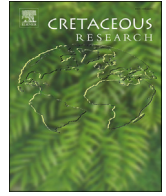




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Short communication

Reassessment of Asian *Mesoneritina* spp. (Gastropoda, Neritidae), with the description of a new genus and species from middle Cretaceous amber of northern Myanmar

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ARTICLE INFO

Article history:

Received 28 April 2022

Received in revised form

30 May 2022

Accepted in revised form 3 June 2022

Available online 11 June 2022

Keywords:

Jurassic

Kachin amber

Neritimorpha

Panneritina gen. nov.*Panneritina ambrae* sp. nov.

ABSTRACT

The genus *Mesoneritina* was first described to contain a single fossil neritid from the Lower Cretaceous of Nebraska, USA. Further Jurassic and Cretaceous neritids from the USA, Greenland, Europe and China were later classified in this genus. However, while the North American species all share similar morphologies, the Chinese forms seem to be a distinct group. In this study, we review the Chinese species presently classified in *Mesoneritina* and erect a new genus to contain them, *Panneritina* gen. nov. (with the exception of one species, now classified as *Bellamyia liaoningensis* comb. nov.). We also describe a new species, *Panneritina ambrae* sp. nov., from the middle Cretaceous Kachin amber of northern Myanmar. The new genus contains the following species: *P. ambrae* sp. nov., *P. crassa*, *P. dakangensis*, *P. gansuensis*, *P. nanshanensis*, *P. opima*, and *P. pustula*.

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1. Introduction

The genus *Mesoneritina* Yen, 1946 was first described to contain *Neritella nebrascensis* Meek & Hayden, 1861, a fossil neritid from the Lower Cretaceous of Nebraska, USA. Further Cretaceous neritids from the USA, previously assigned to the genera *Neritina* Lamarck, 1816 or to its junior synonym *Neritella* Gray, 1847 (Yen, 1946), were later moved to *Mesoneritina*. Likewise, new fossil species from the USA, Greenland, Europe and China (including Jurassic strata) were described and classified in *Mesoneritina* (Table 1).

As it currently stands, *Mesoneritina* has implied large temporal duration and spatial distribution, as well as morphological inconsistencies among its species. While the American species all share similar morphologies, the other species seem to belong to distinct groups, consistently differently from American *Mesoneritina* spp.

In this study, we review the Chinese species presently classified in *Mesoneritina* and, based on their differences to the North

American species, erect a new genus to contain them: *Panneritina* gen. nov. We also describe a new species, *Panneritina ambrae* sp. nov., based on specimens from Myanmar preserved in amber.

2. Material and methods

The material studied in the present work (including the new species) stem from the following paleontological collections: MGUH, Natural History Museum of Denmark, University of Copenhagen (Copenhagen, Denmark); NIGPAS, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Nanjing, China); USNM, Smithsonian National Museum of Natural History (Washington, D.C., USA). The specimens preserved in amber from Myanmar in the NIGPAS collection were legally obtained in 2015 (Supplementary File 1).

The type material of three Chinese taxa (*P. dakangensis*, *P. gansuensis*, and *P. mica*) was housed in the collections of the Institute of Mineral Resources (Chinese Academy of Geological Sciences) and the Xi'an Geological Survey Center (China Geological Survey). This material could not be located during the present study and the specimens are potentially lost.

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Table 1

Species of *Mesoneritina* and *Panneritina* gen. nov., with their respective type locality, stratum and chronostratigraphic horizon. Synonymized names (*M. stantoni* and *P. mica*) are shown indented.

Taxon	Type locality and stratum	Horizon
<i>Mesoneritina</i> Yen, 1946		
<i>M. ajkaensis</i> Bandel & Kiel, 2003	Hungary, Bakony Mountains, Ajka Mountains (Ajka Coal Formation)	Upper Cretaceous (Santonian/Campanian)
<i>M. bannisteri</i> (Meek, 1873)	USA, Utah, Coalville	Upper Cretaceous
<i>M. groenlandensis</i> Yen, 1958	Greenland, Nuussuaq Peninsula, Ujaragtorssuaq ("Unit C")	Upper Cretaceous
<i>M. morrisonensis</i> Yen, 1952	USA, Colorado, Ladder Canyon & Utah, Green River (Morrison Formation)	Upper Jurassic/Lower Cretaceous
<i>M. naticiformis</i> (White, 1878)	USA, Wyoming, Cokeville & Sulphur Creek (Bear River Formation)	Lower Cretaceous
<i>M. stantoni</i> (White, 1895)	USA, Wyoming, Cokeville & Twin Creek (Bear River Formation)	Lower Cretaceous
<i>M. nebrascensis</i> (Meek & Hayden, 1861)	USA, Nebraska, Wind River	Lower Cretaceous
<i>M. subhercynica</i> (Mertin, 1939)	Germany, Harz Mountains, Quedlinburg	Upper Cretaceous ("lower Senonian")
<i>Panneritina</i> gen. nov.		
<i>P. ambrae</i> sp. nov.	Myanmar, Kachin State, Myitkyina, Tanaing, Noiye Bum Village (unnamed stratum)	Middle Cretaceous (upper Albian/lower Cenomanian)
<i>P. crassa</i> (H.-Z. Pan, 1982)	China, Gansu Province (Xinminbao Group)	Lower Cretaceous
<i>P. dakangensis</i> (Y.-T. Pan, 1978)	China, Sichuan Province, Jiangyou (Tianba Formation)	Lower Jurassic
<i>P. gansuensis</i> (W. Yu & F. Guo, 1982)	China, Gansu Province (Xinminbao Group)	Lower Cretaceous
<i>P. mica</i> (W. Yu & F. Guo, 1982)	China, Gansu Province (Xinminbao Group)	Lower Cretaceous
<i>P. nanshanensis</i> (H.-Z. Pan, 1984)	China, Sichuan Province, Guangyuan (Guangyuan Group)	Middle Jurassic
<i>P. opima</i> (W. Yü, 1974)	China, Sichuan Province, Jiangyou (Ziliujing Formation)	Lower Jurassic
<i>P. pustula</i> (H.-Z. Pan, 1980)	China, Zhejiang Province, Jiande (Hengshan Formation)	Lower Cretaceous
Excluded species		
<i>Bellamyia liaoningensis</i> (X.-H. Yu, 1987) comb. nov.	China, Liaoning Province, Yixian (Banlashan Formation)	Lower Cretaceous

Photographs of the specimens were taken with a Zeiss AXIO Zoom V16 microscope at NIGPAS. The images presented here are digitally stacked composites (of circa 50 focal planes each) created with the software Helicon Focus 6 (Helicon Soft Ltd., Ukraine). Figures were prepared with the aid of Corel PHOTO-PAINT 2017 (Corel Corporation, Canada) and Adobe Photoshop CS6 (Adobe Inc., USA).

Additionally, the fossils preserved in amber (NIGP, 180007) were scanned in the micro-CT lab of NIGPAS using a 3D X-ray microscope, Zeiss Xradia 520 versa, which uses CCD-based objectives to achieve higher spatial resolution. A CCD-based 0.4× objective was used, providing isotropic voxel sizes from 0.5 mm with the help of geometric magnification. During the scan, the running voltage for the X-ray source was set at 50 kV and a thin filter (LE2) was used to avoid beam-hardening artefacts. To get a high signal-to-noise ratio, 2001 projections over 360° were collected and the exposure time for each projection was set at 3 s. Volume data processing was performed with the software Vgstudio Max (v. 3.0, Volume Graphics, Germany).

3. Systematic paleontology

Superfamily: Neritoidea Rafinesque, 1815

Family: Neritidae Rafinesque, 1815

Genus *Panneritina* gen. nov.

ZooBank reg. nr. urn:lsid:zoobank.org:act:876E791B-39E3-4ECA-A4D4-EE55DEF2278A.

Type species: *Panneritina ambrae* sp. nov.

Contained species: *P. ambrae* sp. nov., *P. crassa* (H.-Z. Pan, 1982), *P. dakangensis* (Y.-T. Pan, 1978), *P. gansuensis* (W. Yu & F. Guo, 1982), *P. nanshanensis* (H.-Z. Pan, 1984), *P. opima* (W. Yü, 1974), *P. pustula* (H.-Z. Pan, 1980).

Etymology. The genus name is a homage to Prof. Huazhang Pan, who has made outstanding contributions to the research of gastropod fossils in China. Grammatical gender: feminine.

Diagnosis. Spire taller and more pronounced (relatively to other neritids); body whorl typically larger and taller; aperture typically more vertically positioned.

Description. Shell small, neritoid, globular; imperforate; apparently smooth/unsulptured. Shell spire going from relatively pronounced to very short and small. Spire whorls with a less convex profile in relation to body whorl. Suture well-marked. Body whorl making up most of the shell, typically rounded, tall and wide. Aperture large, positioned vertically to obliquely (diagonally) positioned in relation to columellar axis. Callus present on parietal area of aperture.

Distribution. Central and eastern China, northern Myanmar.

Time span. From the Early Jurassic (*P. dakangensis* and *P. opima*) to middle Cretaceous (*P. ambrae* sp. nov.).

Discussion. This Asian group of fossil neritids can be distinguished from American and European *Mesoneritina* spp. by their typically taller and more pronounced shell spire, the larger and taller body whorl, and the more vertically positioned aperture.

The *Mesoneritina* spp. from the USA (Table 1; type specimens in the USNM) have proportions more akin to recent freshwater neritids, with a narrow body whorl and proportionately large aperture. *M. naticiformis* further differs by displaying a keeled shoulder. Likewise, *M. subhercynica* from the Late Cretaceous of Germany has a very modern appearance, including the shell's color pattern (Mertin, 1939: pl. 4, fig. 3). *M. groenlandensis* (holotype and paratype in the MGUH), from Greenland, has a higher spire and vertical aperture, but has a shouldered body whorl, rendering it much different from the present Asian species. Possibly, *M. groenlandensis* should also be excluded from *Mesoneritina*. The same can be argued for *M. ajkaensis* (Bandel and Kiel, 2003: pl. 3, figs. 1–6), from Hungary, which vastly differs from North American and Asian fossils, as well as from *M. subhercynica*, by its flattened spire, short and wide body whorl, and laterally positioned aperture.

The features described above for the Mesozoic Asian fossils also allow their distinction from most extant freshwater neritids, from Asia and elsewhere. As such, they support the creation of a separate genus to house them, *Panneritina* gen. nov.

Almost all previously described Chinese species assigned to *Mesoneritina* are herein transferred to this new genus (Table 1), with the exception of *M. liaoningensis* (X.-H. Yu, 1987). The latter species was originally only tentatively assigned to *Mesoneritina* and its high multi-whorled spire and overall bulimoid shell (Yu, 1987: pl. 12, fig. 4) is more akin to the Viviparidae genus *Bellamyia* Jousseaume, 1886,

known from fossil deposits of similar age in China (Yu, 1987) to present day Eastern Asia. As such, the new classification *Bellamyia liaoningensis* (X.-H. Yu, 1987) comb. nov. is proposed here.

Species diagnosis.

- Spire high and regular-sized; aperture more vertically positioned: *P. ambrae* sp. nov.
- Spire high and small; aperture more vertically positioned: *P. opima*.
- Spire high and small; shell globular; body whorl wide; aperture more obliquely positioned: *P. dakangensis*.
- Spire short and regular-sized; body whorl short; aperture large, obliquely positioned: *P. nanshanensis*.
- Spire short and regular-sized; body whorl wide; aperture very large, obliquely positioned: *P. gansuensis*.
- Spire short and small; aperture more obliquely positioned: *P. crassa*.
- Spire short and small; shell large; body whorl narrow; aperture very large: *P. pustula*.

Panneritina ambrae sp. nov. (Fig. 1A–E).

ZooBank reg. nr. urn:lsid:zoobank.org:act:113CC8F2-DCA1-4A38-8E81-4E6122454781.

Type material. NIGP 180007, holotype and paratype (both specimens are contained within the same piece of amber, the holotype being the larger one; Fig. 1A–C, E).

Type locality and stratum. Myanmar, Kachin State, Myitkyina District, Tanaing Township, Noije Bum Village (approximate coordinates 26°15'N, 96°33'E), from a former amber mine. Unnamed horizon from middle Cretaceous (upper Albian or lower Cenomanian). U–Pb dating of zircons from the volcanoclastic matrix of the amber provided a maximum age of circa 99 Ma for the deposits (Shi et al., 2012); ammonites found in the amber-bearing horizon indicate a late Albian to early Cenomanian age (Cruickshank and Ko, 2003; Yu et al., 2019).

Etymology. The specific epithet means “of amber”, referring to the fossil’s origin.

Diagnosis. Spire high and prominent in comparison to congeners. Aperture more vertically positioned in relation to previous whorl. *Description.* Shell neritoid, globular. Protoconch lightly bulbous; number of whorls uncertain, but potentially only one; transition to teleoconch unclear. Shell smooth. Spire raised and prominent for genus. Suture shallow, but well-marked; subsutural region of whorls slightly raised. Whorl profile only lightly convex on spire, but body whorl markedly convex and rounded. Aperture large, semi-circular; insertion on the median region of whorl. Peristome simple, but with slight thickening (arranged in two parallel lines) where the columellar region meets the callus. Parietal callus large, extending to the interior of shell. Shell imperforate.

Distribution. Known only from type locality and stratum.

Remarks. *Panneritina ambrae* sp. nov. is the only species in the genus that occurs outside China. It can be easily diagnosed from its congeners by its more raised and prominent spire and the more “vertically” positioned (i.e., more parallel to columellar axis) aperture in relation to previous whorl. The most similar species to *Panneritina ambrae* sp. nov. are *P. dakangensis* and *P. opima*, given their somewhat raised spire and the overall more globular shape of the shell. However, the latter two species belong to the Lower Jurassic of China, while the Burmese *P. ambrae* sp. nov. dates from the middle Cretaceous.

Panneritina crassa (H.-Z. Pan, 1982) (Fig. 1F, G).

Mesoneritina crassa Pan in Guo et al., 1982: 28, pl. 12, figs. 1, 2.

Type material. NIGP 44769, holotype.

Type locality/stratum. China, Gansu Province (Xinminbao Group, Lower Cretaceous).

Distribution. Known only from type locality and stratum.

Remarks. *P. crassa* is the Chinese species with the best-preserved specimen, showing the shell, spire and whorl profiles, even though the aperture is only partially preserved.

Panneritina dakangensis (Y.-T. Pan, 1978).

Mesoneritina dakangensis Pan, 1978: 421, pl. 136, fig. 7.

Type material. Potentially lost.

Type locality/stratum. China, Sichuan Province, Jiangyou (Tianba Formation, Lower Jurassic).

Distribution. Known only from type locality and stratum.

Remarks. As pointed out by Pan (1978), this species is very similar to *P. opima*, described from the same locality (but different stratum; Table 1). *P. dakangensis* has a more globular shell and a proportionately wider body whorl, as well as a more circular aperture, than *P. opima*. Its smaller size could mean that it is a juvenile or subadult of *P. opima*. However, the lack of type specimens and the low resolution of the original illustration of *P. dakangensis* do not allow a proper assessment of whether it is synonymous with *P. opima*. For the moment, we prefer the conservative approach of maintaining them as separate species.

Panneritina gansuensis (W. Yu & F. Guo, 1982).

Mesoneritina gansuensis Yu & Guo in Guo et al., 1982: 29, pl. 12, figs. 3, 4.

Mesoneritina mica Yu & Guo in Guo et al., 1982: 29, pl. 12, figs. 5, 6.

Type material. Potentially lost.

Type locality/stratum. China, Gansu Province (Xinminbao Group, Lower Cretaceous).

Distribution. Known only from type locality and stratum (Table 1).

Remarks. The species *P. mica* was described in the same publication as *P. gansuensis*, having the same type locality (Guo et al., 1982). The original photographs (Guo et al., 1982: pl. 12, figs. 3–6) represent a juvenile (*P. gansuensis*) and an adult (*P. mica*) of the same species.

Panneritina nanshanensis (H.-Z. Pan, 1984) (Fig. 1H, I).

Mesoneritina nanshanensis Pan, 1984: 428, pl. 1, figs. 1, 2.

Type material. NIGP 53426, holotype.

Type locality/stratum. China, Sichuan Province, Guangyuan (Guangyuan Group, Middle Jurassic).

Distribution. Known only from type locality and stratum.

Remarks. *P. nanshanensis* is the species with the most distinct morphology in the genus, with a shorter but wider body whorl, although the suboptimal preservation of the fossil might be exaggerating some of these features.

Panneritina opima (W. Yü, 1974) (Fig. 1J, K).

Mesoneritina opima Yü, 1974: 372, pl. 198, figs. 12, 13.

Type material. NIGP 22768, holotype.

Type locality/stratum. China, Sichuan Province, Jiangyou (Ziliujing Formation, Lower Jurassic).

Distribution. Known only from type locality and stratum.

Remarks. See discussion of *P. dakangensis* above.

Panneritina pustula (H.-Z. Pan, 1980) (Fig. 1L, M).

Mesoneritina pustula Pan in Yü & Pan, 1980: 143, pl. 1, figs. 1, 2.

Type material. NIGP 36263, holotype.

Type locality/stratum. China, Zhejiang Province, Jiande (Hengshan Formation, Lower Cretaceous).

Distribution. Known only from type locality and stratum.

Remarks. *P. pustula* is easily identified by its large circular aperture and narrow, almost laterally compressed, body whorl.

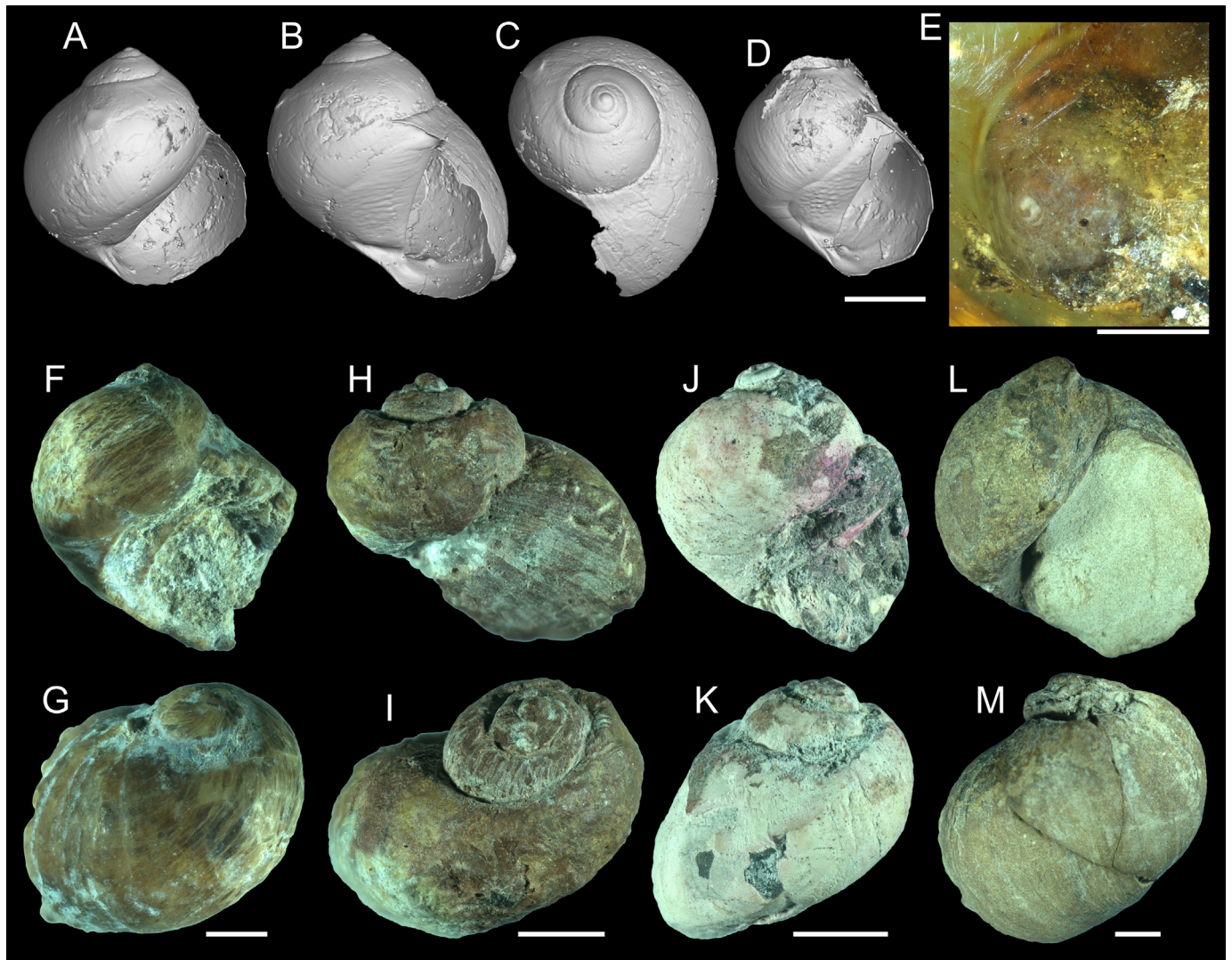


Fig. 1. *Panneritina* spp.; scale bars = 2 mm. **A–E.** *P. ambrae* sp. nov., NIGP 180007. **A–C.** Micro-CT images of holotype in apertural, oblique lateral, and oblique apical views. **D.** Micro-CT image of paratype in apertural view. **E.** Photograph of the piece of amber showing the holotype within, in oblique apical view. **F–G.** *P. crassa* (H.-Z. Pan, 1982), NIGP 44769 holotype, in apertural and oblique dorsal/apical views. **H–I.** *P. nanshanensis* (H.-Z. Pan, 1984), NIGP 53426 holotype, in apertural and oblique dorsal/apical views. **J–K.** *P. opima* (W. Yü, 1974), NIGP 22768 holotype, in apertural and dorsal views. **L–M.** *P. pustula* (H.-Z. Pan, 1980), NIGP 36263 holotype, in apertural and dorsal views.

4. Discussion

Traditionally, many Mesozoic and Cenozoic fossil land and freshwater gastropod species from China (and Asia in general) have been placed in European or North American genera, usually out of convenience and as a provisional classification. Further complicating factors are the sub-optimal preservation of many of those fossils, which in most cases consist only of internal molds and/or incomplete specimens, and the impossibility of finding some of the type specimens. While the wide distribution across Eurasia and North America might represent a biological reality for some genera, the classification of many Asian species needs to undergo taxonomic revision, particularly the freshwater gastropods. Considering what a Herculean task this is, a sensible approach is to tackle one case at a time.

Here, the Chinese species previously classified in the Mesozoic genus *Mesoneritina* were revised and transferred to the newly described genus *Panneritina* (with the exception of one species, now *Bellamyia liaoningensis* comb. nov.). A new species from northern Myanmar, preserved in amber, is also described herein:

P. ambrae sp. nov. Therefore, *Panneritina* is circumscribed as a Mesozoic Asian genus, distributed from central and eastern China to northern Myanmar, and spanning a time period from the Early Jurassic to the middle Cretaceous (Table 1). *Mesoneritina*, on the other hand, is restricted to North American species and the German species *M. subhercynica*, spanning the Late Jurassic to the Late Cretaceous (Table 1). Two species, *M. groenlandensis* from Greenland and *M. ajkaensis* from Hungary (Table 1), likely do not belong in *Mesoneritina* and are in need of revision.

5. Concluding remarks

Panneritina gen. nov. is herein defined, being diagnosed by the proportionally taller and more pronounced spire of the shell (relatively to other neritids), the typically larger and taller body whorl, and the typically more vertically positioned aperture. The new genus contains the following species: *P. ambrae* sp. nov., *P. crassa* (H.-Z. Pan, 1982), *P. dakangensis* (Y.-T. Pan, 1978), *P. gansuensis* (W. Yu & F. Guo, 1982), *P. nanshanensis* (H.-Z. Pan, 1984), *P. opima* (W. Yü, 1974), and *P. pustula* (H.-Z. Pan, 1980).

Funding

This research was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000), the Second Tibetan Plateau Scientific Expedition and Research (2019QZKK0706), and National Natural Science Foundation of China (42125201, 41688103).

Acknowledgements

We are very grateful to Arden R. Bashforth and Laura J. Cotton (MGUH) and Mark S. Florence and Kathy Hollis (USNM) for information and photographs of the type specimens housed in the collections under their care; and to Eduardo Koutsoukos and an anonymous reviewer for the helpful comments and suggestions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2022.105274>.