

THE EARLY CAMBRIAN HELCIONELLOID MOLLUSC *ANABARELLA VOSTOKOVA*

by ALEXANDER P. GUBANOV *and* JOHN S. PEEL

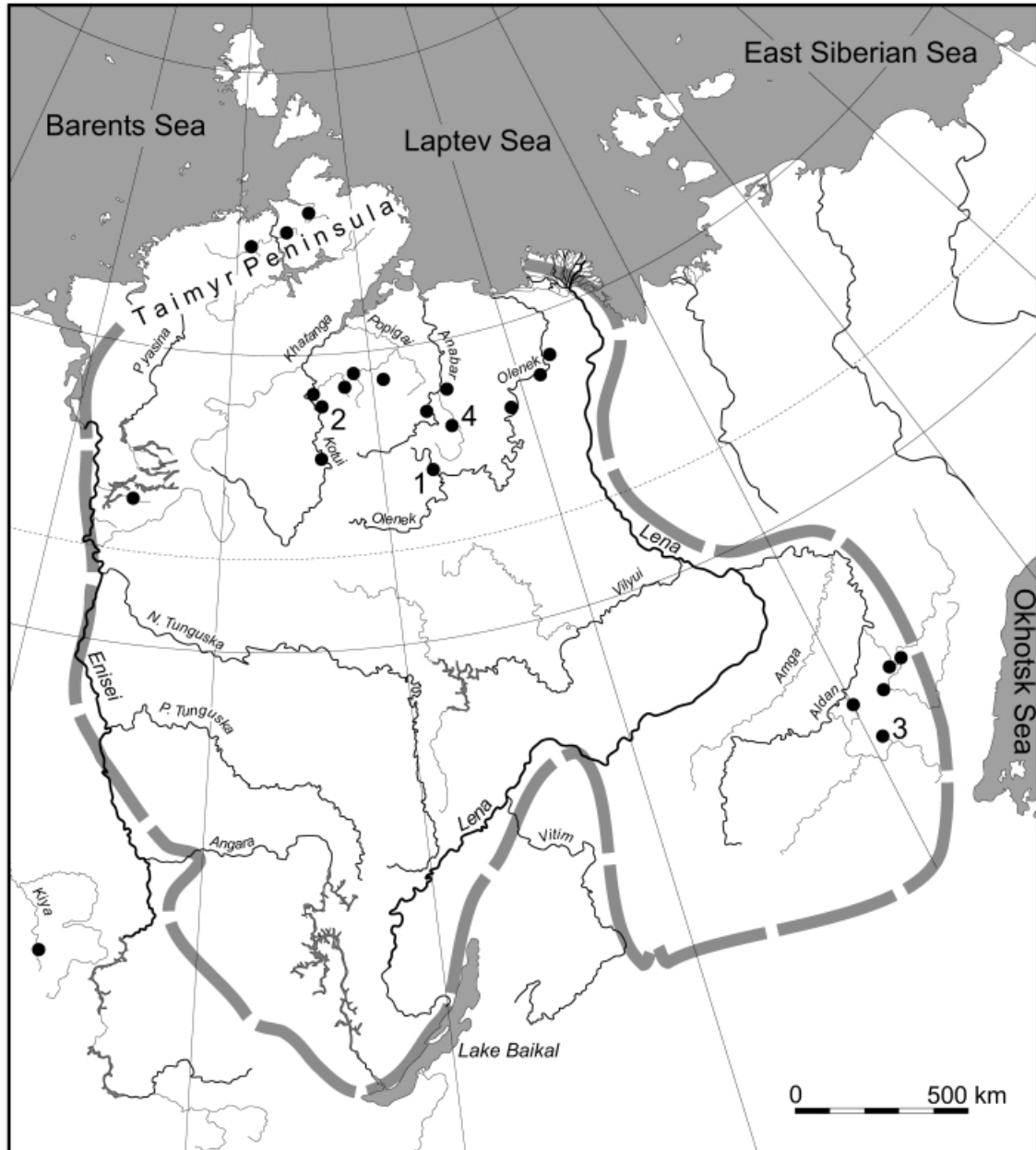
ABSTRACT. One of the oldest known helcionelloid molluscs, *Anabarella Vostokova*, is redescribed on the basis of type material from the lower Cambrian of north Siberia. Published records of the type species, *Anabarella plana* Vostokova, show a very wide range in morphology, but studies of variation through ontogeny and in taphonomy confirm assignment to a single variable species. Other described species are reviewed.

KEY WORDS: helcionelloids, Lower Cambrian, *Anabarella*, taxonomy.

EVOLUTION of the first shelled helcionelloid molluscs was to a large extent driven by rapid adaptation to the new environments that succeeded the severe life conditions of the Late Neoproterozoic. The end Neoproterozoic witnessed the most extensive (both in time and space) glaciation known from the geological record (Eerola 2001), an accompanying decrease in sea level (Knoll and Walter 1992), and oceanic anoxia (Kimura and Watanabe 2001). At the beginning of the Cambrian, the environment dramatically changed, perhaps due to global warming. An increase in plankton biomass stimulated the development of complex ecological webs and the rapid diversification of planktonic and benthic organisms, known as the 'Cambrian Explosion' (Valentine *et al.* 1999). Increased flow of nutrients boosted faunal abundance along with competition for food and living space, and stimulated search for under-exploited ecological niches, such as within the bottom sediment and in the near-bottom water layer.

Anabarella Vostokova, 1962 was the first mollusc adapted to a semi-infaunal mode of life (Gubanov *et al.* 1999). Its type species, *Anabarella plana* Vostokova, 1962, is one of the oldest known molluscs and was possibly derived from *Oelandiella Vostokova*, 1962, a more globose form with prominent transverse ribs (Gubanov and Peel 1999). *Anabarella* is a conspicuous member of one of the most prominent groups of Small Shelly Fossils which appeared in the Cambrian Explosion, namely the molluscan Class Helcionelloida (Peel 1991*a, b*). Although widely reported from a number of separate localities, *Anabarella plana* is based on poorly preserved and inadequately described material from north Siberia (Vostokova 1962). It appeared in the late Nemakit-Daldynian (Khomentovsky and Karlova 1993) and existed only until the late Tommotian (early Cambrian), having produced a series of morphologically distinct forms. These forms have been treated in the literature as different species by some authors, or just as variation of the same species (Landing *et al.* 1989). *Anabarella plana* is most abundant in the lower Tommotian of the Siberian Platform (Vostokova 1962; Rozanov *et al.* 1969; Val'kov 1987; Missarzhevsky 1989), and Taimyr (Vostokova 1962; Bezzubtsev *et al.* 1979) (Text-fig. 1), in the possibly uppermost Nemakit-Daldynian Bayangol Formation of Mongolia (Esakova and Zhegallo 1996), and in the lower Cambrian of Sierra Morena of Spain (Gubanov 1998; Vidal *et al.* 1999). Scattered finds are reported from the lower Cambrian of Poland (Lendzion and Posti 1983), Estonia (Gubanov 1998; Mens and Isakar 1999), Newfoundland (Landing *et al.* 1989), Kuznetsk Alatau (Pospelov *et al.* 1995), and China (He and Yang 1982; Jiang 1982; Xing *et al.* 1983).

Anabarella represents an evolutionary transition from the benthic helcionelloid *Oelandiella* to the bivalve-like infaunal *Watsonella* Grabau, 1900 and probably to the truly bivalved *Fordilla* Barrande, 1881 and *Pojetaia* Jell, 1980 (Runnegar and Pojeta 1974; Gubanov *et al.* 1999; see also Gubanov 1998; Kouchinsky 1999; Vidal *et al.* 1999; Carter *et al.* 2000; Gubanov and Peel 2000). These dramatic evolutionary changes developed within a short period of time around the Nemakit-Daldynian/Tommotian



TEXT-FIG. 1. Map of the Siberian Platform, showing localities for *Anabarella plana* in the Lower Cambrian. 1, the Kengede (Kenya) River; 2, the Kotui River; 3, the Selinde River; 4, the Malaya Kuonamka River. Grey dashed line is the edge of the Siberian Platform.

boundary where *Anabarella plana* itself determines a very narrow stratigraphical interval in Siberia constrained between its first appearance just after the first record of *Oelandiella* in the *Purella antiqua* Biozone and the appearance of *Watsonella crosbyi* (= *Heraultipegma sibirica*) that is the index fossil of the biozone bearing its name (Brasier 1989; Missarzhevsky 1989; Khomentovsky and Karlova 1993;

Val'kov 1987; Gubanov 1998, 2002). The shift from an epifaunal to an infaunal mode of life is possibly rooted in a rapid increase of competition for food on the water/sediment interface after the first diversification of life (Gubanov and Peel 1999). Landing (1989) has provided direct evidence for an infaunal mode of life for *W. crosbyi* by his description of *in situ*, vertically oriented molluscs from the lower Cambrian of Newfoundland.

GEOLOGICAL RECORD

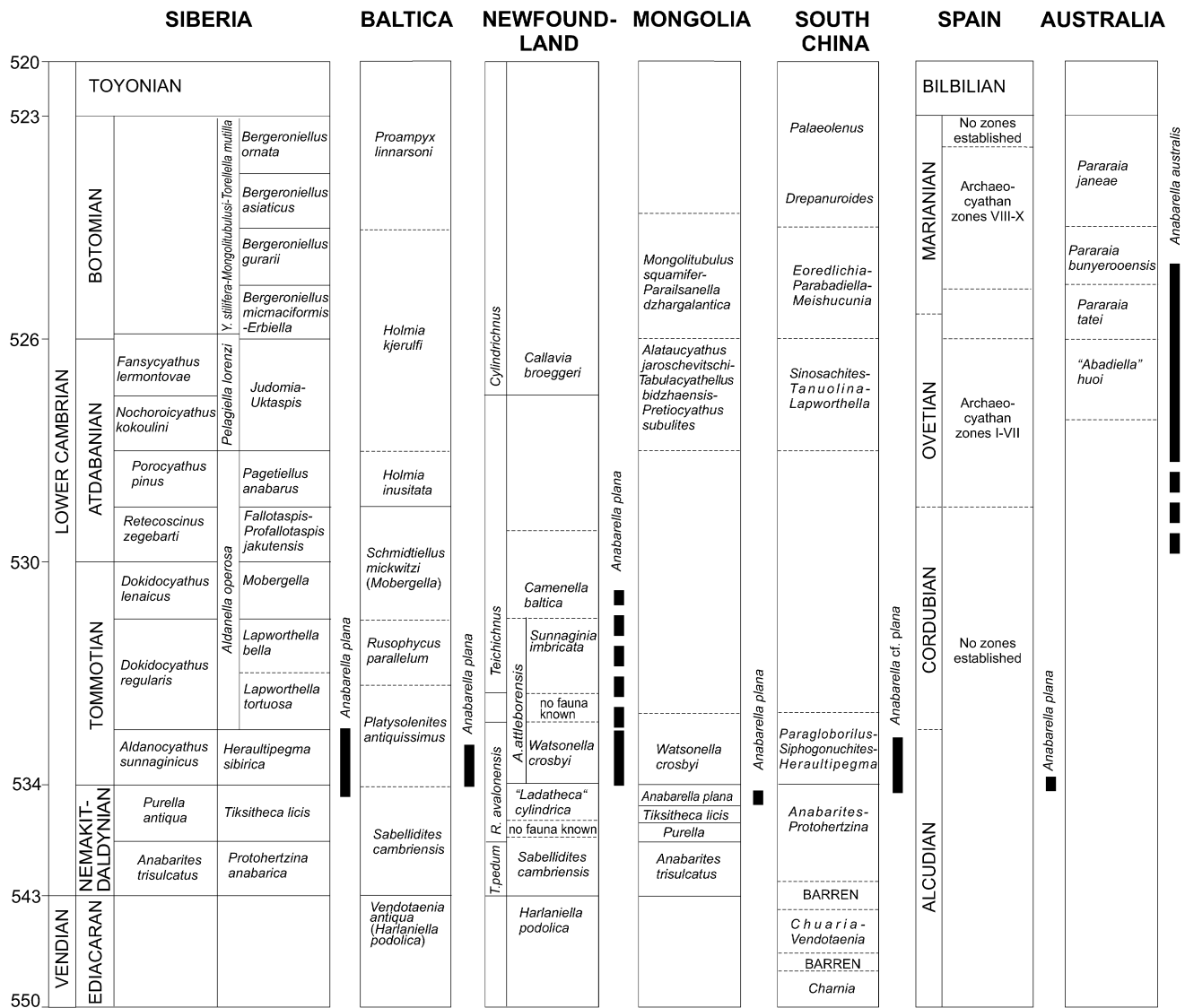
The earliest known *Anabarella plana* is derived from the upper Nemakit-Daldynian *Purella antiqua* Zone (Khomentovsky and Karlova 1993) (Text-fig. 2) in the northern Siberian Platform. *Anabarella* probably appeared even earlier in Mongolia, though there is some uncertainty concerning the age determination of the strata in which it occurs. Voronin *et al.* (1982) and Esakova and Zhegallo (1996) suggested a Tommotian age, but more probably the age is late Nemakit-Daldynian (Brasier *et al.* 1996; Gubanov 1998, 2002), an interval that is possibly missing in some places in Siberia. *Anabarella* from Spain may be late Nemakit-Daldynian or early Tommotian in age (Vidal *et al.* 1999), though there is a lack of reliable biostratigraphic evidence. *Anabarella* from the north-western Russian Platform (Lendzion and Mens 1983; Mens and Isakar 1999) occurs together with *Aldanella* that correlates this part of the Lontova Formation to the lower Tommotian *Watsonella crosbyi* (= *Heraultipegma sibirica*) Zone (Gubanov 1998, 2002). In Newfoundland, *Anabarella* appears in the uppermost part of the *Watsonella crosbyi* Zone of the Chapel Island Formation (Landing *et al.* 1989). It is documented through the uppermost part of Member 3 of the Cuslett Formation (middle *Camenella baltica* Zone), although this record is not well founded due to poor preservation of the very sparse material. *Anabarella* has been also identified from the assemblage Zone II of the Meishucunian Stage in China (Jiang 1982), with the described mollusc showing very similar shell proportions to the holotype of *A. plana*.

Two additional species of *Anabarella* have been described from China (Luo *et al.* 1982; Xing *et al.* 1983), but the poor illustrations fail to provide firm evidence for their validity or for the synonymy with *A. plana* proposed by Landing *et al.* (1989). Both of these species of *Anabarella* occur together with *Watsonella* (described as *Heraultipegma varensalensis* by Xing *et al.* 1983, and *H. yannensis* by He and Yang 1982) that are perhaps synonyms of *W. crosbyi* (Landing *et al.* 1989); they can be considered coeval with records of *A. plana* from other areas.

The youngest known specimens of *Anabarella* were described from Australia by Bengtson *et al.* (1990). *Anabarella australis* Runnegar, in Bengtson *et al.* 1990 and *A. argus* Runnegar, in Bengtson *et al.* 1990 were recovered from the Atdabanian part of the Parara and Ajax limestones (Bengtson *et al.* 1990). Parkhaev (in Gravestock *et al.* 2001) has extended this range into the Botomian. Similar specimens are known from the Bastion Formation of north-east Greenland (Christian Skovsted, pers. comm. 2002). Molluscs questionably determined as *Anabarella* are also known from the uppermost lower Cambrian Lemdad Formation in Morocco (Geyer *et al.* 1995) and from the middle Cambrian Montejimi Formation in Australia (Kruse 1998).

Anabarella indecora Missarzhevsky, 1969 (Rozanov *et al.* 1969) from the lower Tommotian of Siberia was also recognised in the lower Cambrian *Strenuella* Limestone (= Comley Limestone) by Hinz (1987). Missarzhevsky (1989) subsequently transferred this species to the genus *Mellopegma* Runnegar and Jell, 1976.

The molluscs described herein mostly come from the north-east part of the Siberian Platform (Text-fig. 1). The best preserved samples were obtained from rocks collected by V. V. Missarzhevsky from the locality M 410/84 (spot 2 in Text-fig. 1) along the Kotui River just above the Tommotian basal member (see Rozanov *et al.* 1969, pp. 36–39). Phosphatized internal moulds are from lower Tommotian strata exposed along the Selinde and Malaya Kuonamka rivers (Text-fig. 1). Described material is stored in the Geological (GIN) and Palaeontological (PIN) Institutes, Russian Academy of Sciences, Moscow; CNIGR Museum (CNIGRM), St.-Petersburg; Yakutian Geological Museum (YGM), Yakutsk; the Swedish Museum of Natural History (SMNH), Stockholm; and the Palaeontological section of the Museum of Evolution (PMU), Uppsala.



TEXT-FIG. 2. Correlation chart for Lower Cambrian and stratigraphical distribution of *Anabarella plana* (modified from Gubanov 2002) and *A. australis* (from Bengtson *et al.* 1990; Gravestock *et al.* 2001).

SYSTEMATIC PALAEOONTOLOGY

Class HELCIONELLOIDA Peel, 1991a

Order HELCIONELLIDA Geyer, 1994

Family HELCIONELLIDAE Wenz, 1938

Genus ANABARELLA Vostokova, 1962

Type species. *Anabarella plana* Vostokova, 1962 from the Lower Cambrian of north Siberia.

Diagnosis. Small, bilaterally symmetrical univalve mollusc with the involute, rapidly expanding, laterally compressed shell coiled through about one whorl; shell smooth or slightly ornamented by closely spaced transverse growth lines.

Discussion. *Anabarella* differs from genera such as *Latouchella* Cobbold, 1921, *Oelandia* Westergård, 1936, *Oelandiella* Vostokova, 1962 and *Shabaktiella* Missarzhevsky, in Missarzhevsky and Mambetov 1981 by its strongly laterally compressed, rapidly expanding smooth or slightly ornamented shell. The genera *Mellopegma* Runnegar and Jell, 1976 and *Stenothecca* Salter, in Hicks 1872 possess similar laterally compressed shells but these do not exceed half a whorl. Helcionelloids such as *Aldanella* Vostokova, 1962, *Barskovia* Golubev, 1976, *Bestashella* Missarzhevsky, in Missarzhevsky and Mambetov 1981, *Kistasella* Missarzhevsky, 1989, *Pelagiella* Matthew, 1895, *Philoxenella* Vostokova, 1962, *Nomgoliella* Missarzhevsky, in Missarzhevsky and Mambetov 1981 and *Yuwenia* Runnegar, 1981 have a clearly asymmetrical, relatively slowly expanding shell, though *Bestashella*, *Kistasella* and *Yuwenia* show a very elongated, laterally compressed shell cross section comparable with that of *Anabarella*.

Anabarella plana Vostokova, 1962

Plates 1–3; Text-figure 3

- 1962 *Anabarella plana* Vostokova, p. 56, pl. 2, fig. 1.
 1969 *Anabarella plana* Vostokova; Rozanov *et al.*, p. 144, pl. 2, fig. 3; pl. 4, figs 4–6.
 1982 *Anabarella plana* Vostokova; Zhegallo, in Voronin *et al.*, p. 45, pl. 1, figs 6–7.
 1982 *Anabarella exigua* Zhegallo, in Voronin *et al.*, p. 45, pl. 1, fig. 8.
 1982 *Anabarella plana* Vostokova; Jiang, pp. 191–192, pl. 20, fig. 11.
 1983 *Anabarella plana* Vostokova; Lenzion and Posti, p. 126, pl. 94, fig. 8.
 1987 *Anabarella plana* Vostokova; Val'kov, p. 121, pl. 16, figs 2–3.
 1989 *Anabarella plana* Vostokova; Landing *et al.*, pp. 755–756, figs 9.4, 10.11–12.
 1995 *Anabarella plana* Vostokova; Esakova and Ermak, in Pospelov *et al.*, p. 204.
 1996 *Anabarella plana* Vostokova; Zhegallo, in Esakova and Zhegallo, p. 170, pl. 20, figs 1–2.
 1996 *Anabarella exigua* Zhegallo; Zhegallo, in Esakova and Zhegallo, p. 170, pl. 20, fig. 3.
 1999 *Anabarella* cf. *A. plana* Vostokova; Gubanov, in Vidal *et al.*, p. 142, figs 4–5.

Holotype. CNIGRM No. 8361–8 from the Lower Cambrian of the Kenyada (Kengede) River, the western tributary of the Olenek River, north Siberia.

Material. YGM 165/22 (one specimen), the lower part of the Emyaksin Formation, Ulakhan-Tyulen River, north Siberia; GIN 3593/726 (one specimen), SMNH Mo 160430–160431 (two specimens), PMU SIB 1013–1022 (ten specimens), all from Medvezhin Formation, Kotui River, north Siberia; PMU SIB 1023–1025 (three specimens), Pestrotsvetnaya Formation, Selinde River, south-east Siberia; PMU SP 0001–0006 (six specimens), Santa Lorenzo de Calatrava, Sierra Morena, Spain; PIN 3302/1575 (one specimen), PMU MON 0001–0002 (two specimens), sample T17, locality Taishir 1, Bayangol Formation, Mongolia. Numerous specimens from Siberia, Spain and Mongolia have been examined in residues.

Description. The shell is small, up to 10 mm in diameter, rapidly expanding, univalve, tightly coiled through one whorl, bilaterally symmetrical and strongly laterally compressed. The initial part of the shell is advolute or loosely coiled; the later shell is slightly involute. The outer surface is ornamented by fine comarginal growth lines and shallow

irregularly spaced folds as well as by fine, barely visible, spiral striations in some samples. The aperture is narrow in plan view with a length/width ratio of about 4; its margins are convex when viewed laterally. The internal mould is smooth with a hook-shaped initial part.

Preservation. Preservation is strongly dependent on the type of rock containing the specimens, as well as on the method of fossil extraction. Chemical methods of using a weak acid usually have been employed to treat phosphatized calcareous rocks where molluscs are usually preserved as internal moulds and quite rare as external moulds. Very often phosphatization does not exactly replicate the form of the original shell and may include shell overgrowths as well. For instance, specimens of the Spanish *Anabarella* are heavily phosphatized and the thickness of phosphatization around the original shell varies extensively. Phosphatization may begin with the organic matter of the shell or with the soft tissue of the molluscs. It can also include the shell itself, and can penetrate into the matrix surrounding the shell. Algal or bacterial overgrowths of the shell are also readily phosphatized.

Phosphatization may replicate very fine features of the shell or soft tissue, but such cases are rare and require very gentle treatment in acid. In the case of *A. plana*, the best-preserved samples (Pl. 1; Text-fig. 3C–F) were obtained by mechanical preparation of non-phosphatized limestone, though preservation in these cases depends on the degree of recrystallization. The outer surface of recrystallized shell is often more strongly bound to the matrix than is the inner smoother surface of the shell interior, with the result that internal rather than external moulds are usually extracted by mechanical breakage.

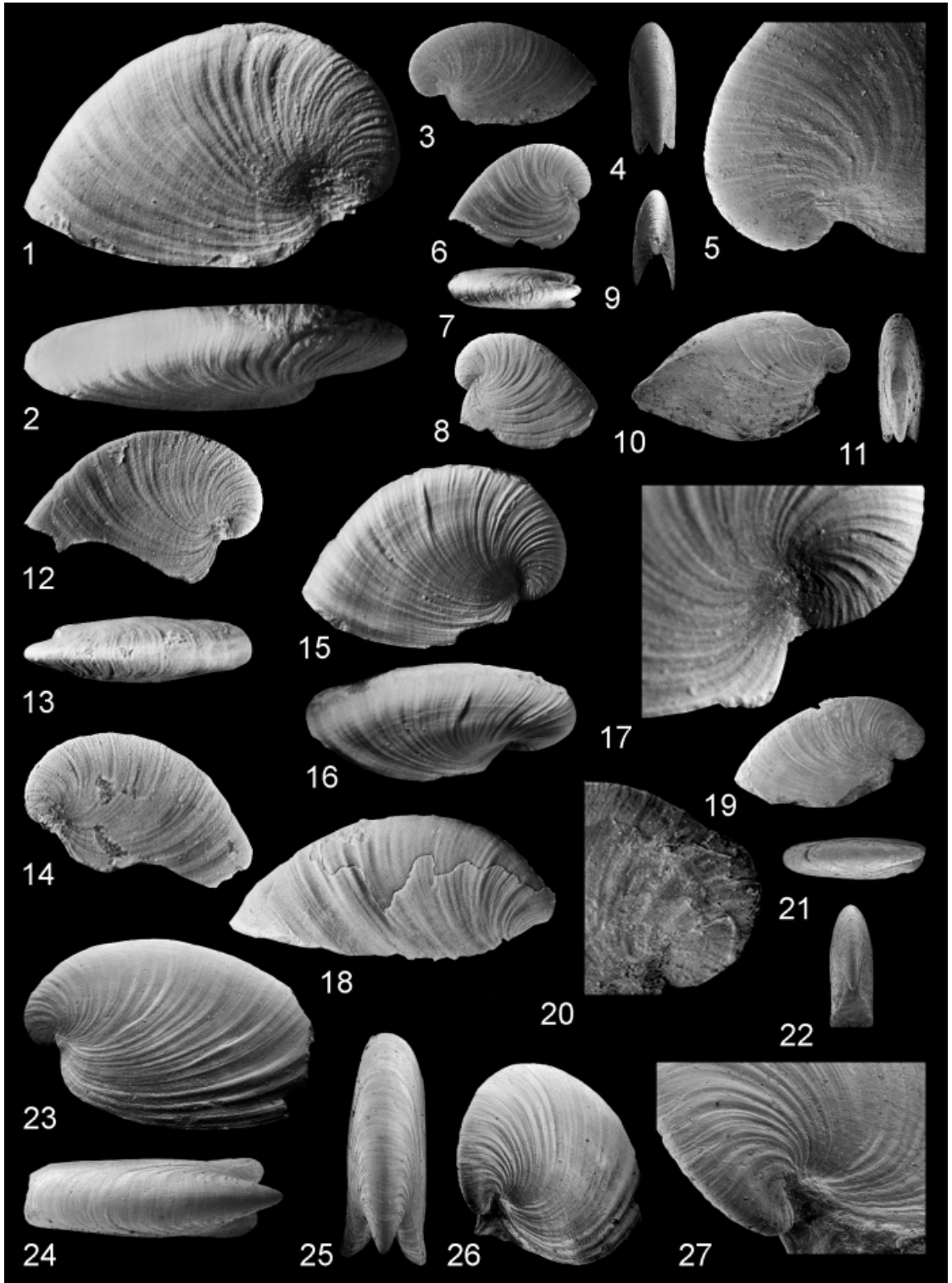
It is widely known that molluscs preserved as internal and external moulds can look quite different (cf. Runnegar and Pojeta 1985) which can confuse their determination. Internal moulds of *Anabarella plana* have a smoother surface with very gentle rugae; growth lines are present only on the external surface of the shell (Pl. 1, fig. 18). The holotype of *A. plana* is evidently an internal mould with a very smooth surface and barely visible comarginal rugae (Text-fig. 3A–B). The initial shell of *A. plana* also looks strikingly different in internal and external moulds. The apex of internal moulds is beak-like, framing a hook which is not in contact with the rest of the internal mould (Pl. 2, figs 1–10, 12–14), while the external shell clearly shows the slightly involute coiling in which the initial shell is partly covered by the later one (Pl. 1, figs 5, 11, 27; Text-fig. 3D–F).

Discussion. The holotype (Text-fig. 3A–B) is a small, poorly preserved, laterally compressed univalve shell with a smooth, slightly eroded surface. Lateral surfaces are almost flat with weakly developed comarginal rugae convex toward the aperture. The maximum length is about 8 mm; the height is 6 mm. The initial shell and the posterior part of the latter whorl are partly broken and the exact position of the initial part of the whorl relative to the apertural margin is not known.

Two other specimens mentioned in the original description are not preserved in the collection. According to Vostokova (1962), the holotype is the best-preserved specimen among five studied

EXPLANATION OF PLATE I

Figs 1–27. *Anabarella plana* Vostokova, 1962 from the Medvezhin Formation, Kotui River, north-west Siberia. All light photographs. 1–2, GIN 3593/726. 1, left lateral view; 2, dorsal view; both $\times 10$. 3–5, PMU SIB 1014. 3, lateral view; $\times 10$. 4, posterior view; $\times 10$. 5, lateral view of umbilical part showing contact between initial and apertural part of the whorl; $\times 30$. 6–9, PMU SIB 1018. 6, left lateral view from the left; 7, right lateral view from the right; 8, dorsal view; 9, posterior view; all $\times 10$. 10–11, PMU SIB 1016. 10, lateral view; 11, posterior view; both $\times 10$. 12–14, PMU SIB 1017. 12, left lateral view from the left; 13, right lateral view; 14, dorsal view; all $\times 10$. 15–17, PMU SIB 1019. 15, lateral view; 16, dorso-lateral view showing spiral ribs; both $\times 10$. 17, lateral view showing contact between initial and apertural part of the whorl; $\times 25$. 18, PMU SIB 1015; $\times 7.5$. 19–22, PMU SIB 1020. 19, lateral view; $\times 10$. 20, lateral view showing contact between initial and apertural part of the whorl; $\times 30$. 21, dorsal view; 22, posterior view; both $\times 10$. 23–27, PMU SIB 1013. 23, lateral view; 24, dorsal view; 25, posterior view; 26, postero-lateral view; all $\times 10$. 27, postero-lateral view showing contact between initial and apertural part of the whorl; $\times 25$.



specimens. A dorsal view of one of the specimens illustrated by Vostokova (1962, pl. 2, fig. 3) indicates that the shell is elongate with a length/width ratio of about 4.5.

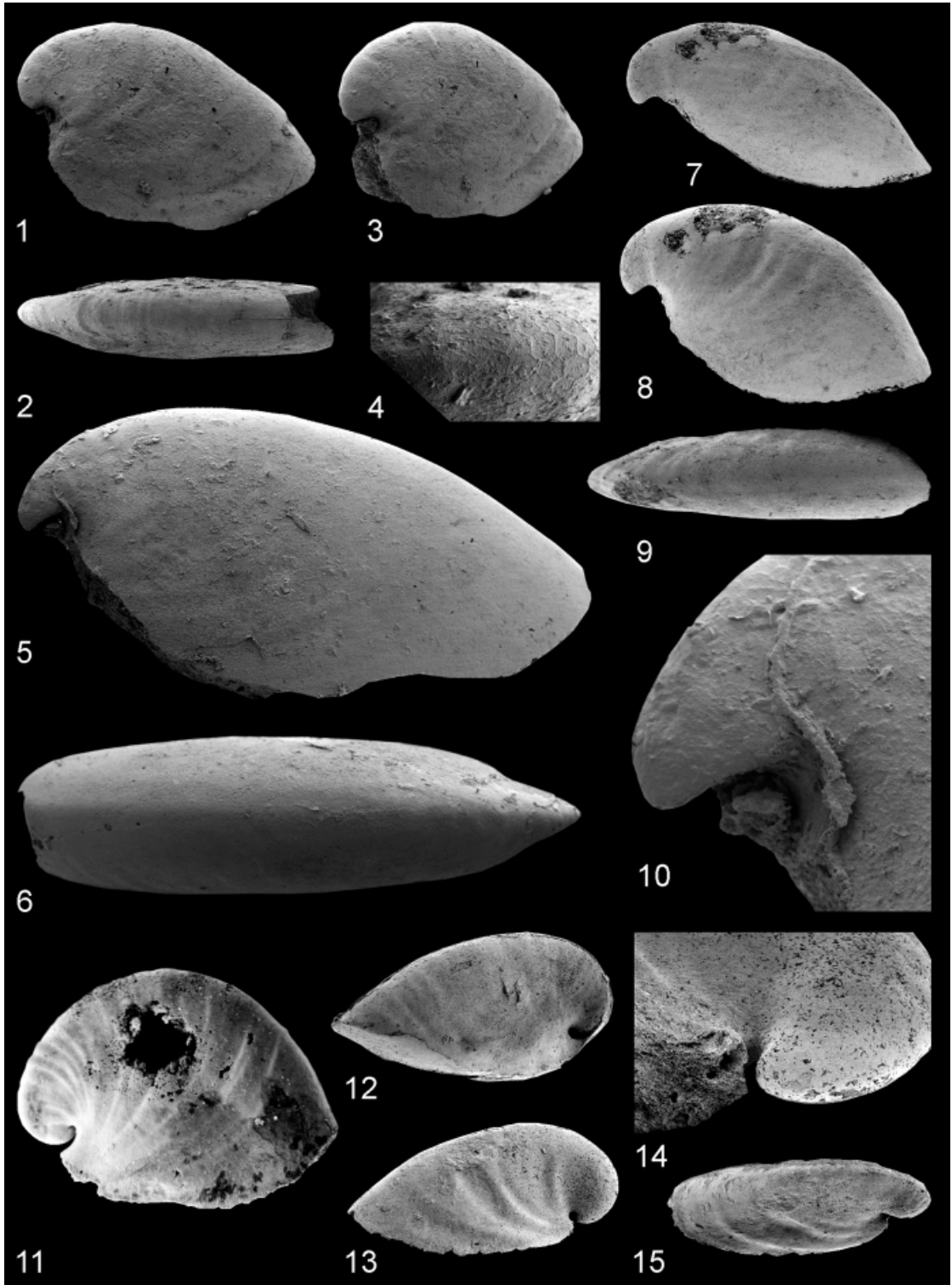
Well-preserved molluscs from the area close to the type locality, and from sections along the Anabar, Kotui, Olenek and Malaya Kuonamka rivers of the north-east part of the Siberian Platform were described by Missarzhevsky (Rozanov *et al.* 1969; Missarzhevsky 1989) and Val'kov (1987). These specimens (Pl. 1, figs 1–2; Text-fig. 3C–F) clearly show closely-spaced comarginal growth lines that sometimes form irregular or almost regularly-spaced rugae and gentle spiral striations. The initial shell is lifted above the plane of the aperture. The posterior margin of the aperture is bent upward and partly covers the initial shell, such that the shell is slightly involute. The anterior margin is also slightly arched upward on account of the adaperturally convex form of the lateral apertural margins. Both specimens illustrated by Missarzhevsky (Rozanov *et al.* 1969, pl. 2, fig. 3; Pl. 1, figs 1–2 here) and Missarzhevsky (1989, pl. 4, fig. 1) show similar shell proportions to the holotype with a rate of shell expansion (ratio of whorl radius to the radius one whorl previously) of about 10 and a length/height ratio of about 1.25. Two large shells from the Anabar River section were illustrated by Val'kov (1987, pl. 16, figs 2–3; Text-fig. 3C–F here) and the one of these which exceeds the size of the holotype shows higher values of about 14 and 1.7, respectively.

Other specimens in Missarzhevsky's collection from the Kotui River section, as well as newly recovered shells from the same sample, demonstrate the quite high variability of *A. plana*. Shell expansion varies from 10 to 13 and the length/height ratio from 1.25 to 1.7. Ontogenetic changes are also conspicuous. Thus, for specimen PMU SIB 1013 (Pl. 1, figs 23–27) the length/height ratio changes from 1.25 in the early shell to 1.8 at a late growth stage, and the ratio of the shell expansion from 8 to 13. The curvature of growth lines when viewed laterally also becomes shallower in later growth stages (Pl. 1, fig. 23).

Although too few specimens are available to support a proper statistical analysis, it is evident that *A. plana* shows considerable morphological variation. This variation ranges from relatively slowly expanding, ribbed shells which closely resemble the morphology of *Oelandiella* (Gubanov and Peel 1999; Gubanov *et al.* 1999; Pl. 3 here) to rapidly expanding and less coiled forms (Gubanov *et al.* 1999; Kouchinsky 1999) that approach the morphology of *Watsonella* (Pl. 2, figs 1–10; Text-fig. 3H). Unfortunately, the holotype of *A. plana* is poorly preserved, but in terms of its lateral shape it is very similar to two molluscs from the Kotui River locality illustrated by Missarzhevsky (*in* Rozanov *et al.* 1969, pl. 4, fig. 4) and Missarzhevsky (1989, pl. 6, fig. 1). Due to the excellent preservation we use one of the specimens obtained from Missarzhevsky's sample as a basis for comparison with other material (Pl. 1, figs 15–17). Not all illustrated *A. plana* from Siberia (Rozanov *et al.* 1969; Val'kov 1985; Missarzhevsky 1989) are different from the holotype, but the existing collections show a great deal of variability within the species. Molluscs from the same sample in Missarzhevsky's collection and newly extracted shells show significant variation in shell form (Pl. 1). Shell expansion and, as a result, the length/height ratio vary as much as almost twice within the population (Pl. 1, figs 1, 23). Considerable variation of morphology also occurs during the ontogeny of some individuals (Pl. 1, figs 3, 10, 15). Usually it is seen as an increase in whorl expansion, though some samples show an irregular pattern of ontogenetic growth (Pl. 1, figs 19–20; Pl. 3, fig. 1) that could be pathological or reflect a response to unfavourable environmental change. Specimens morphologically close to the holotype demonstrate no visible change during ontogeny, and the shape of the shell and form of the spire remain similar for the juvenile and adult shell (Pl. 1, figs 1, 15).

EXPLANATION OF PLATE 2

Figs 1–15. *Anabarella plana* Vostokova, 1962, internal moulds from the Lower Cambrian of the Selinde River, south-east Siberia (1–10) and Mongolia (11–15). 1–4, PMU SIB 1022. 1, lateral view; 2, dorsal view; 3, postero-lateral view; all $\times 35$. 4, enlarged dorsal surface showing casts of calcitic shell prisms; $\times 140$. 5–6, 10, PMU SIB 1023. 5, lateral view; 6, dorsal view; both $\times 35$. 10, enlarged initial part showing beak-like apex; $\times 140$. 7–9, PMU SIB 1024. 7, lateral view; 8, dorso-lateral view showing lateral comarginal rugae; 9, dorsal view; all $\times 35$. 11, PIN 3302/1575; lateral view; $\times 40$. 12, PMU MON 0001; lateral view; $\times 35$. 13–15, PMU MON 0002. 13, lateral view; 14, ventro-lateral view to show posterior part of the aperture and its contact with initial whorl; both $\times 35$. 15, dorso-lateral view; $\times 120$. All SEM photographs.



The coarse preservation of *A. plana* from Spain (Pl. 3) contrasts strongly with the well-preserved Siberian material. The heavy phosphatization of the Spanish shells obscures some morphological features but enhances preservation potential. On average, the Spanish molluscs are larger than molluscs from other areas, although this difference is probably largely taphonomic. They have been concentrated on the bedding surfaces with clear hydrodynamic sorting. Morphological differences include coarser rugae which form crude ribbing and a shallower curve of the apertural margin in lateral aspect that results in a lower elevation of the initial whorl above the plane of the aperture when compared with the Siberian molluscs. Some individuals, however, possess a similar shell form to Siberian *A. plana* (Pl. 3, figs 8, 11, 14–15). The largest shells from Spain show a decrease in whorl expansion that possibly indicates a gerontic stage of development (Pl. 3, figs 1–3).

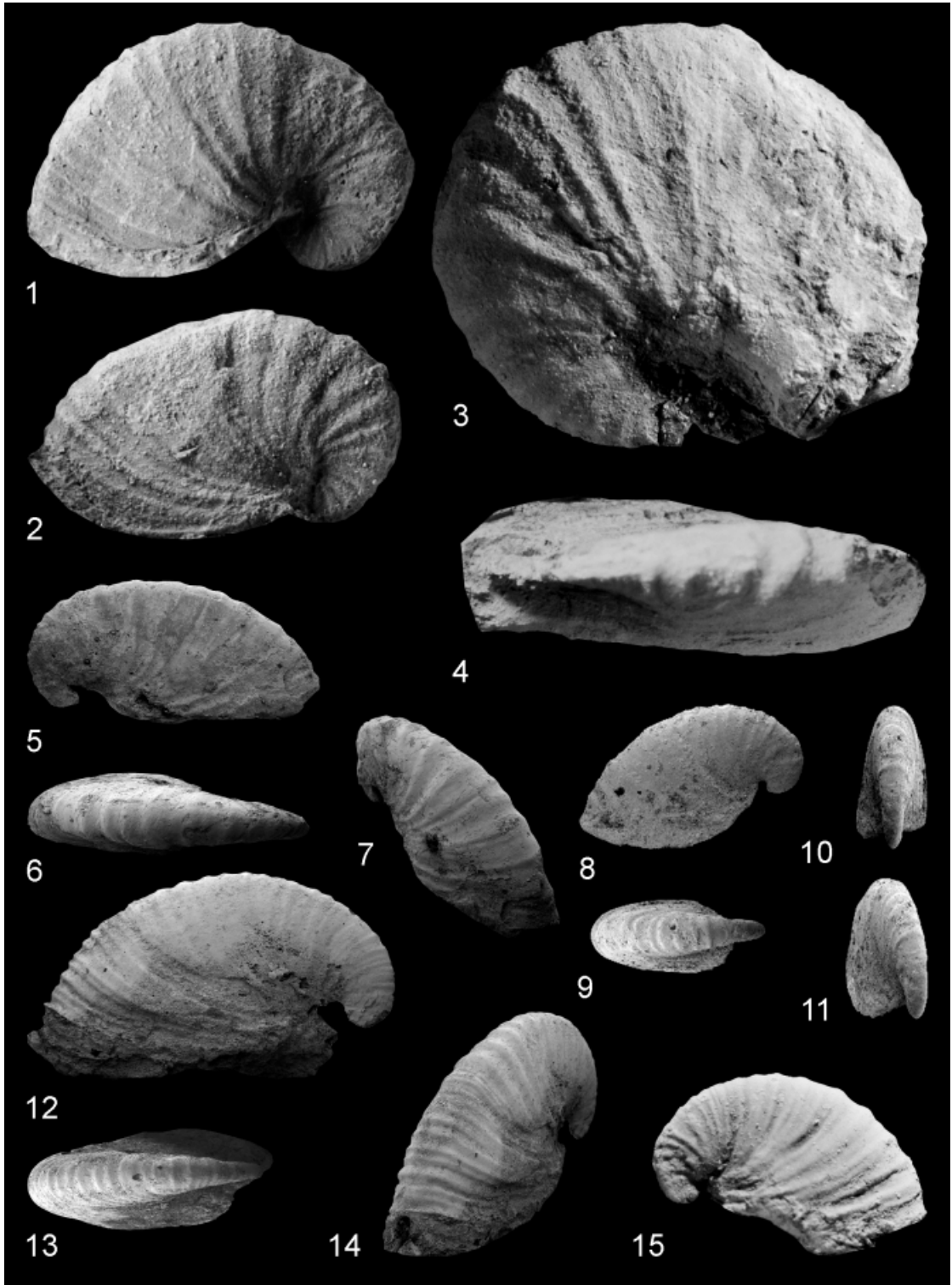
Preservation of the phosphatized shells of *A. plana* from the lower Cambrian of Mongolia is better than in Spain and reveals more morphological detail. In shell form, the Mongolian specimen illustrated by Zhegallo (*in* Esakova and Zhegallo 1996, pl. 20, fig. 1) (Pl. 2, fig. 11) is similar to the holotype (Text-fig. 3A–B), though it is much smaller and has an evolute shell without contact between the initial whorl and the later shell. Some small shells from Siberia show that involute coiling appears in a later stage of development (compare Pl. 1, figs 6 and 27). A species described from Mongolia as *A. exigua* Zhegallo, 1982 (Voronin *et al.* 1982; Esakova and Zhegallo 1996, pl. 20, fig. 3) represents a rather poorly preserved internal mould that resembles specimens of *A. plana* with a high rate of shell expansion. We support Missarzhevsky's opinion that it falls within the morphological variation of *A. plana* (Missarzhevsky 1989). Our own study of numerous molluscs from Mongolia reveals that most specimens of *A. plana* have a much more expanded shell form (Pl. 2, figs 12–13) than the specimen illustrated by Zhegallo (*in* Esakova and Zhegallo 1996) (Pl. 2, fig. 11) and the involute coiling is clearly seen even on the internal mould (Pl. 2, fig. 14).

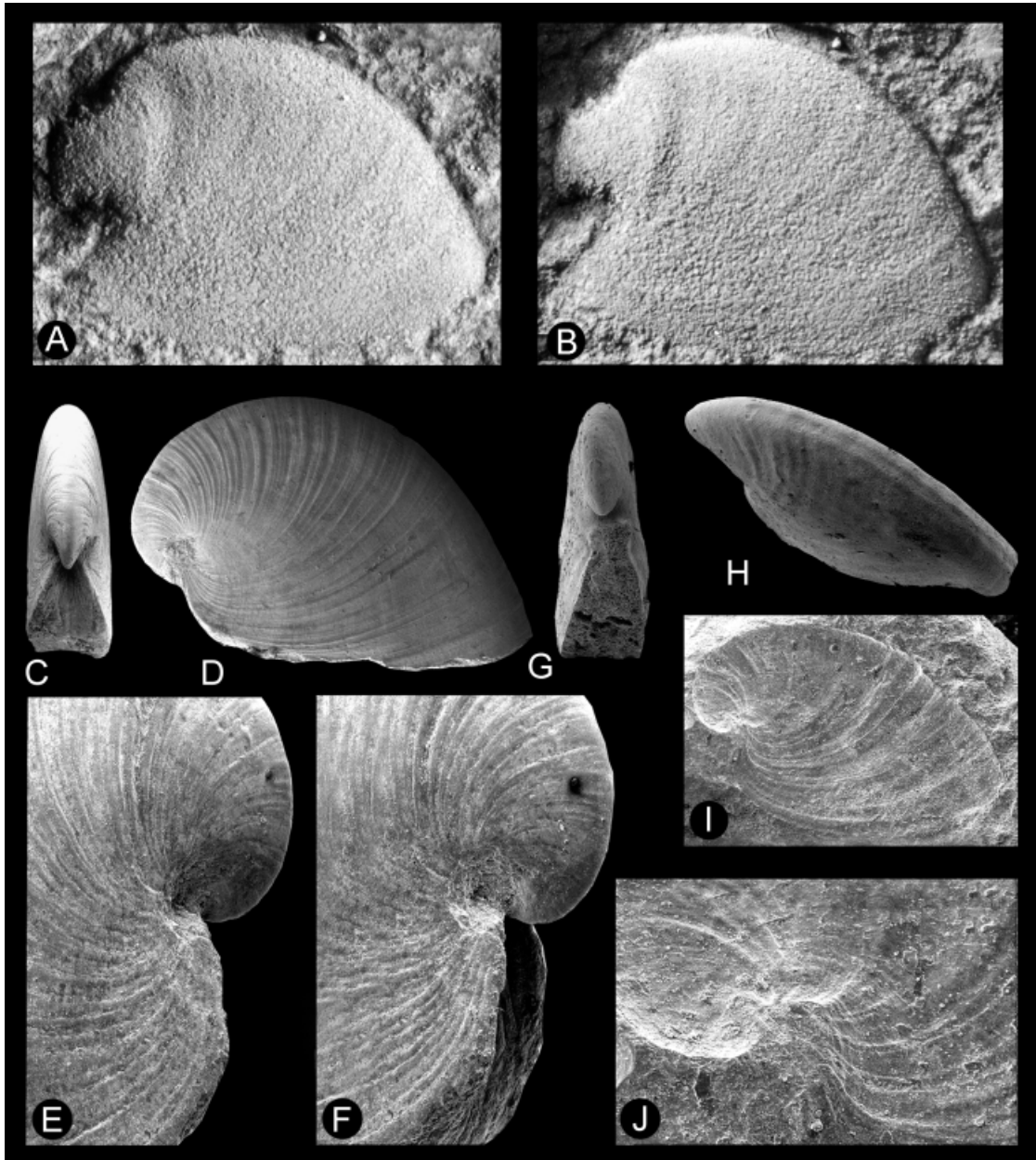
Poor preservation of *Anabarella* from Newfoundland, the Baltic region and the low quality of the published images of Chinese molluscs does not allow detailed comparison. However, the similarity of shape outline, curvature and direction of growth lines, and the laterally very compressed shell suggest that the determinations as *A. plana* are correct.

The geologically youngest record of *Anabarella* is from the Atdabanian of Australia (Bengtson *et al.* 1990) where two new species were described: *A. australis* Runnegar, *in* Bengtson *et al.* 1990 (Bengtson *et al.* 1990, pp. 244, 251, figs 163A, 164A–G) and *A. argus* Runnegar, *in* Bengtson *et al.* 1990 (Bengtson *et al.* 1990, p. 251, fig. 164H–N). The first species is known from well-preserved phosphatized shells as well as an internal mould. The second species is known only from internal moulds. Recently Parkhaev (*in* Gravestock *et al.* 2001) showed that *A. argus* is a morphologically extreme form in *Anabarella* populations in Australia and must be considered as a synonym of *A. australis*. He has also extended the geological record of *A. australis* to the Botomian. While the morphology of the *A. australis* shell resembles *A. plana*, the internal moulds have a different outline (Bengtson *et al.* 1990, fig. 164C–F). It has a smaller shell size and the initial shell is also smaller. The involute overlapping of the initial shell by the later shell started much earlier and is expressed to a greater degree. The shape of the internal mould of *A. australis* is also rather different from the shape of *A. plana*.

EXPLANATION OF PLATE 3

Fig. 1–15. *Anabarella plana* Vostokova, 1962 from the Lower Cambrian of Sant Lorenzo de Calatrava, Sierra Morena, Spain. 1, PMU SP 0001, light photograph; lateral view; $\times 7.5$. 2, PMU SP 0002, light photograph; lateral view; $\times 7.5$. 3–4, PMU SP 0007, light photographs. 3, lateral view; 4, dorsal view; both $\times 7.5$. 5–7, PMU SP 0003, SEM photographs. 5, lateral view; 6, dorsal view; 7, dorso-lateral view; all $\times 7.5$. 8–11, PMU SP 0004, SEM photographs. 8, lateral view; 9, dorso-posterior view; 10, posterior view; 11, postero-lateral view; all $\times 4$. 12–14, PMU SP 0005, SEM photographs. 12, lateral view; 13, postero-dorsal view; 14, antero-lateral view; all $\times 7.5$. 15, PMU SP 0006, SEM photograph; lateral view; $\times 7.5$.





TEXT-FIG. 3. *Anabarella plana* Vostokova, 1962. A–B, CNIGRM No. 8361–8, holotype, showing the sculpture under different light direction; light photographs; both $\times 10$. C–F, YGM 165/22. C, posterior view; D, lateral view; both $\times 10$. E–F, lateral and postero-lateral views to show contact between initial and later whorls; both $\times 30$. G, SMNH Mo 160431, internal mould, posterior view to show the shape of posterior part of aperture; $\times 40$. H, SMNH Mo 160430, dorso-lateral view to show the dorsal groove; $\times 20$. I–J, PMU SIB 1021, external mould to show shape of growth lines close to umbilicus. I, $\times 20$; J, $\times 75$. All SEM photographs.

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