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Woodland in a fluvio-lacustrine environment on the dry Mongolian Plateau during the late Paleocene: Evidence from the mammal bearing Subeng section (Inner Mongolia, P.R. China)

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Abstract

In the understanding of the global faunal turnover during the Paleocene–Eocene transition, an important role has been attributed to the Asian continent, although the Asian fossil record for this period is still incomplete. Here we present a multidisciplinary study of the Subeng section (Inner Mongolia, P.R. China), integrating sedimentological, stratigraphical and diverse palaeontological data, in order to reconstruct the palaeoenvironment and to enhance the understanding of the late Paleocene communities that once thrived on the Mongolian Plateau. The Subeng section starts with the Maastrichtian Iren Dabasu Formation directly covered by the late Paleocene Nomogen Formation. This Nomogen Formation is composed of typical lacustrine deposits at the base, covered by fluvio-lacustrine deposits at the top. Both types of deposits provided rich ostracod and charophyte assemblages, closest to those of the Naran Member, Naran Bulak Formation of Mongolia. Palynomorphs from the lake sediments suggest a local flora at Subeng more wooded and closed than reported from elsewhere in this region. The fluvio-lacustrine deposits of the Nomogen Formation have yielded a vertebrate fauna especially rich in mammals. The mammal fauna from Subeng is close to that from Bayan Ulan and typical for the Gashatan Asian Land Mammal Age. The presence of reworked pedogenic carbonate nodules and mud aggregates suggests an at least seasonally dry regional climate. Combined sedimentological and palaeontological data suggest the late Paleocene Nomogen Formation at Subeng was an isolated woodland in a fluvio-lacustrine environment, representing a locally humid environment on the semi-arid Mongolian Plateau. The mammal fauna reflects these differences and shows a number of relatives to mammals from the more humid northeastern Chinese biotic province as well as some North American immigrants.

Keywords: Paleocene; Nomogen Formation; Gashatan; Erlian Basin; Inner Mongolia; China

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1. Introduction

The Paleocene/Eocene (P/E) boundary is a major turning point in Earth's history with sudden biotic changes in the marine and terrestrial realm. Across the northern hemisphere continents, a wave of modern mammal groups appeared at the beginning of the Eocene, at the expense of archaic forms that progressively became extinct.

These faunistic changes are associated with a sudden climate pulse, known as the Paleocene–Eocene Thermal Maximum (PETM) caused by a massive release of greenhouse gasses into the atmosphere. This event is reflected in the isotopic record by a consistent negative spike in the $^{13}C/^{12}C$ ratio and this carbon isotope excursion (CIE) has been chosen as the boundary criterion for the P/E boundary (Gradstein et al., 2004 and references therein; Magioncalda et al., 2004).

Rich fossil mammal localities of the P/E-boundary interval have been intensely studied in North America (Gingerich, 2000, 2001, 2003) and Europe (Hooker, 1998; Smith, 2000). They have clearly demonstrated the sudden appearance of modern mammal groups over the entire northern hemisphere. However, the geographic origin of these modern mammals has not yet been discovered. Several hypotheses have been proposed and many of these attribute an important role for the Asian continent (Krause and Maas, 1990; Beard, 1998; Bowen et al., 2002; Ni et al., 2004), although the Asian fossil record for this period is still very incomplete. Therefore late Paleocene and early Eocene Asian mammal sites have been a popular research topic in recent years (Wang et al., 1998; Ting et al., 2003). Traditionally, the P/E boundary in Asia is correlated to the boundary between the Gashatan and the Bumbanian Asian Land Mammal Ages (ALMA). The Gashatan faunas are best represented in the Gashato site and the Zhigden and Naran Member from Naran Bulak site in Mongolia and in the Bayan Ulan and Nomogen sites in Inner Mongolia, China. The best representatives for the Bumbanian ALMA are found within the Bumban Member of Naran Bulak in Mongolia, the Wutu Formation in East China and the Upper Lingcha Formation in South China (Ting et al., 2003).

The Subeng (Subon) locality was discovered in 1976, during field prospections in the Bayan Ulan and Nomogen area by Chinese scientists from the Institute of Vertebrate Paleontology and Paleoantropology (IVPP) and the Inner Mongolia Museum (IMM). Although Russell and Zhai (1987) mentioned the locality, no material from the Subeng locality was published. At the occasion of the Sino–Belgian Dinosaur expeditions (Bultynck and Dhondt, 1998, 1999, 2001), the Subeng region was re-explored by one of us (T.S.) in 1995 and a level rich in mammal remains was discovered. This level was sampled during fieldwork in 2000, 2001 and 2004, with the description of a new genus from the Subeng locality (Smith et al., 2004).

Although the Mongolian Plateau houses many interesting Paleogene mammal sites, only few sedimentological, micropalaeontological and paleoenvironmental studies have been conducted. The mammal bearing level at Subeng is situated within a well-exposed section that has also yielded numerous microfossils, molluscs, fish, amphibians, lizards, turtles, eggshells, and silicified wood fragments, which makes the section ideally suited for such studies. The present paper aims to give a summary of the Subeng section, integrating the sedimentological, stratigraphical and diverse palaeontological data. Thereby, we try to reconstruct the palaeoenvironment and to enhance the understanding of the late Paleocene communities that once thrived on the Mongolian Plateau.

2. Geological setting

The Subeng section is situated near the Chinese–Mongolian border, within the Inner Mongolia autonomous province, P.R. China (Fig. 1, A). In this region an extensive sedimentary basin system comprises several basins, a.o. the Erlian Basin in which the studied section is located (Fig. 1, B). The sedimentary basin system in the Chinese–Mongolian border region is dominantly infilled with late Mesozoic sediments (Meng et al., 2003 and references therein). However upper Paleocene, Eocene and Oligocene strata are well developed in the Erlian Basin (Bureau of Geology and Mineral Resources of Nei Mongol autonomous region (BGMRNMAR), 1991).

The Subeng locality is situated 20 km southwest of the city of Erlianhot (Fig. 1, C). In an incline on the plateau, gullies have eroded the Quaternary cover, exposing the Tertiary sediments. In these outcrops three lithological units are observed (Fig. 1, D). The lower unit 1 is situated at the very base of the incline, and it is separated from the middle unit 2 by a hiatus that is obscured by runoff sediments. The transition from unit 2 to the upper unit 3 is continuously exposed.

The regional geological map (BGMRNMAR, 1991) identifies these three units respectively as the upper Cretaceous Iren Dabasu Formation and the Tertiary Nomogen and Bayan Ulan formations. Here however, we adopt the view of Meng et al. (1998), who no longer consider the Bayan Ulan beds as a separate formation, but as the upper part of the Nomogen Formation.

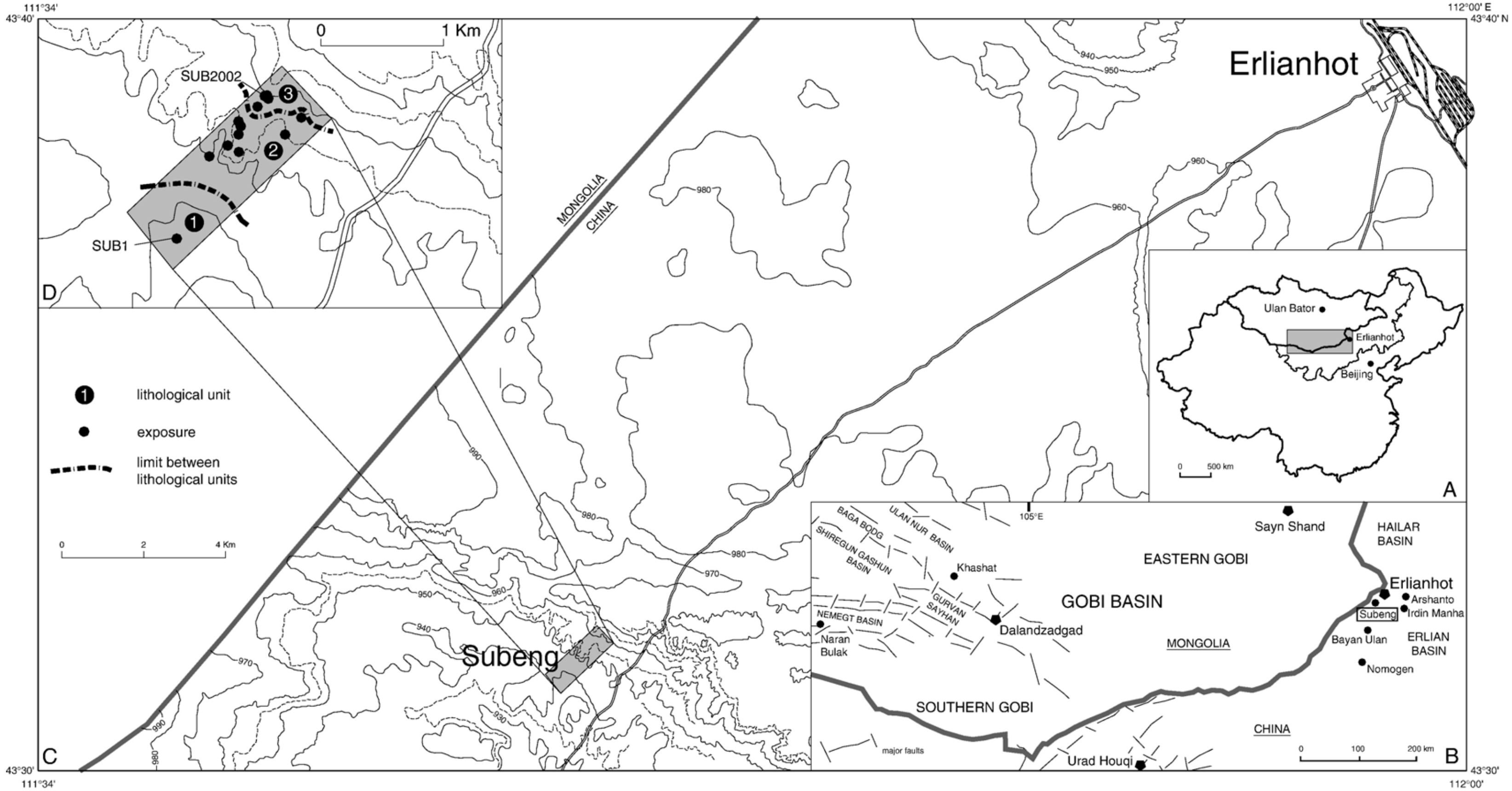

Fig. 1. A, inset map showing the location of the town Erlianhot in Inner Mongolia, China, grey rectangle indicates the area enlarged in B; B, map of the Gobi Basin with main cities (⬟) and important mammal sites (●); C, topographic map with the Subeng mammal site 20 km southwest from Erlianhot; D, detail of the Subeng section.

3. Sedimentary Geology

3.1. Unit 1 (Iren Dabasu Formation)

Although this unit crops out in a vast area according to the geological map, it is only temporarily exposed in a man-made, 0.6-m deep trench at the base of the section. Two contrasting lithologies have been observed: a 0.05-m thick black, organic-rich clay covered by a white silt (Fig. 2). The fossil content of this exposure is limited to the palynomorphs retrieved from the organic-rich clay. This layer is interpreted as a histosol indicative of wetland conditions during deposition (Mack et al., 1993).

Conversely, in its type area around the Iren Nor salt lake (Berkey and Morris, 1927), the Iren Dabasu Formation presents only ferric and vertic gleyed calcisols (Van Itterbeeck et al., 2005).

3.2. Unit 2 (Nomogen Formation)

The green mudstones and white to yellowish limestones of unit 2 are exposed in the middle part of the Subeng section (Fig. 2). The limestones display an irregular fissility more or less parallel to the bedding plane. On these planes ostracod shells are abundant and can be observed with the naked eye. In thin section these limestones can be characterized as ostracodal packestones (Fig. 3.2). Charophyte gyrogonites occur in minor quantities while calcified charophyte stems have not been observed. The limestone near the top of the unit is somewhat different: it has a massive thickness of 20 cm and can be classified as an ostracodal wackestone (Fig. 3.3). Besides ostracods and charophytes, this layer has also yielded numerous gastropods but the vertebrate content is limited to rare fish teeth.

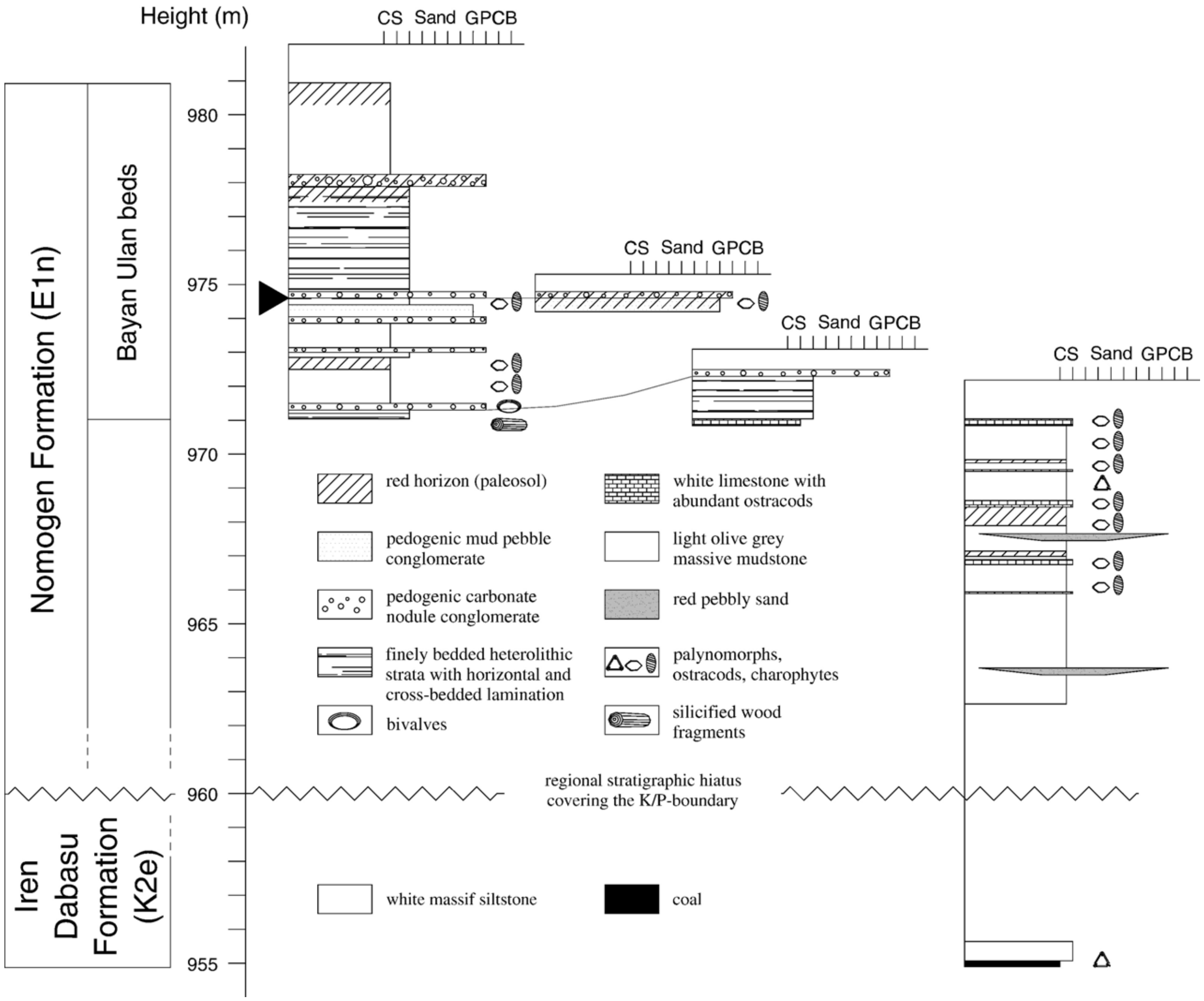

Fig. 2. Lithostratigraphic column of the Subeng section, ▶ indicates the mammal bearing horizon.

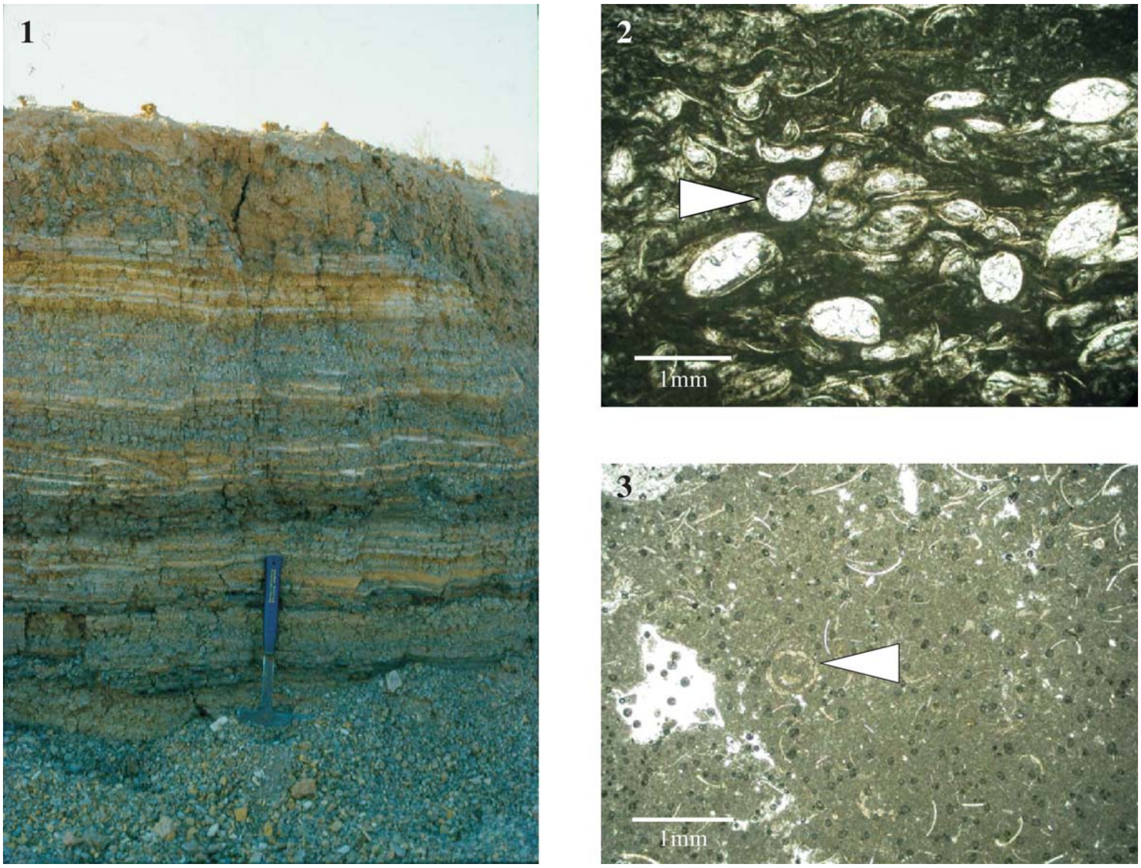

Fig. 3. Sediments of unit 2: 1, typical finely laminated strata with an alternation of greenish marls and white limestones, the dark organic-rich layers near the base have yielded a rich palynomorph assemblage; 2, thin section of ostracodal packstone; 3, thin section of ostracodal wackestone; arrows indicating charophytes.

The mudstones yield a similar fossil content, although in minor quantities, compared to the limestone layers. The mudstones are dominantly greenish, although black, organic-rich layers and red layers have been observed. The clay mineralogy of these mudstones has been defined by standard X-ray diffraction techniques which include untreated, glycolated and heated diffraction patterns. The dominant clay minerals are smectite and illite with minor kaolinite occurrences. There are no significant differences in clay mineralogy in the mud layers with a different colour.

Mudstones and limestones have been observed in two facies associations. In the first, they display a nearly undisturbed, fine cm-scale lamination (Fig. 3.1). It is within this association that the dark, organic-rich marls have been observed. The second association also shows an alternation of limestones and mudstones. However, in this case, both lithologies form uniform, massive beds with thicknesses ranging from 5 to 20 cm for the limestones and up to 120 cm for the mudstones. Within this second association, reddish mudstone layers have been observed, but dark, organic-rich layers are completely absent. Also within this second association two red, coarse pebbly sand lenses with a lateral extension of 2–3 m and a fining upward trend have been observed.

Both associations represent typical freshwater, lacustrine deposits, an interpretation corroborated by the fossil content of these layers (see Section 4). The rhythmically laminated sediments of association 1 are typical deeper water lacustrine deposits. The preservation of laminae indicates the absence of a bioturbating bottom fauna, which is typical for the deeper part of a stratified lake with anoxic bottom layers (Platt and Wright, 1991). The alternation of mudstone and limestone sedimentation is caused by an interplay between influx of siliciclastic material and biogenic carbonate production. During phases of high siliciclastic input in the lake, carbonate production is low due to the lowered light penetration in the suspension-rich waters and mudstones are deposited. During phases of low siliciclastic input, carbonate production is high due to


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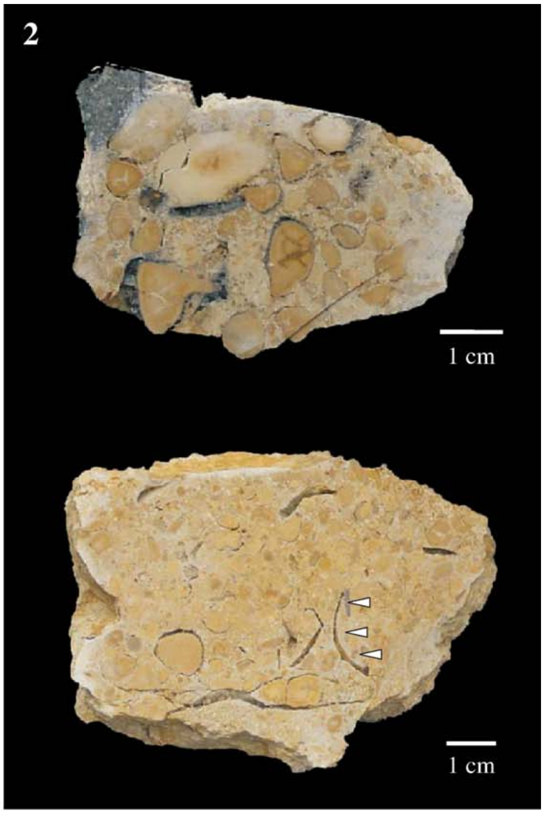
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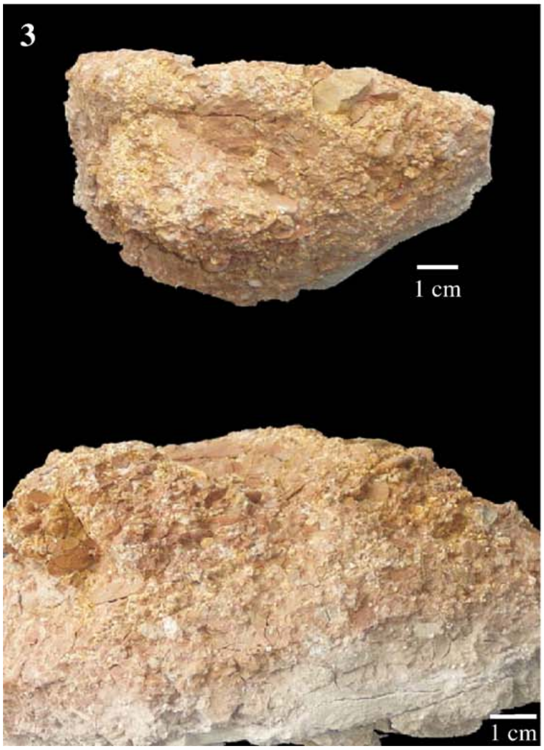
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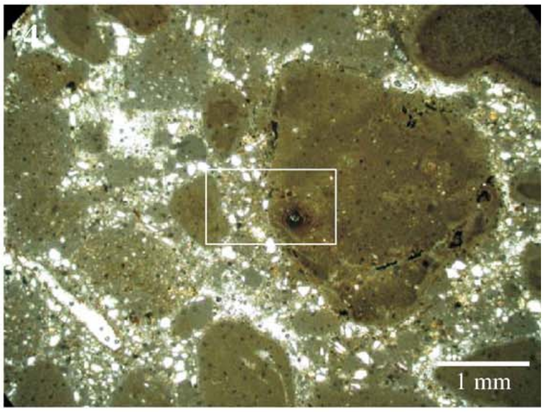
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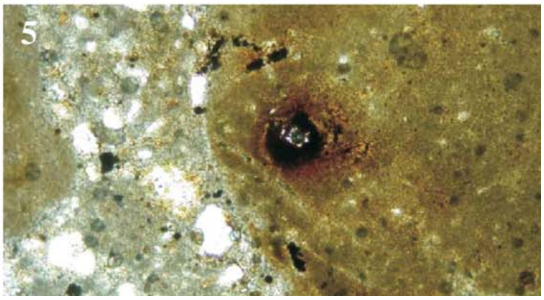
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the enhanced light penetration in the clear lake waters resulting in limestone sedimentation. These processes play on different scales as can be deduced from Fig. 3.1. On a small scale, they cause the alternation of the separate mudstone and limestone laminae. On a larger scale, they cause groups of laminae that are dominated by one of the lithologies. For example, the top of this exposure is clearly dominated by limestone laminae compared to the rest of the outcrop.

The second association of mudstones and limestones is typical for shallow, nonstratified lacustrine environments. Bioturbation prevents the preservation of the smallscale lamination and only the large-scale variation (or dominance) is preserved. Due to fluctuations in the lake level, these shallow environments can temporarily be subaerially exposed resulting in the red coloring of the mudstones. No pedogenic features have been observed within the limestones. The red sandy lenses observed within this second association are interpreted as turbidity flows caused by large influxes of siliciclastic material within the lake. The most likely source is a larger river feeding the lake, but due to the limited exposure area it has not been observed.

3.3. Unit 3 (Bayan Ulan Beds, Nomogen Formation)

Unit 3 is exposed in the upper part of the section and displays the highest variability in both lithology and fossil content. The exposure of unit 3 is covered by a weathered horizon with a lag deposit enriched in silicified wood fragments, and as such its extent can easily be traced in the landscape. These fragments are poorly preserved but they can be attributed to gymnosperms (Gerrienne, pers. comm.). Unit 3 mainly consists of massive mudstones and finely bedded heterolithic sand-, silt- and claystones. The latter strata have a colour varying between yellowish gray (5Y8/1) and light olive gray (5Y6/1), and show both horizontal and cross-bedded laminations. The massive mudstones are light olive gray (5Y5/2), and strongly resemble those of unit 2 in outward appearance, but clearly differ in clay mineralogy and fossil content. The unit 3 mudstones contain smectite, illite and kaolinite like the lacustrine mudstones, but also small amounts of chlorite. Their fossil content is dominated by charophytes, while the muds of unit 2 are dominated by ostracods.

The deposits described above are intercalated with pebble layers and some levels have a pebble fraction exclusively consisting of pedogenic carbonate nodules forming a conglomerate (Fig. 4.4, 4.5). On one occasion, such a conglomerate forms the basal infill of a channel with a lateral extent of 20 m and a maximum depth of 1.25 m. The pedogenic nature of the pebbles has been proven by the occurrence of rhizocretons in thin sections. Most of the carbonate nodule layers are friable but some are well cemented and have proven to be also rich in bivalve molds. Other of these coarser levels contain a mixture of mud pebbles varying from 1 to 10 mm in size and sandsized carbonate particles (Fig. 4.3). The mud pebbles are well rounded with a flattened shape and a colour similar to the adjacent mudstones. The carbonate particles are white to yellowish and both biogenic (gyrogonites, ostracods, charophyte stems) and pedogenic in origin. A total of 1750 kg of these coarser layers were screenwashed for vertebrate fossils (Fig. 4.1).

As in unit 2, several red-coloured horizons have been recognized throughout unit 3 in all the different sediment types. They are often associated with slickensides and the presence of iron nodules and can be interpreted as palaeosols. The different coarse-grained lithologies in unit 3 indicate fluvial activity; and the large amount of gyrogonites and calcified charophyte stems are typical for marginal lacustrine environments, with still or slowly running waters (Corillion, 1975; Tappan, 1980). Unit 3 is therefore identified as marginal lacustrine/fluvial system that is a part of the lake during high lake levels. During low lake levels, soils are formed within the subaerially exposed sediments and fluvial activity reworks the altered sediments.

During the periods with the lowest lake levels soil formation is even observed within the sediments of unit 2.

The fluvial system described here is not the trunk channel feeding the lake as its deposits do not contain the coarse siliciclastic grains observed in the unit 2 turbidite deposits. The mud pebbles deposited in unit 3 are clearly transported as bedload and not in suspension. Rust and Nanson (1989) were the first to describe this kind of bedload transport and they considered the mud pebbles as reworked pedogenic mud aggregates. The co-occurrence with reworked pedogenic carbonate nodules in Subeng section also clearly corroborates their pedogenic nature. No in situ mud aggregates or carbonate nodules have been observed and their main region of origin is unexposed. According to Rust and Nanson (1989), the mud aggregates form under a

Fig. 4. Sediments of unit 3: 1, Exposure of screenwashed mammal-bearing level, a typical pedogenic carbonate nodule conglomerate; 2, cemented pedogenic carbonate nodule conglomerate with bivalve steinkerns (indicated by arrows); 3, Pedogenic mud aggregates; 4, Thin section through pedogenic carbonate nodule conglomerate, white rectangle indicates enlarged of 5; 5, detail of pedogenic carbonate nodule with root trace.

Table 1
List of charophyte taxa observed in unit 3, Subeng section

- Order Charales Lindley, 1836
  - Suborder Charineae Feist and Grambast-Fessard, 1991
    - Family Clavatoraceae Pia, 1927
      - Subfamily Clavatoroideae Pia, 1927 emend. Grambast, 1969
        - Genus *Caenoclavator* Wang and Lu, 1982
          - *Caenoclavator hubeiensis* Wang and Lu, 1982
    - Family Characeae Agardh, 1824
      - Subfamily Charoideae Migula, 1897
        - Genus *Grovesichara* Horn af Rantzien, 1959
          - *Grovesichara changzhouensis* Huang and S. Wang in Wang, 1978
          - *Grovesichara kielani* Karczewska and Ziembinska-Tworzydlo, 1972
        - Genus *Peckichara* Grambast, 1957
          - *Peckichara varians* Grambast, 1957
          - *Peckichara lefeldi* Karczewska and Ziembinska-Tworzydlo, 1973
          - *Peckichara subsphaerica* Lin and Z. Wang, 1982
        - Genus *Neochara* Z. Wang and Lin, 1978
          - *Neochara huananensis* Z. Wang and Lin, 1978
        - Genus *Nemegtichara* Karczewska and Ziembinska-Tworzydlo, 1972
          - *Nemegtichara prima* Karczewska and Ziembinska-Tworzydlo, 1972
          - *Nemegtichara secunda* Karczewska and Ziembinska-Tworzydlo, 1972
          - *Nemegtichara quarta* Karczewska and Ziembinska-Tworzydlo, 1972
        - Genus *Gobichara* Karczewska and Ziembinska-Tworzydlo, 1972
          - *Gobichara deserta* Karczewska and Ziembinska-Tworzydlo, 1972
          - *Gobichara nigra* Karczewska and Ziembinska-Tworzydlo, 1972
          - *Gobichara tenera* Karczewska and Ziembinska-Tworzydlo, 1972
          - *Gobichara rubra* Karczewska and Ziembinska-Tworzydlo, 1972
          - *Gobichara latielliptica* Lu and Luo, 1990
        - Genus *Sphaerochara* Mädler, 1952 emend. Horn af Rantzien, 1959 emend. Horn af Rantzien and Grambast, 1962
          - *Sphaerochara minutissima* (Mädler, 1955) n. comb.
        - Genus *Collichara* S. Wang and Z.R. Zhang, 1982
          - *Collichara taizhouensis* S. Wang and Z.R. Zhang, 1982
          - *Collichara xiaohekouensis* S. Wang and Zhang, 1982
        - Genus *Microchara* Grambast, 1959
          - *Microchara* cf. *vestita* Castel, 1969
        - Genus *Pseudolatochara* Z. Wang, 1978
          - *Pseudolatochara ovatoides* Huang and Zhang, 1984
          - *Pseudolatochara* sp.
        - Genus *Maedleriella* Grambast 1957
          - *Maedleriella* sp.
        - Genus *Mesochara* Grambast, 1952
          - *Mesochara* sp.
        - Genus *Stephanochara* Grambast, 1959
          - *Stephanochara lauta* (Liu, 1987) comb. nov.
          - *Stephanochara cuniformis* (Zhang, 1978) comb. nov.
          - *Stephanochara stipitata* (Liu, 1987) comb. nov.
          - *Stephanochara grambasti* (Karczewska and Ziembinska-Tworzydlo, 1972) comb. nov.
          - *Stephanochara grandiceps* (Wang, 1981) comb. nov.
        - Genus *Chara* Linnaeus, 1753
          - *Chara* spp.

climate with at least seasonally hot and dry periods in clay-rich layers containing at least a minor amount of swelling clays, the ideal conditions to generate vertisols. Indeed, the dominant clay mineral in these pebbles as in the rest of unit 3 is smectite and the palaeosol horizons do display vertic features like slickensides.

The reworked pedogenic carbonate nodules originate from calcretes that have been described from both Cretaceous (Van Itterbeeck et al., 2005) and Paleocene deposits in the other parts of the basin. In fact, these calcretic carbonate nodules have been used in other outcrops of the Nomogen Formation to locate the P/E boundary based on carbon isotopes (Bowen et al., 2005).

4. Palaeontology

4.1. Charophytes

The mammal-bearing horizon in the Subeng section has yielded a very rich assemblage of charophytes (see Table 1 for a complete list; see also Fig. 5). At the generic level the charophyte assemblage indicates a Paleocene to Eocene age. Seven genera, *Gobichara*, *Nemegtichara*, *Peckichara*, *Collichara*, *Microchara*, *Pseudolatochara* and *Maedleriella* have a stratigraphic range from the upper Cretaceous into the Eocene (Feist and Grambast-Fessard, 1982, Huang and Zhang, 1984; Huang and Zhao, 1989). The genera *Grovesichara*, *Chara* and *Stephanochara* are typical Cenozoic genera. From a geographical point of view, *Nemegtichara*, *Gobichara*, *Collichara*, *Neochara*, *Caenoclavator* are endemic to China and Mongolia while *Grovesichara*, *Chara*, *Stephanochara* and *Peckichara* have a cosmopolitan distribution.

One of the most abundant species is *Grovesichara changzhouensis*. This species is generally considered as a biostratigraphic marker of Paleocene to early Eocene strata in China (Tang and Di, 1991). Two specimens were attributed to *Caenoclavator hubeiensis* (Fig. 5, 11–13) that had thus far only once been observed in the lower Eocene (Wang and Lu, 1982). However, another species, *C. naomugenensis* has been reported from the late Paleocene Nomogen Formation (Liu, 1987). *Caenoclavator* is the only Cenozoic representative of the family Clavatoraceae; although the validity of the genus has been contested (Lu, 1997), we continue to use it here

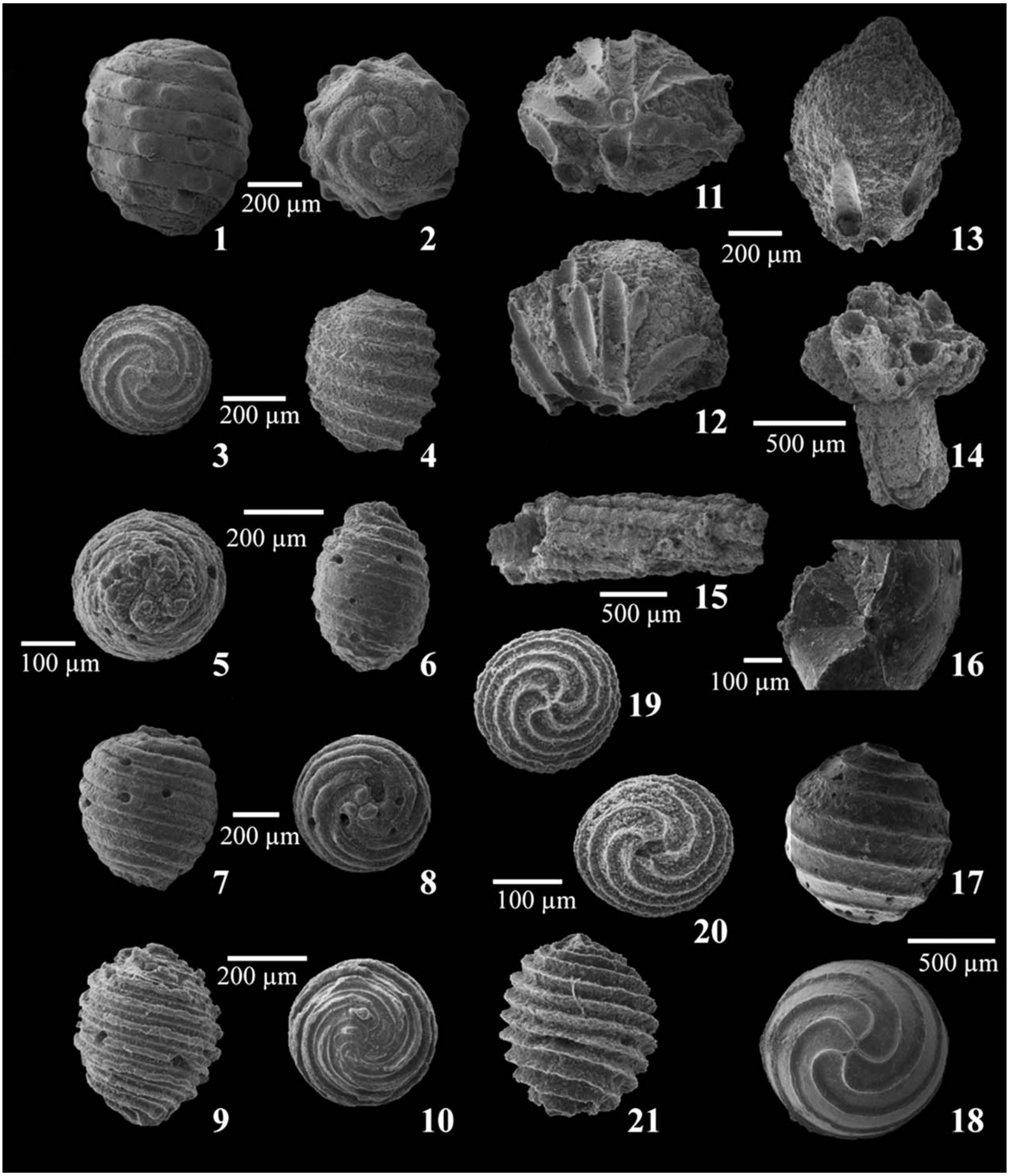

Fig. 5. Charophytes of the mammal bearing horizon: 1, *Neochara huananensis*, lateral view; 2, idem, apical view; 3, *Nemegtichara prima*, apical view; 4, idem, lateral view; 5, *Collichara taizhouensis*, apical view; 6, idem, lateral view; 7, *Peckichara lefeldi*, lateral view; 8, idem, apical view; 9, *Gobichara deserta*, lateral view; 10, idem, apical view; 11, *Caenoclavator hubeiensis*, basal view; 12/13, idem, lateral view; 14/15, *Charaxis* sp.; 16, *Grovesichara changzhouensis*, detail of basal plate; 17, idem, lateral view, 18, idem, apical view; 19, *Sphaerochara minutissima*, apical view; 20, idem, basal view with composed basal plate; 21, idem, lateral view.

for lack of an alternative. The current material doesn't allow a detailed study of this genus.

The charophyte assemblage from unit 3 most closely correlates with that from the late Paleocene Naran Member of the Naran Bulak Formation (Nemegt Basin, Mongolia). From the 19 species in 9 genera present at Naran Bulak (Karczewska and Ziembinska-Tworzydlo, 1972), 12 species in 6 genera were also found at Subeng. So, the charophyte flora of the mammal-bearing horizon in the Subeng section clearly indicates the correlation of these beds with the Naran Member of the Naran Bulak Formation and suggests a late Paleocene age.

The charophyte flora of unit 2 is similar though fairly poor (both in specimens and species) compared with the flora of unit 3. The most important difference is the absence of *Grovesichara changzhouensis*.

The charophyte flora of the Nomogen and Iren Dabasu formations has been studied by Liu (1987). The data for this publication were compiled from different localities in the Shalamulun area in Inner Mongolia. For the Nomogen Formation, some of the data were gathered in a locality named 'Subeng' (Liu, 1987, p. 131–133), but any information on the exact location is lacking and it is unclear if Subeng in Liu (1987) equals the section studied in the present work. Liu (1987) considers the Nomogen Formation and the Bayan Ulan Formation as two separate formations, probably corresponding to unit 2 and unit 3 as described in the present work. Both levels as identified by Liu (1987) are very similar, differing mainly by the presence of *Obtusochara laticonia* Xinlun et al., 1978 and *Maedlerisphaera* in the Bayan Ulan 'Formation'. Although these two species are absent in our unit 3, the rest of our unit 3 assemblage is very similar in composition to that of the Bayan Ulan Formation sensu Liu, 1987.

4.2. Ostracods

The ostracods of unit 2 and unit 3 are very similar but unit 2 is richer in specimens. The ostracod assemblage of unit 3 (Bayan Ulan Beds, Nomogen Formation) at the Subeng mammal site consists of nine species belonging to six genera (Table 2; see also Fig. 6). The genus *Caganella* is endemic to Mongolia and is only known from the Paleocene (Khand, 2000, Fig. 1). The presence of the genus *Cypris* indicates that the age of the sediments can be no older than the Paleocene (Guan, 1988, Fig. 1) or even the late Paleocene (Khand, 2000, Fig. 1).

Table 2
List of ostracod taxa observed in unit 3, Subeng section

- Subclass Ostracoda Latreille, 1806
  - Order Podocopida G.W. Müller, 1894
    - Suborder Cytherocopina Gründel, 1967
      - Superfamily Cytheroidea Baird, 1850
        - Family Limnocytheridae Klie, 1938
          - Subfamily Limnocytherinae Klie, 1938
            - Genus *Limnocythere* Brady, 1868
              - *Limnocythere nemegtensis* Szczechura, 1971
          - Subfamily Timiriaseviinae Mandelstam, 1947 emend. Colin and Danielpol, 1980
            - Genus *Timiriasevia* Mandelstam, 1947
              - *Timiriasevia naranbulakensis* Szczechura, 1971
              - *Timiriasevia ulanbulakensis* Szczechura, 1971
              - *Timiriasevia subengensis* Van Itterbeeck and Bultynck, 2004
              - *Timiriasevia* sp.
    - Suborder Cypridocopina Jones, 1901
      - Superfamily Cypridoidea Baird, 1945
        - Family Ilyocyprididae Kaufmann, 1900
          - Genus *Ilyocypris* Brady and Norman, 1889
            - *Ilyocypris multinoda* Yang in Hou et al., 1982
        - Family Cyprididae Baird, 1845
          - Subfamily Cypridinae Baird, 1845
            - Genus *Cypris* O.F. Müller, 1776
              - *Cypris dashzevegi* (Khand, 1976)
        - Family Notodromadidae Kaufmann, 1900
          - Genus *Cyprois* Zenker, 1854
            - *Cyprois xuyiensis* Zhou and Chen in Hou et al., 1982
        - Family uncertain
          - Genus *Caganella* Szczechura, 1971
            - *Caganella oblonga* Khand, 1976

Seven of the nine ostracod species are shared with the Naran Member of the Naran Bulak Formation (Szczechura, 1971; Khand, 1976, 1987): *Caganella oblonga*, *Timiriasevia subengensis*, *T. naranbulakensis*, *T. ulanbulakensis*, *Timiriasevia* sp., *Limnocythere nemegtensis* and *Cypris dashzevegi*. However, from these seven species, only the latter two have been reported from other strata than the Naran Member. *Limnocythere nemegtensis* has been observed in the Paleocene Xhinzuang Formation and in the late Paleocene upper Shashi Formation, both in China. *Cypris dashzevegi* has often been misidentified as the recent African *C. decaryi*, and under this name it was considered typical for the lower Eocene of China (Van Itterbeeck and Bultynck, 2004 and references therein). The other two species (*Ilyocypris multinoda*, *Cyprois xuyiensis*) have been reported from levels 2–4 from the Funing Group, Jiangsu (Hou et al., 1982). Both the Naran Member of the Naran Bulak Formation and the Funing Group are considered to be late Paleocene in age, although sometimes an early Eocene age has been proposed for the uppermost part of the Funing Group (He et al., 1988).

The ostracod assemblage of the Bayan Ulan Beds at the Subeng site confirms the correlation of these beds with the Naran Member of the Naran Bulak Formation and also suggests a late Paleocene age.

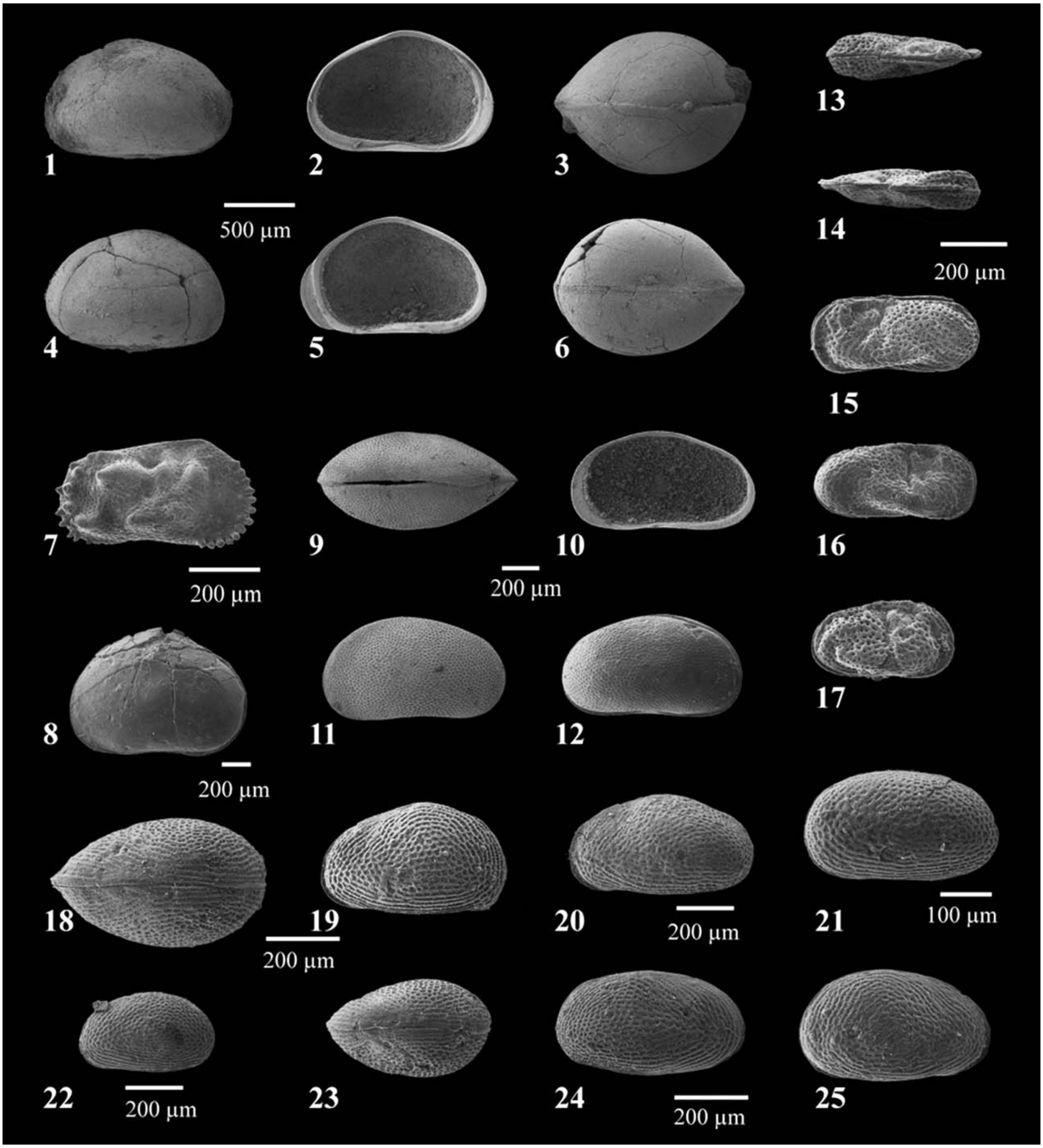

Fig. 6. Ostracods of the mammal bearing horizon: 1–6, *Cypris dashzevegi*: 1, adult, left valve, external view; 2, adult, left valve internal view; 3, adult, carapace, dorsal view; 4, adult, right valve, external view; 5, adult, right valve, internal view; 6, adult, carapace, ventral view. 7, *Ilyocypris multinoda*, right valve, external view. 8, *Cyprois xuyiensis*, carapace, left external view. 9–12, *Caganella oblonga*: 9, carapace, dorsal view; 10, right valve, internal view; 11, left valve, external view; 12, carapace, right external view. 13–17, *Limnocythere nemegtensis*: 13, ♂, carapace, dorsal view; 14, ♀, carapace, dorsal view; 15, ♂, left valve, external view; 16, ♀, carapace, right external view; 17, juvenile, carapace, right external view. 18–19, *Timiriasevia naranbulakensis*: 18, carapace, dorsal view; 19, ♂, right valve, external view. 20, *Timiriasevia* sp., left valve, external view. 21, *Timiriasevia ulanbulakensis*, right valve, external view. 22–25, *Timiriasevia subengensis*: 22, ♀, left valve, external view; 23, carapace, dorsal view; 24, ♂, carapace, right external view; 25, ♀, right valve, external view.

4.3. Palynomorphs

4.3.1. Unit 1 (Iren Dabasu Formation)

According to the regional geological map, the sediments of unit 1 belong to the late Cretaceous Iren Dabasu Formation and the taxonomically diverse palynospectrum of unit 1 is indeed typical for this age. The assemblage (Fig. 7) is dominated by gymnosperm pollen (approximately 70%), mainly bisaccate pollen of the conifer families Pinaceae and Podocarpaceae.

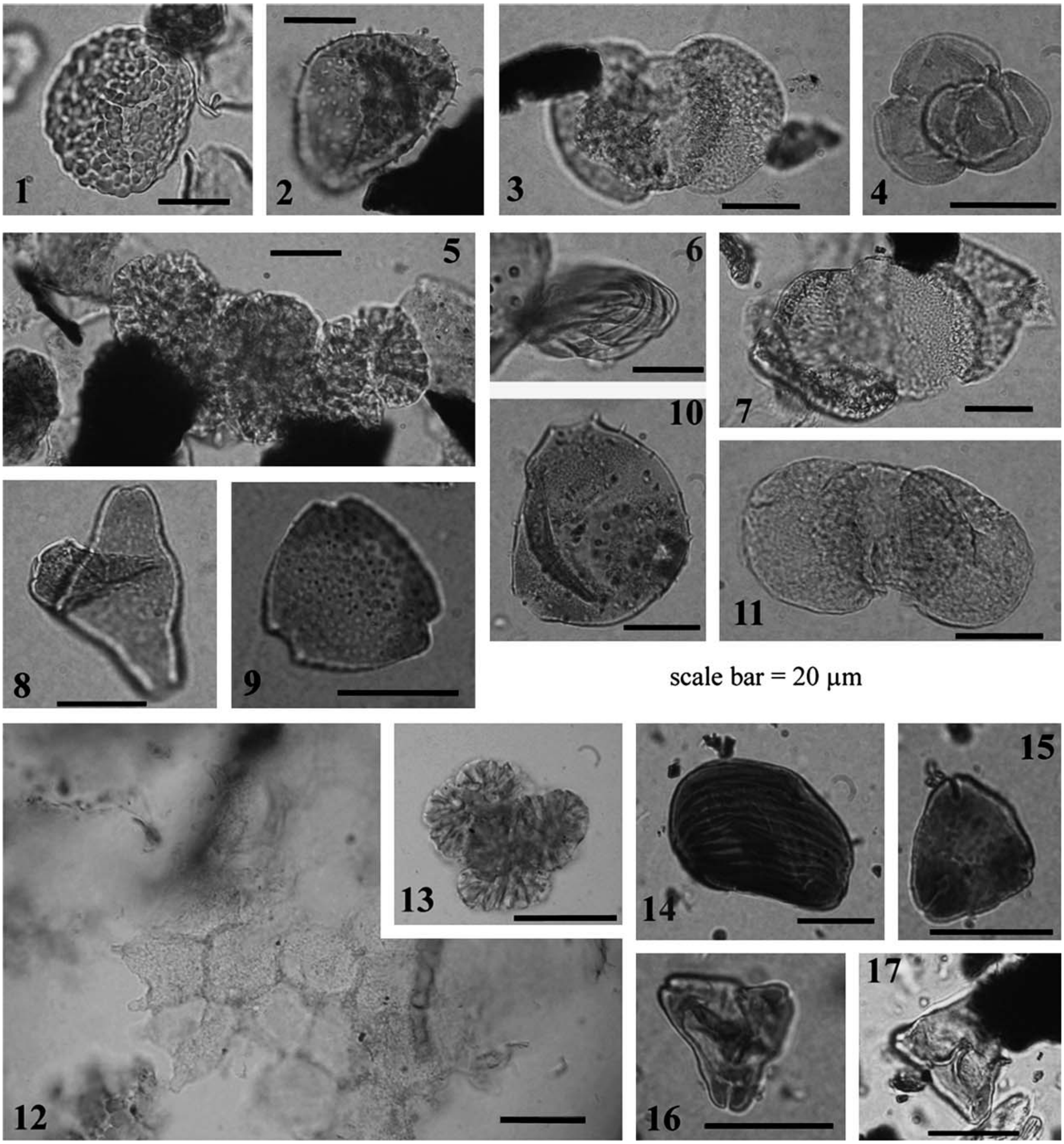

Fig. 7. Overview of the palynological assemblages in the Subeng section (scale bar = 20 µm): 1–11 Palynomophs of unit 1: 1, *Leptolepidites verrucatus*; 2, *Selaginella* sp.; 3, *Podocarpidites* sp.; 4, 5, *Botryococcus* sp.; 6, *Ephedripites* sp.; 7, *Pinuspollenites* sp.; 8, *Fibulapollis mirificus*; 9, *Triatriopollenites echinatus*; 10, 11, 12–17 Palynomorphs of unit 2: 12, *Pediastrum* sp.; 13, *Botryococcus* sp.; 14, *Cicatricosisporites dorogensis*; 15, *Ocullopollis* sp.; 16, *Basopollis* sp.; 17, *Plicapollis plicatus*.

Gnetaceae, Taxodiaceae and Cupressaceae pollen are also common. The angiosperms are reasonably diverse, represented by 56 taxa (28%). Most of them belong to the Normapolles-stemma although a few pollen of the Aquilapollenites-stemma have been recognized (*Aquilapollenites*, *Fibulapollis*). Spores only account for 2.7% of the spectrum.

Botryococcus is abundant, but it does not have any stratigraphical value (Batten and Grenfell, 1996 and references therein) and therefore has not been included in the census data. Nevertheless its abundance corroborates the interpretation of unit 1 as a wetland environment, as suggested also by the sedimentological data. Given this interpretation of unit 1 as a wetland, the low abundance of spores recorded in this assemblage is enigmatic (Table 3). Possibly the real diversity and abundance of ferns in the local vegetation is masked by the large dominance of bissacate pollen, in spite of our large sample (Frederiksen, 1985, p. 28–29).

Based on the distribution of Normapolles and Aquilapollenites type pollen, two palynofloral provinces are distinguished in the northern hemisphere during the Cretaceous, the Normapolles and Aquillapollenites provinces (Herngreen and Chlonova, 1981; Herngreen et al., 1996). Both pollen types only co-occur in the boundary zone between the two provinces, such as the Maastrichtian Ashut Formation of Northern Kazakhstan, and the Senonian palynological assemblages of Central Asia and the central part of West Siberia (Chlonova, 1961; Samoilovich, 1961; Polumiskova et al., 1966; Ponomarenko, 1966; Samoilovich, 1977). In China, this boundary runs from 38–39°N in the eastern coastal region to about 44°N in Inner Mongolia (Song and Huang, 1997). The Subeng section (N 43°31′50″, E 111°44′04″) is located directly in this boundary region, forming a new, well-documented site of co-occurrence and confirming the proposed broad ecotone zone between the two floristic provinces. The dominance of Normapolles over Aquilapollenites-type pollen in the Subeng section indicates a closer affinity with the Normapolles province.

Some Chinese authors divide China during the late Cretaceous and Paleocene into three floristic regions: the northeastern, northwestern and southern regions (Sun, 1979; Wang et al., 1990). The Subeng section is located in the boundary of the northeastern and northwestern region, but its palynospectrum best matches the latter. Characteristics for these late Cretaceous palynospectra of northwestern China are the presence of Normapolles like *Basopollis*, *Extratriporopollenites* and *Triatriopollenites echinatus* and secondly, the abundance of *Ephedripites* and some bisaccate pollen (Sun, 1979).

Table 3
Census data of palynomorphs from the Subeng section

	Unit 1		Unit 2	
	#	%	#	%
Spores				
Sphagnumsporites sp.	1	0.16	1	0.30
Selaginella sp.	1	0.16		
Lycopodiumsporites sp.	3	0.48		
Leptolepidites verrucatus Couper, 1953	2	0.32	4	1.20
Osmundacidites sp.	1	0.16		
Leiotriletes sp.	4	0.63	25	7.49
Dyctiophyllidites harrisii Couper, 1953			5	1.50
Cyathidites australis Couper, 1953	1	0.16	1	0.30
Cyathidites minor Couper, 1953			52	15.57
Gleicheniidites senonicus Ross, 1949			8	2.40
Gleicheniidites laetus (Bolchovitina) Bolchovitina 1968			8	2.40
Cicatricosisporites dorogensis Potonié and Gelletich, 1933			5	1.50
Klukisporites variegatus Couper, 1958			5	1.50
Laevigatosporites ovoideis Takahashi, 1961	4	0.63		
Laevigatosporites ovatus Willson and Webster, 1946			14	4.19
	17	2.69	128	38.32
Gymnosperms				
Ginkgocycadophytus sp.	6	0.95	8	2.40
Alisporites bilateralis Rouse, 1959			2	0.60
Pinuspollenites sp.	201	31.85		
Piceapollenites sp.	60	9.51		
Cedripites parvisaccatus (Sauer) Krutzsch, 1971			3	0.90
Cedruspollenites sp.	50	7.92		
Podocarpidites sp.	40	6.34		
Taxodiaceaepollenites hiatus (Potonié) Kremp, 1949			8	2.40
Taxodiaceaepollenites sp.	35	5.55	3	0.90
Cupressaceae	21	3.33		
Ephedripites (*Distachyapites*) sp.	20	3.17		
Ephedripites sp.	1	0.16	1	0.30
Gnetaeceaepollenites ovatus (Pierce) Verbitzkaja, 1979	3	0.48		
Classopollis sp.			2	0.60
	437	69.26	27	8.08
Angiosperms				
Tricolpites hians Stanley, 1965	4	0.63		
Tricolpites sp.			7	2.10
Triporopollenites plicoides Zaklinskaja, 1963			2	0.60
Triporopollenites sp.			4	1.20
Liliacidites variegatus Couper, 1953	4	0.63		
Lixiodendron (=Palmae) sp.	4	0.63		
Quercites sparsus (Martynova) Samoilovich, 1961			2	0.60
Quercuspollenites sp.	2	0.32		
Faguspollenites sp.	3	0.48		
Platanuspollenites sp.	2	0.32		

(continued on next page)

Table 3 (*continued*)

	Unit 1		Unit 2	
	#	%	#	%
Angiosperms				
Caryapollenites sp.	4	0.63	3	0.90
Castaneapollenites sp.	1	0.16	12	3.59
Platycarya sp.	2	0.32		
Corylopsis crassa Lubomirova, 1965	2	0.32		
Corylopsis sp.	4	0.63		
Alnuspollenites sp.	1	0.16		
Carpinuspollenites sp.	1	0.16		
Myricapollenites sp.			1	0.30
Anacolosidites acutullus Cookson and Pike, 1954	1	0.16		
Sparganium sp.	2	0.32		
Ulmoideipites krempii Anderson, 1960	1	0.16		
Ulmoideipites planaeriformis Anderson, 1960	1	0.16		
Ulmoideipites tricostatus Anderson, 1960	2	0.32	2	0.60
Campanulaceae	8	1.27		
Caprifoliaceae	10	1.58		
Eleagnaceae	1	0.16		
Ericaceae	1	0.16		
Hamamelidaceae	1	0.16		
Menispermaceae	1	0.16		
Rubiaceae			3	0.90
Elytranthe striatus Couper, 1953	1	0.16		
Proteacidites xiningensis Sun, Zhao and He, 1980	4	0.63		
Aquilapollenites subtilis Mtchedlishvili, 1961			1	0.30
Aquilapollenites sp.	1	0.16		
Parviprojectus sp.			1	0.30
Fibulapollis mirificus (Chlonova) Chlonova, 1961	15	2.38	2	0.60
Basopollis spp.	30	4.75	4	1.20
Complexiopollis praeatumescens Krutzsch, 1959	8	1.27		
Complexiopollis sp.	11	1.74		
Extratriporopollenites rostratus Scarby, 1968	5	0.79		
Extratriporopollenites aff. *vestifex* Pflug, 1953	5	0.79		
Extratriporopollenites sp.	2	0.32	2	0.60
Interpollis heteroporatus Krutzsch, 1961			3	0.90
Nudopollis terminalis (Thomson and Pflug) Pflug, 1953	3	0.48		
Nudopollis thiergarti (Thomson and Pflug) Pflug, 1953	3	0.48		
Oculopollis praedicatus Weyland and Krieger, 1953			35	10.48
Oculopollis sp.			32	9.58
Plicatopollis plicatus (Potonié) Krutzsch, 1962			31	9.28
Sporopollis trisulcatus Zaklinskaja, 1963	6	0.95		
Sporopollis peneserta Pflug, 1953			2	0.60
Thomsonipollis magnificus (Thomson and Pflug) Krutzsch, 1960	1	0.16		
Angiosperms				
Trudopollis cf. platoides (Pflug) Krutzsch, 1967	2	0.32		
Trudopollis sp.	11	1.74		
Vacuopollis sp.			25	7.49
Triatriopollenites echinatus Sun and Zhang, 1980	2	0.32		
Triatriopollenites plicatus Thomson and Pflug, 1953	1	0.16		
Kuprianipollis santaloides (Zaklinskaja) Komarova, 1980			3	0.90
Kuprianipollis elegans (Zaklinskaja) Komarova, 1980			2	0.60
Plananthus sp.	3	0.48		
	177	28.05	179	53.59
	631	100.0	334	100.0

4.3.2. Unit 2 (Nomogen Formation)

The palynological assemblage of unit 2 is completely different from that observed in unit 1 (Fig. 7). Gymnosperms make up 8% of the assemblage. They are dominated by Taxodiaceae and *Ginkgocycadophytus* while bisaccate pollen are nearly absent (Table 3). Angiosperm pollen are dominant but their diversity is reduced and they are dominated by triporate pollen, mainly by the Normapolles genera *Oculopollis* and *Vacuopollis* (>27%). This extinct group is believed to be part of the Fagales (Sims et al., 1999; Friis et al., 2003). Spores occur fairly frequent with 13 species of ferns representing 38% of the total assemblage.

Because of the high abundance of organic matter in unit 2, palynomorphs were counted in oxidized slides. In the unoxidized slides, we also identified the freshwater algae *Botryococcus* sp. and *Pediastrum* sp. Their presence corroborates the sedimentological interpretation of unit 2 as lake sediments. Compact colonies of *Pediastrum* are known since the early Cretaceous, but the first perforated forms are of Eocene age (Batten, 1996). All the *Pediastrum* colonies observed in unit 2 are of the compact form, not conflicting the inferred Paleocene age.

The palynological assemblage of unit 2 at Subeng has all the characteristics of a typical Paleocene assemblage in this region with a dominance of Normapolles, some relicts of dominant Cretaceous forms like *Aquilapollenites* and *Fibulapollis* and very few modern taxa like *Castaneapollenites*.

During the Paleocene, China is subdivided into 2 floristic provinces (Song, 1996, Fig. 2). Unlike the Northeastern region, the Northwestern floristic province is characterized by the dominance of *Ephedripites* and the abundant occurrence of Normapolles. The Nomogen Formation lies within the Northwestern floristic province, and indeed such palynological assemblages have been described from the Caomuhao gypsum mine in Inner Mongolia (Song and Zhang, 1990). It led these authors to the conclusion that the Mongolian Plateau had a savannah-like vegetation under a semi-arid, subtropical climate with local woodlands during the late Paleocene. The absence of *Ephedripites*, a known xerophyte, indicates that the Subeng section represents such a woodland. This interpretation is corroborated by the high abundance of ferns and the sedimentology, both indicating a humid local environment.

4.4. Mollusca

One of the pedogenic carbonate nodule conglomerate layers of unit 3 (Fig. 2) has yielded 12 bivalve molds, most of them articulated. All specimens (Fig. 8) belong to the exclusively freshwater family Unionidae, but preservation of the specimens limits their identification to the genus level. Most specimens can be attributed to *Cuneopsis* Simpson, 1900, a rare extant genus represented by five species in southern China and Vietnam. Fossil species of *Cuneopsis* have been described from upper Cretaceous deposits of Mongolia (Martinson, 1982, p. 60–61). One specimen probably belongs to *Acuticosta* Simpson, 1900, nowadays represented by two species in China. The size, form and proportions of this specimen resemble *A. chinensis* (Lea, 1868) but more material is needed for a positive identification. One partial specimen probably represents a species of *Lamprotula* Simpson, 1900, an extant genus represented by 14 species. In spite of their occurrence in channel deposits, the dominance of articulated shells is indicative of a calm environment and limited transport. The optimal unionid habitat is a clean, well oxygenated,

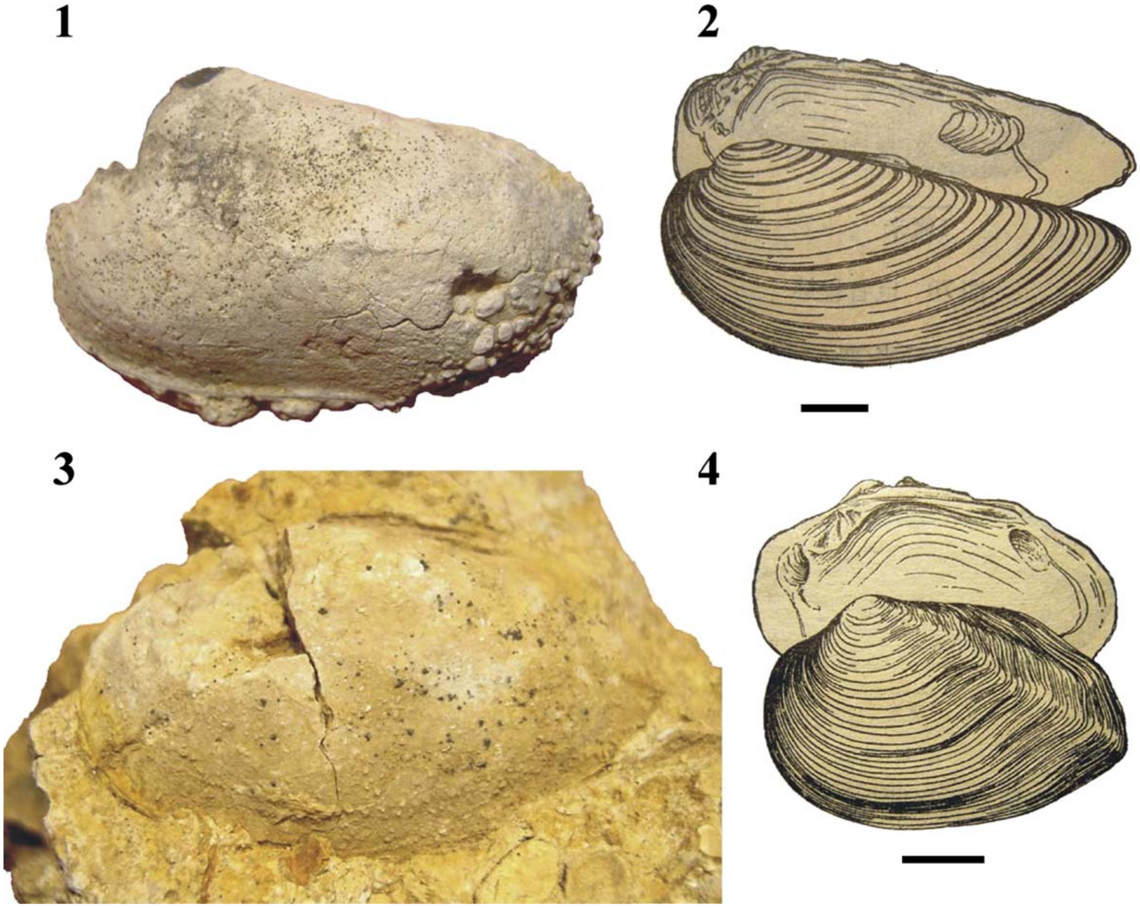

Fig. 8. Molluscs of the Nomogen Formation: 1, *Cuneopsis* sp. ($L=77$ mm) (Unionidae) inner mold, Bayan Ulan Beds, Unit 3 (Subeng, China); 2, Recent *Cuneopsis heudei* (Heude) ($L=71.5$ mm), South China (from Liu, 1979); 3, *Acuticosta* sp. ($L=42$ mm) (Unionidae) inner mold, Bayan Ulan Beds, Unit 3 (Subeng, China); 4, Recent *Acuticosta ovata* (Simpson) ($L=47.5$ mm), South China (from Liu, 1979).

shallow water under an at least seasonally warm climate (Good, 2004, Table 1). The marginal lacustrine/fluvial sediments of unit 3 form the ideal habitat for these unionid molluscs (see Section 3.3).

4.5. Amphibians and lizards

Amphibians and lizards are represented in the Subeng section by a few, well preserved fragments of bones. The preservation of vertebrae neural arches or tooth tips shows that they underwent limited, low energy transport.

The anurans are represented by fourteen humerus distal ends (8 left and 6 right), one right ilium and two maxillae fragments (one left and one right), attributed to discoglossid frogs (Fig. 9.1–.4). One sacral vertebra could belong to a gobiatid frog (Fig. 9.5–.6). Discoglossidae are present in Asia already from the end of the Jurassic (Gao and Wang, 2001). Gobiatidae were present in Asia at least from the early Cretaceous and they were probably dominant among the Asian Cretaceous anurans (Rocek and Nessov, 1993), but this report would be their first Paleocene record.

The caudates (Fig. 9.7–.10) are represented in Subeng by an atlas and an isolated vertebra. The shape of the atlas is generalized among caudates (Estes, 1981), and it is therefore difficult to identify. However, it does not belong to a batrachosauroid (Duffaud, 2000). Otherwise, the vertebra presents salamandrid affinities (Duffaud, 2000). This family is known throughout Laurasia from the end of the Cretaceous (Rage and Hossini, 2000).

Six jaw fragments are attributed to the squamates (Fig. 9.11–.14), and five of them are identified as anguimorphs (Estes, 1983). From these, one incomplete right maxilla and two jaw fragments belong to an anguioid lizard and one left dentary fragment belongs to a varanoid lizard (Estes, 1983; Conrad, 2004). Anguimorphs are present in Asia since the end of the early Cretaceous (Alifanov, 1993). The anguioids are well known in the late Cretaceous and Paleogene of North America and probably appeared in Asia at about the same time (Alifanov, 2000).

4.6. Mammals

The mammal fossils from Subeng are fragile but well preserved and are thought to have undergone only limited transport. An overview of the mammal taxa observed at Subeng is given in Table 4. This fauna is closest to the Chinese mammal faunas from Bayan Ulan and Nomogen (Nomogen Formation), and to the Gashato (Gashato Formation, Mbr I) and Naran Bulak faunas (Naran Bulak Formation, Naran and Zhigden Mbr) in Mongolia. These four faunas are the classical faunas assigned to the Gashatan ALMA (Ting, 1998; Meng et al., 1998; Bowen et al., 2002). These correlations are especially supported by the presence of the arctostylopid *Palaeostylops*, the rodent-like *Tribosphenomys* and the taeniolabidioid multituberculates *Lambdopsalis* and *Prionessus* (Fig. 10), as they are exclusively known from the Gashatan.

The Subeng material contains a few remains of larger animals such as a calcaneum from *Prodinoceras* cf. *plantigradum*, and a femur and lower molar from *Dissacus* cf. *serratus*. However, the Subeng fauna is especially rich in small-bodied forms that are easily missed by surface collecting and are therefore often not or poorly known. The Subeng site is the first Paleocene site on the Mongolian Plateau that has been sampled for mammals by methodical screenwashing. A taphonomical bias is probably responsible for the high abundance of the small taxa. However, their study has already proven to be valuable for the understanding of the late Paleocene Asian mammal faunas and their paleobiogeograpical relations. We described from Subeng the carpolestid plesiadapiform *Subengius mengi* (Fig. 10.1–.2), currently the oldest Asian plesiadapiform (Smith et al., 2004). The nyctitheriid insectivore *Asionyctia guoi* from Subeng is the most completely known Asian nyctitheriid, and allowed us to group all Asian nyctitheriids in a new subfamily Asionyctiinae (Missiaen and Smith, 2005). Both taxa most probably descend from North American ancestors migrating into Asia, and for both taxa early dispersal scenarios during the middle Paleocene were proposed. The small neoplagiaulacid multituberculate *Mesodmops dawsonae* was described from the Bumbanian Wutu Formation in East China (Tong and Wang, 1994). It was suggested that *Mesodmops* is derived from the North American genus *Mesodma*, and migrated into Asia by the late Paleocene. Now a new species of *Mesodmops* is found at Subeng, differing from *M. dawsonae* by a slightly more primitive cusp formula, and by a more slender form. Our findings of *Mesodmops* from Subeng confirm the ideas expressed by Tong and Wang (1994, 1998), and represent the oldest Asian record of ptilodontoid multituberculates. In any case, the occurrence of these mammal taxa clearly indicate that mammal migration was not unidirectional from Asia towards North America as proposed by some authors (Beard, 2002). The identification of arctostylopid tarsal bones from Subeng also suggested faunal interchange between Asia

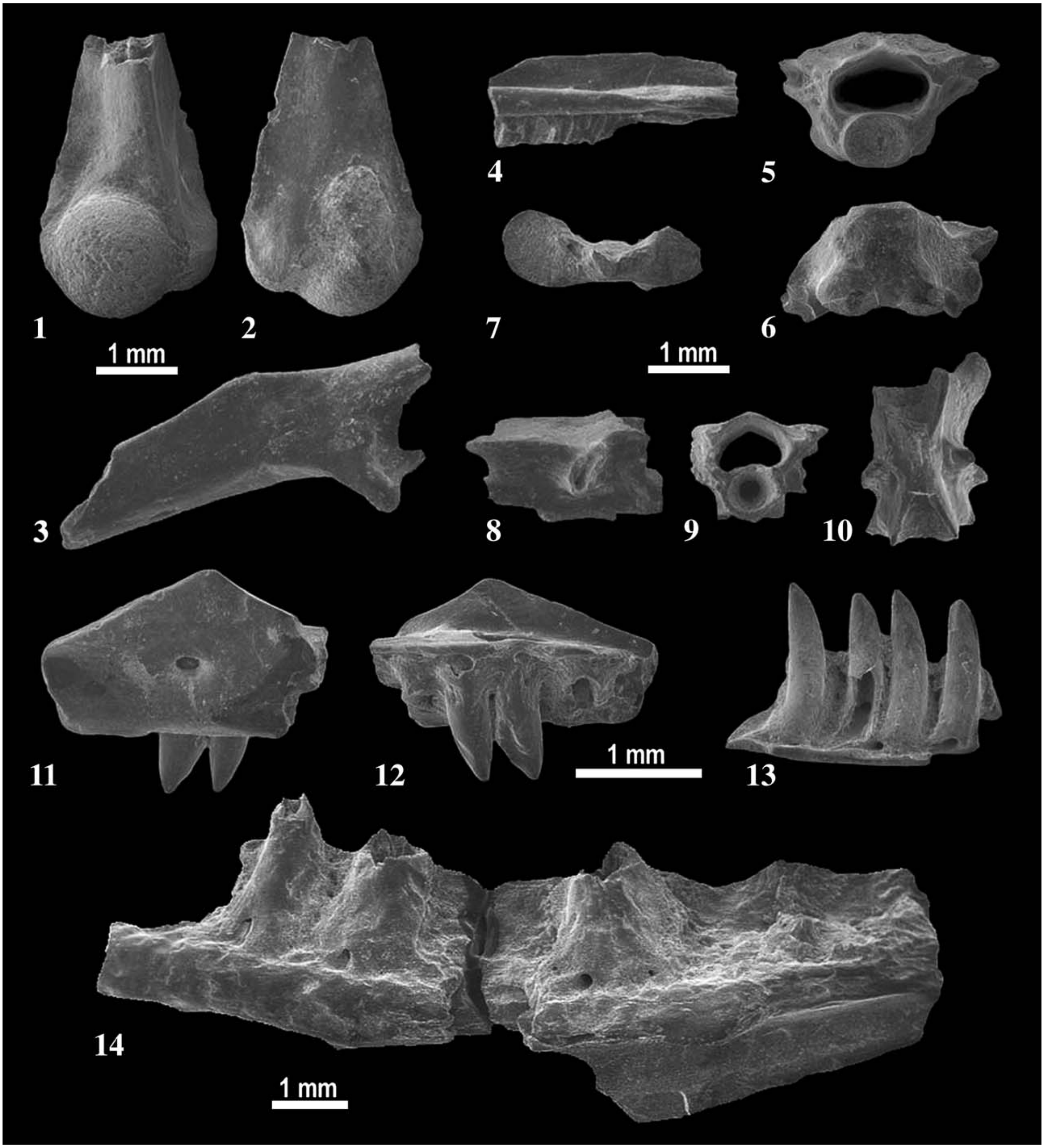

Fig. 9. Gashatan amphibians and lizards at Subeng: 1–10: Amphibians. 1–4: discoglossid frog indet:. humerus distal end in ventral and dorsal views, right ilium in lateral view, right maxilla in lingual view; 5–6: gobiatid frog?: sacral vertebra in anterior and ventral view; 7–10: Caudata indet: atlas in anterior view, vertebra in left lateral, anterior and ventral views. 11–14: Squamates. 11–13: Anguoidea indet.: maxilla in labial and lingual views, jaw fragment in lingual view; 14: Varanoidea indet.: jaw fragment in lingual view.

and North America, but weakened the support for Paleocene interchange between North and South American faunas (Missiaen et al., 2006).

An important number of other small mammals from Subeng represents an undocumented morphological and taxonomical diversity and their study may equally add

Table 4
List of Gashatan mammal taxa at Subeng

- Class Mammalia Linnaeus, 1785
- Infraclass Allotheria Marsh, 1880
    - Order Multituberculata Cope, 1884
    - Superfamily Ptilondontoidea Cope, 1887
      - Family Neoplagiaulacidae Cope, 1887
        - Genus *Mesodmops* Tong and Wang, 1994
          - *Mesodmops* sp. nov.
    - Superfamily Taeniolabidoidea Granger and Simpson, 1929
      - Family Taeniolabididae Granger and Simpson, 1929
        - Genus *Lambdopsalis* Chow and Qi, 1978
          - *Lambdopsalis bulla* Chow and Qi, 1978
        - Genus *Prionessus* Matthew and Granger, 1925
          - cf. *Prionessus lucifer*
- Infraclass Holotheria Wible et al., 1995
- Cohort Placentalia Owen, 1837
  - Grandorder Gliriformes Wyss and Meng, 1996
          - Gliriformes indet.
      - Family Arctostylopidae Schlosser, 1923
        - Genus *Palaeostylops* Matthew and Granger, 1925
          - *Palaeostylops iturus*
      - Family Pseudictopidae Sulimski, 1969
        - Genus *Pseudictops* Matthew, Granger and Simpson, 1929
          - *Pseudictops* cf. *lophiodon*
    - Order Mixodontia Sych, 1971
      - Family Eurymylidae Dashzeveg and Russell, 1988
        - Genus *Eomylus* Dashzeveg and Russell, 1988
          - *Eomylus* cf. *bayanulanensis* Meng et al. 2005
    - Order Rodentiaformes Wyss and Meng, 1996
      - Family Alagomyidae Dashzeveg, 1990
        - Genus *Tribosphenomys* Meng, Wyss, Dawson and Zhai, 1994
          - *Tribosphenomys* cf. *minutus*
  - Grandorder Ferae Linnaeus, 1758
    - Order Cimolesta McKenna, 1975
      - Family Cimolestidae McKenna, 1975
        - Genus *Tsaganius* Russell and Dashzeveg, 1986
          - *Tsganius* sp.nov.
    - Order Carnivora Bowdich, 1821
      - Family Viverravidae Wortman and Matthew, 1899
          - Viverravidae indet.
  - Grandorder Lipotyphla Haeckel, 1866
    - Order Erinaceomorpha Gregory, 1910
          - Erinaceomorpha indet.
    - Order Soricomorpha Gregory, 1910
      - Family Nyctitheriidae Simpson, 1928
          - Nyctitheriidae sp.
        - Genus *Asionyctia* Missiaen and Smith, 2005
          - *Asionyctia guoi* Missiaen and Smith, 2005
      - Family Micropternodontidae Stirton and Rensberger, 1964
        - Genus *Hyracolestes* Matthew and Granger, 1925
          - *Hyracolestes* cf. *ermineus*
  - Grandorder Archonta Gregory, 1910
    - Order Proprimates Gingerich, 1989
    - Infraorder Plesiadapiformes Simons, 1972
      - Family Carpolestidae Simpson, 1935
        - Genus *Subengius* Smith, Van Itterbeeck and Missiaen, 2004
          - *Subengius mengi* Smith, Van Itterbeeck and Missiaen, 2004
  - Grandorder Ungulata Linnaeus, 1766
    - Order Dinocerata Marsh, 1873
      - Family Uintatheriidae Flower, 1876

Table 4 (*continued*)

        - Genus *Prodinoceras* Matthew, Granger and Simpson, 1929
          - *Prodinoceras* sp.
    - Order Mesonychia Matthew, 1937
      - Family Mesonychidae Cope, 1875
        - Genus *Dissacus* Cope, 1881
          - *Dissacus* cf. *serratus* (Chow and Qi, 1978)

significant new insight into the mammal faunas of the Paleocene–Eocene transition in Asia.

5. Age of the Subeng site

From unit 1, only palynomorphs were retrieved, and these clearly indicate a Maastrichtian age, agreeing with the late Cretaceous age proposed for the Iren Dabasu Formation (BGMRNMAR, 1991).

The presence of different fossil groups in both units of the Nomogen Formation allows multiple independent correlations and dating. The unit 2 palynomorphs indicate a Paleocene age based on the dominance of Normapolles, the limited occurrence of relict Cretaceous and modern taxa. Charophyte data suggest a correlation to the late Paleocene Naran Member in Mongolia, while ostracod data show affinities to the Naran Member and to the middle to upper levels of the Funing Group in the late Paleocene of East China. Mammal biostratigraphy clearly places the Subeng fauna in the Gashatan ALMA, correlating it to the nearby Bayan Ulan and Nomogen faunas also from the Nomogen Formation, to the Naran, Zhigden and Gashato faunas in Mongolia, and to the Lower Lingcha fauna in South China (Ting, 1998; Bowen et al., 2002).

A major advance to date the Gashatan faunas was the absolute dating of the Lingcha Formation (Bowen et al., 2002). The Gashatan Lower Lingcha fauna occurs somewhat below the chron C25n/C24r reversal, and the Bumbanian Upper Lingcha fauna was collected close to the minimum of the δC^{13} excursion (Bowen et al., 2002; Ting et al., 2003). This showed that at least part of the Gashatan faunas are late Paleocene, and part of the Bumbanian faunas are early Eocene. The exact limit between the two ALMAs could not be located, but is situated in a 900 kyr uncertainty window containing the Paleocene–Eocene boundary (PEB). More recently, Bowen et al. (2005) made a composite section based on different late Paleocene and early Eocene sections from the Erlian Basin, and correlated this to the Geomagnetic Polarity Timescale. They extend the upper limit of the Gashatan into chron C24r, and possibly even very near to the PEB, and the lower limit of the Gashatan into chron C25r or even C26n. This suggests

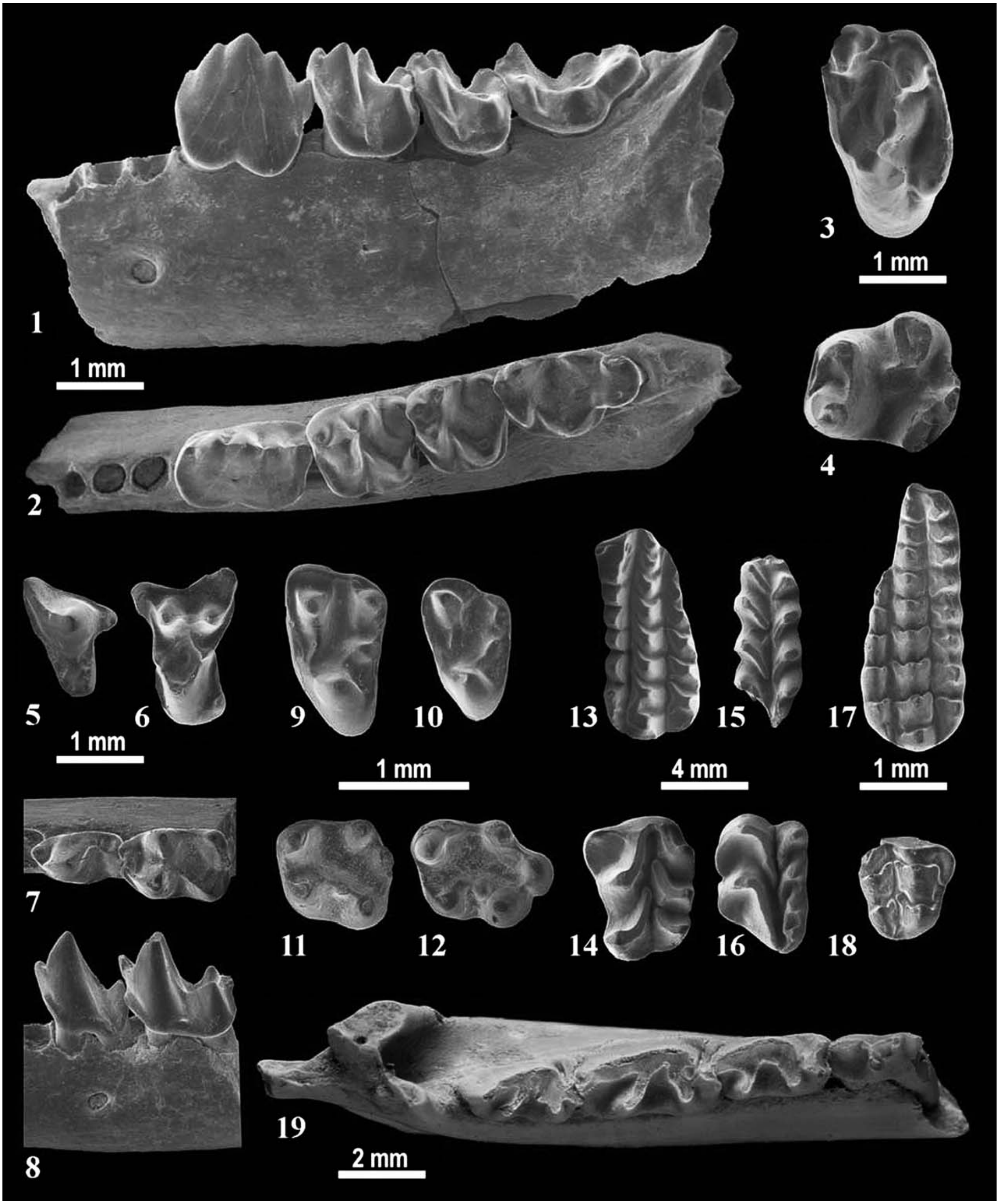

Fig. 10. Gashatan mammals at Subeng: 1–2: *Subengius mengi*: p4–m3 in labial and occlusal view; 3–4: *Eomylus* cf. *bayanulanensis*: M2 and m1 in occlusal view; 5–8: *Asionyctia guoi*: P4 and M1 in occlusal view, p4–m1 in occlusal and labial view; *Tribosphenomys* cf. *minutus*: M2, M3, m2 and m3 in occlusal view; 13–16: *Lambdopsalis bulla*: M1, M2, m1 and m2 in occlusal view; 17–18: *Mesodomops* sp.nov.: M1 and M2 in occlusal view; 19: *Palaeostylops iturus*: p4–m3 in occlusal view.

that the Gashatan ALMA correlates to the complete Clarkforkian and the upper Tiffanian in North America (Gingerich, 2003), and to much of the Thanetian in Europe (Gradstein et al., 2004).

6. Depositional environments and palaeoecology

As suggested also by the sedimentological data and corroborated by abundance of *Botryococcus*, we interpret unit 1 as a wetland environment, although the scarcity of spores is enigmatic. The highly abundant bisaccate gymnosperm pollen as well as *Ephedripites* are interpreted as allochtonous representatives of a relatively nearby upland vegetation.

During the Paleocene, the Subeng region was a fluvio-lacustrine environment in a dry region (Fig. 11) (Song and Zhang, 1990; Meng et al., 1998). The lake was stratified with an anoxic hypolimnion resulting in the preservation of the fine lamination and of organic-rich layers within the distal lake sediments. This original bedding was mostly lost in the proximal lake sediments by bioturbation of the benthic community. The lake ecosystem contained a rich flora of aquatic plants and algae (charophytes, *Botryococcus*, *Pediastrum*) and a rich fauna of ostracods, fish (represented by isolated teeth and vertebrae) and gastropods.

The lake margin is characterised by a system of minor channels and rivers. Within the channel deposits, articulated bivalves occur frequently, indicating calm, clean and well oxygenated waters, and suggesting climate conditions similar to present-day southern China and Vietnam. This zone was vegetated by typical lowland plants like ferns, Taxodiaceae and *Plicatopollis plicatus*. Many of the pollen types from Subeng (*Ginkgocycadophytes*, *Taxodiaceapollenites*, *Castaneapollenites*, *Plicatopollis*, *Caryapollenites*) belong to groups of tree- or shrub-like plants. Moreover, although the biological affinities of the Normapolles pollen from Subeng are uncertain, all recent findings of fossil flowers with attached Normapolles pollens are thought to be members of the Fagales (Sims et al., 1999; Friis et al., 2003), which are also dominantly tree-shaped. The high abundance of ferns is indicative of shady, humid conditions, and may represent the undergrowth in a

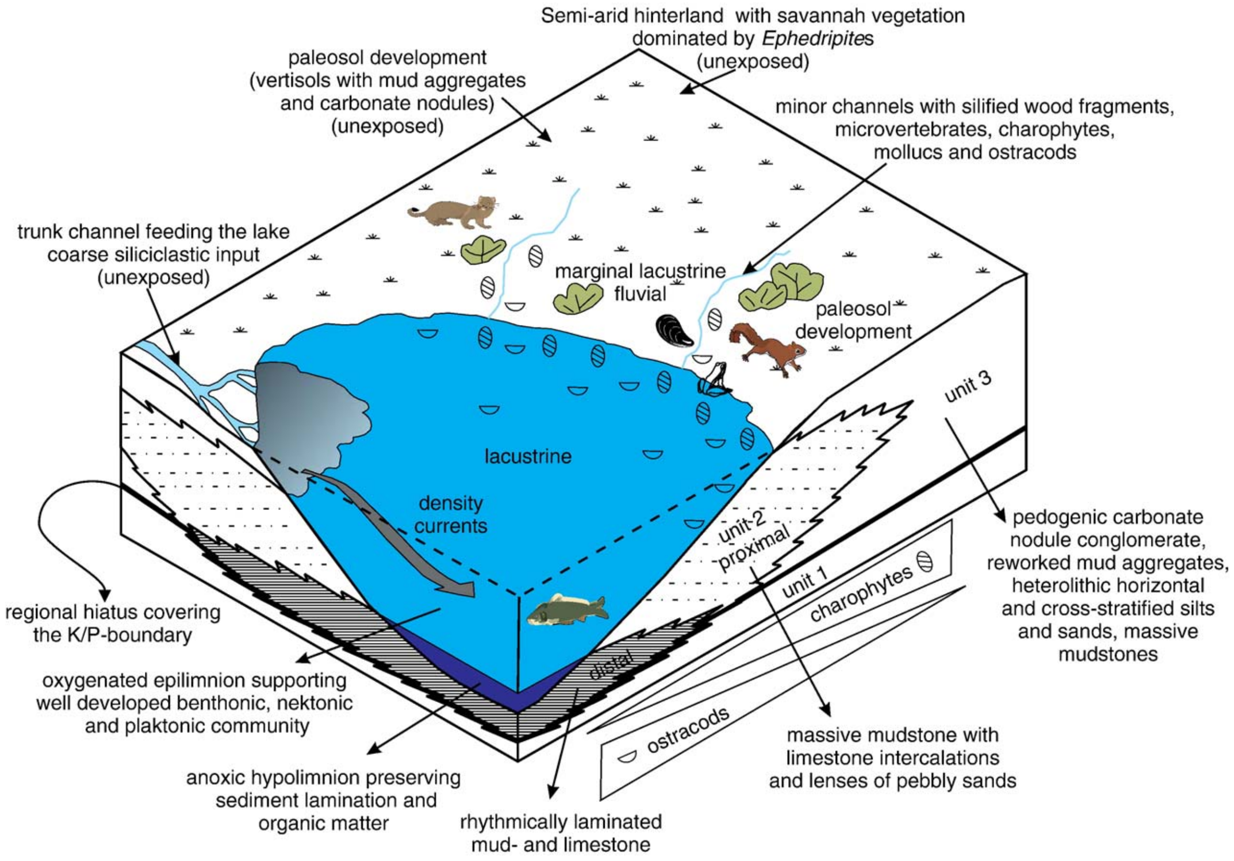

Fig. 11. Paleoenvironmental reconstruction of the Subeng area during the late Paleocene.

relatively woody environment. *Subengius mengi* is a member of the arboreal Plesiadapiformes and therefore certainly seems fit to live in a more forested environment. Among the other small mammals from Subeng, at least also for the nyctitheriids an arboreal mode of life cannot be excluded (Hooker, 2001).

Typical dryland vegetation is hardly represented in the pollen assemblage of the Nomogen formation at Subeng, suggesting a remote origin. The Bayan Ulan beds of the Nomogen Formation at Subeng contain calcrete nodules and mud aggregates, which are generally formed in dryland settings under climates that are at least seasonally hot and dry. However, these calcretes and mud pebbles are not in situ, but were reworked from more distant, unexposed environments. Equally, at Subeng, only limited development of red coloured palaeosols occurred and no gypsum or other evaporites were observed.

Contrastingly, in the nearby Bayan Ulan site the vivid red colour of the sediments was what gave this site its name, and in the Nomogen site the fossils are found in layers containing gypsum and celestite concretions (Russell and Zhai, 1987; Meng et al., 1998). Further away, in western Inner Mongolia, the Nomogen Formation is characterized by gypsum intercalations, with abundant pollen from upland vegetation and up to 30% xerophytic *Ephidripites* (Song and Zhang, 1990; Song, 1996). Therefore, Central Asia has been considered to have an open shrubbery or savanna vegetation in a relatively arid subtropical climate, with only small, dispersed woodlots and without arboreal mammals (Meng et al., 1998). Consequently, the Paleocene Central Asian environments were considered distinctly different from the more humid and forested conditions in southern and eastern areas of China and in Europe and North America (Gingerich, 1989; Song and Zhang, 1990; Meng et al., 1998).

Following our interpretation, the Subeng area represents a locally extensive, more humid woodland on this drier, more open Mongolian Plateau, with both a flora and fauna distinctly different from other Gashatan sites from Central Asia. Most notable are, the Paleocene records of plesiadapiforms and ptilodontoid multituberculates at Subeng, immigrants from North America and the first and oldest Asian members of groups previously only known from the early Eocene Wutu fauna in eastern China (Tong and Wang, 1998). This may suggest that the local palaeoenvironment at Subeng was more similar to the humid, forested conditions in North America and in eastern and southern China than was the case for any other Gashatan fauna known to date.

7. Conclusions

The multidisciplinary study of the Subeng section presented here is the first of its kind in this region and it is a first step into a more complete environmental picture of the Mongolian Plateau.

Based on both sedimentological and palynological data the Iren Dabasu Formation in Subeng is characterised as a wetland environment. Pollen data further confirm a Maastrichtian age for these deposits, and its place on the boundary of the northwestern (‘Normapolles’) and northeastern (‘*Aquilapollenites*’) Chinese palynological provinces.

The Nomogen Formation from Subeng is characterised by the presence of abundant and diverse fossil groups. Ostracod, charophyte, pollen and mammal data together strongly suggest a late Paleocene age, placing it in the Gashatan ALMA. Both sedimentological and palaeontological data suggest a fluvio-lacustrine, relatively humid local environment in a warm to subtropical and semi-arid region. The local flora is more woody and closed than elsewhere in this region. The Subeng area represents an isolated woodland on the dry Mongolian Plateau. The mammal fauna reflects these differences and shows a number of relatives to mammals from the more humid eastern Chinese biotic province, who are known to be North American immigrants. The Subeng mammals thus form a link between the forest adapted faunas in North America and in eastern China Possibly the woody local palaeoenvironment at Subeng was more suitable for the North American immigrants. Therefore we regard the Subeng mammal assemblage as a somewhat peculiar Gashatan fauna, presenting interesting affinities to faunas from both eastern China and North America.

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