circ}\text{C}$ , and was seasonal with warm summers (warm month mean  $19.0\text{--}25.8^{\circ}\text{C}$ ) and cool to cold winters (cold month mean  $-3.0^{\circ}\text{C}$  to  $4.2^{\circ}\text{C}$ ) (Poulter, 2013). The flora of Ardtun on Mull ( $60.5 \pm 0.3$  Ma) is different from the coeval Allt Mor flora, although these two floras share many taxa, in that angiosperms are dominant, and conifers that are common in the Allt Mor assemblage are rare or absent (Poulter, 2013). Additionally, the Ardtun flora also contains thermophilic plants such as *Camptodromites major* (Johnson) Boulter and Kvaček, 1989, *C. multinervatus* (Johnson) Boulter and Kvaček, 1989 and *Amentotaxus gladifolia* (Ludwig) Ferguson, Jähniche and Alvin, 1978, which are absent from Skye (Poulter, 2013). All the above indicates that the subfamily Zeuneropterinae preferred to live in a warm and humid climate.

## 6. Conclusions

Re-description of the holotype of *Hylophalangopsis chinensis* Lin and Huang, 2006 indicates that this species should not be attributed to the family Prophalangopsidae of Hagloidea but to the subfamily Zeuneropterinae of Stenopelmatidae. Some characters preserved in this species show a transition between Aboilinae (Prophalangopsidae) and Stenopelmatoidea, supporting the deduction by Gorochov (2001) that a close relationship exists between Stenopelmatoidea and Aboilinae. Although Zeuneropterinae are systematically debatable within Stenopelmatoidea, some evidence indicates that they are probably a



**Fig. 3.** Paleocene palaeogeographic map showing the locality of *Albertoitus cervirufi* Kevan and Wighton, 1981 (red point 1), of *Zeuneroptera scotica* (Zeuner, 1939) (red point 2), and of *Hylophalangopsis chinensis* Lin and Huang, 2006 (red point 3). Palaeogeographic reconstructions from PaleoMap 2014 for ArcGIS ([www.scotese.com](http://www.scotese.com)). Paleoclimatic zones based on Boucot et al. (2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

group in the superfamily. The close relationship of *Hylophalangopsis* with the other zeuneropterines indicates a middle-late Paleocene age for the lower Niubao Formation, supported by some previous studies. The known zeuneropterines in Canada and Scotland lived in a warm and humid climate, suggesting a similar climate in the Dazhuoma area in the middle-late Paleocene. This inference is supported by the palynological evidence, the palaeobotanical data, and an associated hemipteran insect although northern Tibet was considered by Boucot et al. (2013) to be located in the arid zone in the Paleocene.

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