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Middle Miocene record of *Pliocaenicus changbaiense* sp nov. from Changbai (Jilin Province, China)

KATARZYNA STACHURA-SUCHOPLES*, REGINE JAHN

Freie Universität Berlin, Botanic Garden and Botanical Museum Berlin-Dahlem, Königin-Luise Str. 6–8, 14195 Berlin, Germany

The first record of the genus *Pliocaenicus* from middle Miocene deposits is presented in this paper. This record from Changbai (Jilin Province, China) places the origin of the genus further back into the middle Miocene. The genus has been so far reported from the late Miocene/early Pliocene till Recent. The population from Changbai belongs to the group of *Pliocaenicus* species possessing complex alveolae, such as *P. cathayanus* Wang, *P. jilinensis* Wang and *P. omarensis* (Kuptsova) Stachura-S. et Khursevich. Both *P. cathayanus* and *P. jilinensis* have been described from China (Pliocene deposits), and are only known from the type locality. The third species, *P. omarensis* is reported from Eurasia and Africa (age range: late Miocene-Pleistocene). In this report we describe *P. changbaiense*, a new species from China, and focus on those characters having the potential for developing further an evolutionary and taxonomical concept in *Pliocaenicus*. We anticipate that these will contribute to our understanding of the driving forces of diatom dispersal.

Key words: Diatom, *Pliocaenicus changbaiense*, ultrastructure, alveolae, Miocene, China

Introduction

The relatively newly established genus *Pliocaenicus* Round and Håkansson emend. Khursevich and Stachura-Suchoples was erected to accommodate two fossil species of cyclotelloid diatoms (ROUND and HÅKANSSON 1992). Four further species were transferred at the same time. Today the genus contains nine species, both fossil and extant (FLOWER et al. 1998, WANG 1999, TANAKA and NAGUMO 2004, STACHURA-SUCHOPLES and KHURSEVICH 2007, STACHURA-SUCHOPLES et al. 2008, this paper). The genus description, biogeographical distribution of the species and a key for identification have been published elsewhere (KHURSEVICH and STACHURA-SUCHOPLES 2008).

In this study, we focus on a middle Miocene population of *Pliocaenicus* species from China. These specimens represent the oldest known record of the genus and place the ori-

* Corresponding author, e-mail: k.stachura@bgbm.org

gin of the genus further back to ca. 13 Ma. For China, this is the record of the third representative of the genus *Pliocaenicus*. The first observations were done by WANG (1999), who described *P. cathayanus* and *P. jilinensis* from fossil deposits lacking sufficient geological data, however Pliocene? is suggested. Both species are so far only known from the type locality (Jilin Province, China). Besides *P. cathayanus* and *P. jilinensis*, from Asia are reported: (i) extinct, *P. nipponicus* Tanaka et Nagumo and *P. omarensis*, and extant: *P. costatus* (Loginova, Lupikina et Khursevich) Flower, Ozornina et Kuzmina and *P. seczkinae* Stachura-S., Genkal et Khursevich. Moreover, recent studies indicate that the distribution of the genus *Pliocaenicus* is restricted to the Northern Hemisphere, and the living populations are reported from Asian arctic and mountain zones exclusively (KHURSEVICH and STACHURA-SUCHOPLES 2008, STACHURA-SUCHOPLES et al. 2008).

Here we present ultrastructural observations of *Pliocaenicus* specimens from Changbai Shan and focus on characters that might have the potential to be of importance for further understanding of evolutionary processes and for the development of the taxonomical concept of the genus. In addition, this will contribute to diatom biogeographical studies.

Materials and methods

The investigated samples were collected from a deposit in Badaogou, Changbai, Jilin Province (China) situated near the border with North Korea. Changbai Shan – Changbai Mountains (China) or Baekdu Mountains (Korea) – is a mountain range on the border between China and North Korea (41°41' to 42°51' N; 127°43' to 128°16' E). There, plant-bearing diatomites of the Manshancun Formation were intercalated between basalt flows. In the 1980s, radiometric dating of olivine-basalts indicated ca. 13.4 Ma. for the basalts (KOVAR-EDER and GE SUN 2009). The diatomites yield foliage with excellent cuticle preservation. The flora is a mixture of deciduous and evergreen angiosperm taxa and conifers. Also, the pollen flora is very well preserved. Herbaceous plants occur in low abundances (KOVAR-EDER and GE SUN 2009).

The diatom samples were cleaned in 30% H_20_2 solution, and then washed several times with distilled water. The permanent diatom slides were mounted in Naphrax. Light microscope (LM) observations were made using a Zeiss Axioplan microscope. For scanning electron microscope (SEM) observations specimens were mounted on aluminum stubs and sputter-coated with gold-palladium. The SEM observations were made with SEM Philips 515 at the BGBM, Berlin-Dahlem. The terminology follows KHURSEVICH and STACHURA-SUCHOPLES (2008).

Results

Pliocaenicus changbaishanense Stachura-Suchoples and R.Jahn sp. nov.

Holotype: B 400040653 as represented in figure 11, deposited at the herbarium of the Botanical Museum Berlin-Dahlem (B).
Isotype: B 400040653a, deposited at the Research Center of Paleontology and Stratigraphy of Jilin University in Changchun, China.
Original material: B 400040654, mixed sample from type locality.
Type locality: a deposit in Badaogou, Changbai County (Jilin Province, China).

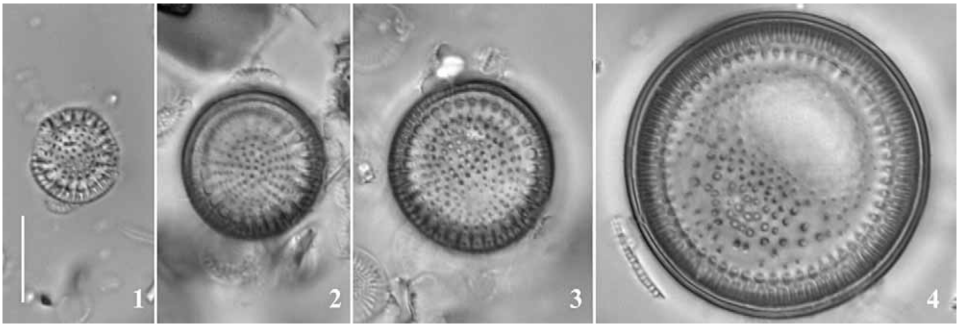
Age and Distribution: Miocene, known only from the type locality.
Etymology: The species name refers to the type locality, Changbai in China.

Diagnosis:

Pliocaenicus changbaiense differt a P. cathayanus et P. jilinensis positione fultoportularum marginalium in costis crassioribus et absentia alveolarum simplicium. Pliocaenicus changbaiense a P. omarensis differt absentia alveolarum simplicium, costis secundariis male evolutis hyalinis, et aperturis fultoportularum marginalium ad basin interstriarum latiorium.

Diagnosis:

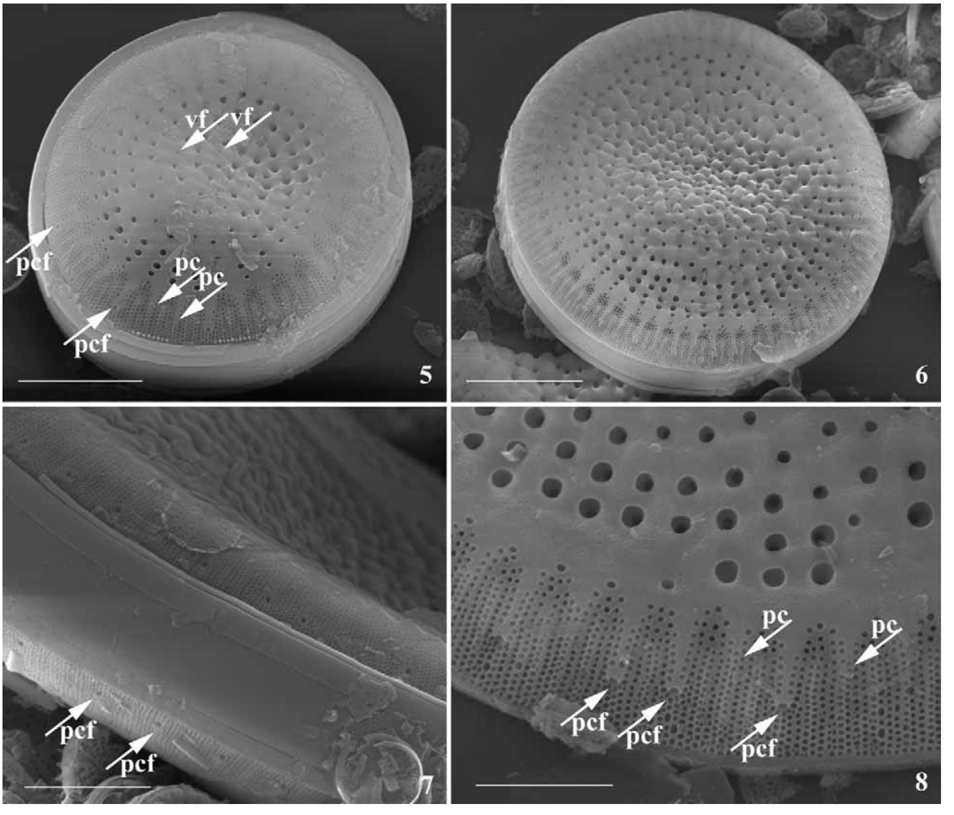
Valves round, diameter 10–36 µm. Valve face more or less transversely undulated; smooth to colliculate. Areolae in single rows radiating from valve centre to mantle, 10–12 along the radius, no distinct interstriae in between. Valve face areolae with internal domed cribra. Mantle puncta smaller than those on the valve face, arranged in fascicles divided by V-like shape interfascicles. Fultoportulae possess three satellite pores. Valve face fultoportulae (from 3 to15) set out in circular pattern; externally, open by smaller puncta than areolae. Mantle fultoportulae on each second-third, really on each or on each fourth costa. Externally, mantle fultoportulae open on the base of wide hyaline strips; internally, located on each second-third thick costa, rarely on each one or each fourth. Alveolae complex with secondary poorly developed secondary costae (folds), restricted to the valve mantle. A single raised rimoportula located in the submarginal zone of the valve face. Externally, the rimoportula opening difficult to detect. On the valve surface granules can be present.



Pl. 1. *Pliocaenicus changbaiense* specimens from middle Miocene, Changbai, China. LM, scale bar= 10 µm.

The frustules are round (Figs. 1–4). The diameter varies from 10 to 36 µm. Number of costae ranges from 7 to 8 in 10 µm. The valve face is usually transversely undulated. Areolae, c. 10–12 along the radius, are usually arranged in single rows without fascicles, an irregular pattern can be observed (Fig. 4).

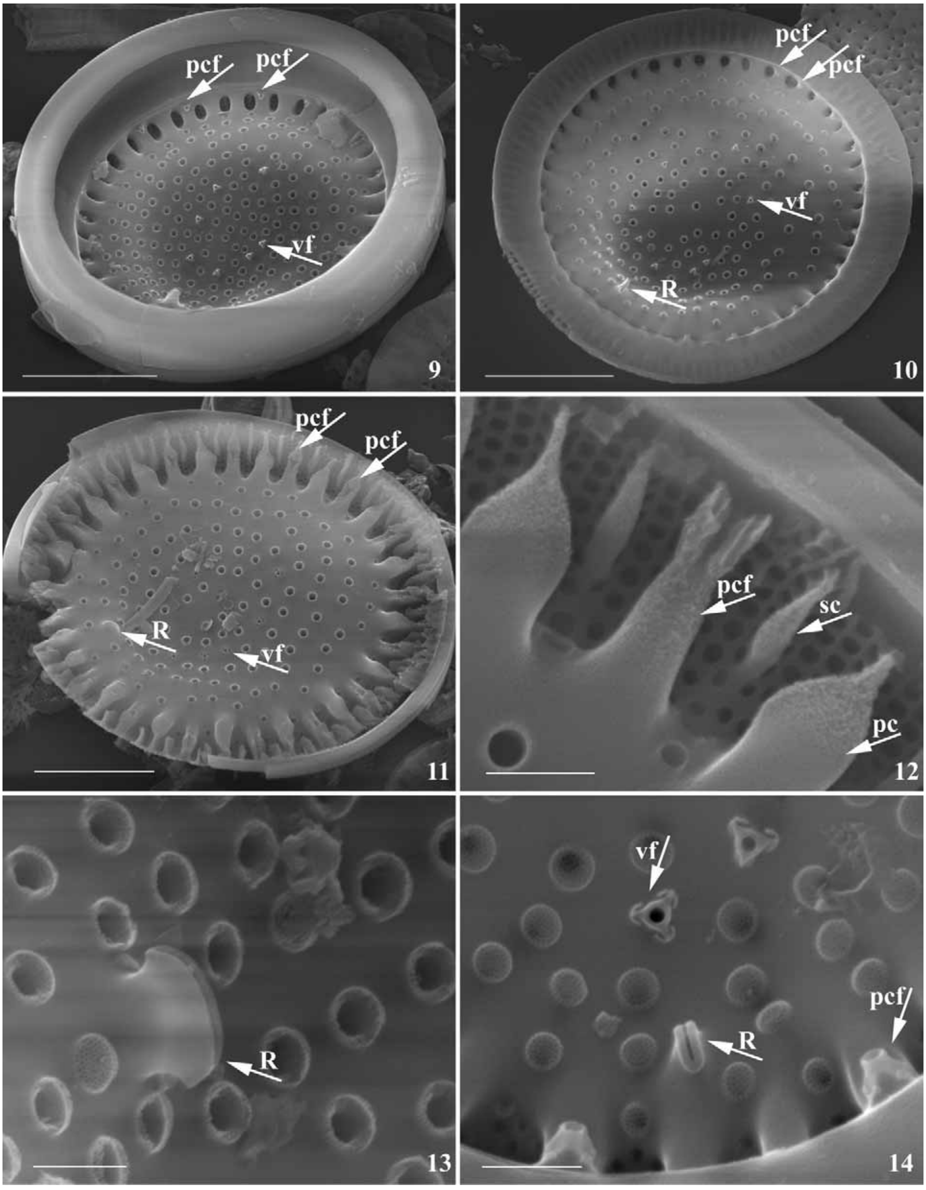
Valve usually round, transversely undulated (Figs. 5, 6). Externally, relief of the external valve face smooth or colliculate (Figs. 6–7); areolae loculate, arranged in radiate striae, sometimes irregular (Figs. 5, 6, 8); on the mantle, the vertical rows of fine puncta are



Pl. 2. *Pliocaenicus changbaiense* specimens from middle Miocene, Changbai (China), external valve view. Scale bars: 10 µm (Fig. 6), 7 µm (Fig. 5), 6 µm (Fig. 7), 4 µm (Fig. 8). The transversely undulated valves, relief of the valve face smooth (Fig. 5) or colliculate (Fig. 6). Areolae loculate, irregular or arranged in radiate striae. Note external openings of fultoportulae (Fig. 5): valve face (arrow vf) and mantle, on the base of wide hyaline strips (arrow pcf), and shorter hyaline strips without openings of fultoportulae. The valve mantle with vertical rows of fine puncta arranged in fascicles, divided by V-like shape hyaline strips that do not go to the valve edge :shorter without opening of fultoportulae (arrow pc) or longer with opening of mantle fultoportulae at the base of (arrow pcf) (Fig. 7). The pseudofenestral-like structure on the valve face/ mantle junction. The girdle band without ornamentation (Fig. 8).

grouped in fascicles divided by hyaline interfascicles that do not go to the valve edge (Figs. 7, 8); pseudofenestral-like structures on the valve face/mantle junction (Figs. 7, 8); valve face fultoportulae lacking external tubuli (Fig. 5), mantle fultoportulae open at the base of wide hyaline strips (Figs. 7, 8).

Internally, areolae with domed cribra (Fig. 14). Alveolae complex with secondary thin poorly developed costae (folds) (Figs. 11, 12). The marginal fultoportulae located on each second-third primary thick costa, rarely on each or each fourth (Figs. 9–12, 14). Valve face fultoportulae (from 3 to15 in the valve face) positioned in circular pattern (Figs. 9–11). Mantle and valve face fultoportulae have three satellite pores (Figs. 9–11, 14). A single, raised rimoportula (Figs. 10, 11, 13, 14) located in the marginal zone of the valve face.



Pl. 3. *Pliocaenicus changbaiense* specimens from middle Miocene, Changbai (China), internal valve view. The internal view of the valve surface showing the valve face (arrow vf) and mantle fultoportulae with three satellite pores located on thick costae (arrow pcf), and rimoportula (arrow R) (Figs. 9–11). Holotype B 4000 (Fig. 11). Note: structure of complex alveolae. Details on complex alveolae structure, note costae bearing fultoportulae (arrow pcf), costae non-bearing fultoportulae (arrow pc), and poorly developed secondary costae (arrow sc) (Fig. 12). The valve surface with a single raised rimoportula (arrow R) located in the submarginal zone of the valve (Figs. 13, 14). Valve face fultoportulae (arrow vf) and mantle fultoportulae with three satellite pores on thick costae (arrow pcf), areolae with internal domed cribra (Fig. 14). Scale bars: 9 μm (Fig. 10), 8 μm (Fig. 9), 6 μm (Fig. 11), 1 μm (Figs. 12–14).

Discussion

The genus *Pliocaenicus* is defined by seven characters as proposed by KHURSEVICH and STACHURA-SUCHOPLES (2008), see also ROUND and HÅKANSSON (1992):

(i) areolae not fasciculate on valve face;
(ii) external mantle fasciculate with opening of fultoportulae on interfascicle;
(iii) external openings of mantle fultoportulae lacking tubuli;
(iv) external openings of valve face fultoportulae lacking tubuli on the valve surface;
(v) external openings of rimoportula lacking tubuli;
(vi) marginal costae with centrifugal 'roofing over';
(vii) internal valve face with domed cribra.

The specimens observed possess all characters to be accommodated in *Pliocaenicus*. Additionally, ultrastructural observations on *P. changbaiense* (Figs. 5–14) revealed typical characters for the group of *Pliocaenicus cathayanus-jilinensis-omarensis* (KHURSEVICH and STACHURA-SUCHOPLES 2008). These species can be characterized as having:

(i) both, simple and complex alveolae; or only complex (as in *P. changbaiense*: see figures 11, 12)
(ii) externally, narrow interfascicles (costae) on the mantle that do not go to the valve edge;
(iii) internally, mantle fultoportulae located on thick or thin recessed costa;
(iv) valve diameter of 5–47 µm.

All these characters are observed in *P. changbaiense*. The comparison of morphometric and morphological characters is given in table 1 and 2 respectively (see also key for taxonomic identification in KHURSEVICH and STACHURA-SUCHOPLES 2008). In general, the range of the valve diameter of our population varies significantly and overlaps with all the species forming the complex alveolae group. For example, the smallest measured specimen of *P. changbaiense* is 3.6 times smaller than the biggest observed valve. The number of areolae in 10 µm and the number of puncta rows in the mantle fascicles in specimens from Changbai is slightly lower than in the other three species. At this point it is necessary to stress that, in the case of less pronounced hyaline areas without external opening of fultoportula (e.g. *P. jilinensis*) or very narrow interstriae (e.g. *P. omarensis*) the measurement of

Tab. 1. Morphometric data and information on *Pliocaenicus* species group with complex alveolae.

	Valve diameter [µm]	Areolae in 10 µm	Costae in 10 µm	Rows of puncta in mantle fascicle	Valve face fultoportulae
P. cathayanus[1)]	14–44	14–16	c. 6	7–9	several (8–12)
P. jilinensis[1)]	7–19	c.12[4]	c. 6[4]	15–20; c. 7*	several
P. omarensis[2)]	5–47	10–28	7–15	c. 11; c. 7*	several (2–8)
P. changbaiense[3)]	10–36	10–12	c. 7–8	c. 6–7	several (3–15)

After [1] – WANG (1999), [2] – *sec*. KHURSEVICH and STACHURA-SUCHOPLES (2008), [3] – this paper, [4] – TANAKA and NAGUMO (2004), * – from reference papers.

number of rows of puncta between interstriae can give misleading results (for illustration see e.g. figures 5–8, see also table 1). In *P. changbaiense* the number of costae in 10 µm is similar to *P. cathayanus* and *P. jilinensis*, and in the lowest range to *P. omarensis*. All species posses low number of valve face fultoportulae. The above presented comparison of morphometric data indicates that fine structural observations are necessary for identification on the species level.

The main diagnostic character in the species of the group II.2. (*Pliocaenicus cathayanus-jilinensis-omarensis*) is the occurrence of both simple and complex alveolae (KHURSEVICH and STACHURA-SUCHOPLES 2008). In *P. cathayanus* and *P. jilinensis* the mantle fultoportulae are located on recessed costae (WANG 1999). This character is indicated in the diagnosis of *P. cathayanus* (WANG 1999: 126). In the case of *P. jilinensis* in the diagnosis it is written. »every second, third or fourth costa bearing a fultoportula (WANG 1999: 127), however later on WANG (1999: 128) added:...« those fultoportula-bearing costae are also recessed like those of *P. cathayanus*«. In *P. changbaiense*, mantle fultoportulae are located externally at the base of wide hyaline strips (Figs. 5–8), and internally on thick costae (Figs. 9, 10). The alveolae cross section observations indicate that the secondary costae are located between the primary costae (Figs. 11, 12). The secondary costae are poorly developed (folds) and are located on the valve mantle. These characters differentiate *P. changbaishanense* from *P. cathayanus* and *P. jilinensis*. Complex alveolae as observed in *P. omarensis* are restricted by thick bearing mantle fultoportulae costae, while between them the much thinner well developed secondary costae are located (KHURSEVICH and STACHURA-SUCHOPLES 2008). This character differentiates *P. omarensis* from *P. changbaiense*. Besides, the specimens observed possess only complex alveolae, in contrast to *P. cathayanus*, *P. jilinensis* and *P. omarensis*, which have both simple and complex alveolae (as suggested by KHURSEVICH and STACHURA-SUCHOPLES 2008). However, this character should be further investigated, for example in *P. cathayanus* secondary costae can be seen between primary costae (WANG 1999: Fig. 17). Therefore, additional investigation on complex alveolar structures of other species can reveal new important data. Unfortunately, we were not able to re-investigate type material of *P. cathayanus* and *P. jilinensis*. Furthermore, as suggested by e.g. LOSEVA (1981) and KHURSEVICH and STACHURA- SUCHOPLES (2008) additional observations on worldwide reported populations of *P. omarensis* are required.

In all three species from China the external openings of mantle fultoportulae are positioned at the base of wider hyaline strips, while shorter hyaline strips reflect the internal costae non-bearing fultoportulae. In *P. omarensis* the hyaline strips are narrow. Additionally, different patterns of valve face fultoportulae are observed in the case of *P. changbaiense*, *P. cathayanus* and *P. jilinensis* in contrast to *P. omarensis* (circular: WANG 1999: Figs. 16–18, 24; this paper: Fig. 5; arc: KHURSEVICH and STACHURA-SUCHOPLES 2008: Figs. 30–33). The number of valve face fultoportulae of all species from the complex alveolae group is three. In the case of mantle fultoportulae in *P. cathayanus,* WANG (1999) wrote that they probably possess no satellite pores, however KHURSEVICH and STACHURA-SUCHOPLES (2008) suggested that they can have three satellite pores. For *P. jilinensis* WANG (1999) did not mention the number of satellite pores of mantle fultoportulae, KHURSEVICH and STACHURA-SUCHOPLES (2008) also suggested the presence of three satellite pores. The presence of a fenestrate structure is a diagnostic character in *P. cathayanus;* a similar structure called a pseudo-fenestrate structure, is a character observed in *P.*

Tab. 2. Ultrastructural features of *Pliocaenicus* species group with complex alveolae.

	Alveolae	Areolae	Valve face fultoportulae	Mantle fultoportulae	Rimoportula
	structure	arrangement	a) structure, b) location	a) structure, b) position, c) localisation	a) structure, b) localisation
P. cathayanus[1,2]	simple and complex	Radiate, single rows	a) three-(four) satellite pores b) ring in central area	a) none (?), three (?) satellite pores b) internally, on thin recessed costae	a) single, sessile or raised b) near the base of an internal costa
P. jilinensis[1,2]	simple and complex	radiate, single rows	a) three satellite pores b) ring in central area	a) three? satellite pores b) internally, on recessed costae, c)	a) single, raised b) near the base of an internal costa
P. omarensis[2]	simple and complex	radiate, single rows	a) three satellite pores b) arc within central depression	a) three satellite pores b) internally, on thick costae, c)	a) single, sessile or raised b) near or at the base of an internal costa
P. changbaishanense[3]	complex	irregular, radiate, single rows	a) three satellite pores b) ring in central area	a) three satellite pores b) internally, on thick costae, c) on each (1)2–3(4) costa	a) single raised b) near the base of an internal costa or in submarginal zone

After [1] – WANG (1999), [2] – KHURSEVICH and STACHURA-SUCHOPLES (2008), [3] – this paper

jilinensis (terminology after WANG 1999). The pseudofenestral structure is also observed in *P. costatus*, *P. omarensis* and *P. seczkinae*. Similar to the pseudofenestral structure a cluster of less orderly organized areolae is located at the valve face/mantle junction in *P. changbaiense*.

Now, the key for the identification of *Pliocaenicus* species can be extended (for details see KHURSEVICH and STACHURA-SUCHOPLES 2008). We suggest that *P. changbaiense* is the closest related to *P. omarensis*. Here, we also added the position of the rimoportula on the valve face as one of the diagnostic character for the species accommodated in the group II.2.

Extention of the key for identifying of *Pliocaenicus changbaiense* within group II. 2 (KHURSEVICH and STACHURA-SUCHOPLES 2008).

Group II. Valves round, rarely elliptical, transversely undulate. Alveolae simple or both simple and complex. Valve face and mantle fultoportulae with two or three satellite pores. One sessile or raised rimoportula near or at the base of an internal costa or in the chambered region.

2. Alveolae both simple and complex or only complex. One sessile or raised rimoportula on the valve face (submarginal zone). Diameter of valves 5–47 μm. Externally interstriae on the mantle do not go the valve edge. Internally, mantle fultoportulae located on thick or thin recessed costa.

A. Internally, mantle fultoportulae located on thick costae.

a. both simple and complex (with thin recessed costae) alveolae . . . . . . *P. omarensis*

b. complex alveolae with poorly developed secondary costae . . . . . . *P. changbaiense*

B. Internally, mantle fultoportulae located on thin recessed costae.

Our results indicate that detailed investigations of alveolae, especially cross sections would be valuable, helping to develop further the concept in *Pliocaenicus* species possessing complex alveolae. Moreover, as revealed by STACHURA-SUCHOPLES et al. (2008), detailed ultrastructural observations on valve face fultoportulae have already differentiated *Pliocaenicus seczkinae* – the species reported so far only from Holocene and Recent populations from Lake El' gygytgyn (Chukotka, Russia) – from *P. costatus*, which is widely distributed and known from the late Miocene to Recent. Independently, previous studies on the genus *Pliocaenicus* also documented morphological variability on population/species level observed in *P. costatus* (e.g. GENKAL et al. 2001, STACHURA-SUCHOPLES 2006), *P. omarensis* (GASSE 1980, see also KHURSEVICH and STACHURA-SUCHOPLES 2008) and *P. seczkinae* (STACHURA-SUCHOPLES et al. 2008). In the population of *P. changbaishanense* variable characters are e.g.: a valve face relief (smooth: Figs. 5, 8 to colliculate: Figs. 6, 7) and presence (Fig. 5) or absence (Figs. 6–8) of granules.

In conclusion, this study extends the biostratigraphical, biogeographical and evolutionary knowledge on the genus *Pliocaenicus*. The oldest record of the genus *Pliocaenicus*, according to a preliminary dating of the deposit in Changbai (which needs to be reconfirmed in the future), places the origin of the genus further back into the middle Miocene. This would be similar to the origin of other freshwater genera in the family Thalassiosiraceae Lebour emend. Hasle such as, *Cyclostephanos* Round, *Mesodiction* Theriot et Bradbury, *Stephanodiscus* Ehrenberg or *Conticribria* Stachura-Suchoples et D. M. Williams (STACHURA-SUCHOPLES and WILLIAMS in press). Further, detailed ultrastructural observations on representatives of *Pliocaenicus* will contribute to a refined species concept of the genus. They will also contribute to our understanding of evolutionary processes at the generic and inter-generic levels and diatom biogeography.

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