NOTES ON THE PERMIAN KALENTERID BIVALVIA GENUS NETSCHAJEWIA
LICHAREV, 1925 AND RELATED FORMS

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ABSTRACT

The identity of the Permian kalenterid Netschajewia Licharev, 1925 has been uncertain because its author indicated it could be regarded as a replacement name for the preoccupied Modiolodon Netschajew, 1894 yet Newell (1957) treated Netschajewia as a subgenus of Stuchbursia Etheridge Jr., 1900, and designated a type species different from that proposed by La Rocque and Newell (1969) for Modiolodon Netschajew. Netschajewia is confirmed as a replacement name for Modiolodon, thereby invalidating Newell’s (1957) erroneous type designation (misidentified type species) for Netschajewia. The names Ivanovia Astafieva-Urbajtis in Astafieva-Urbajtis and Ramovš, 1978 and Astafia Goncharova, 2013 are objective junior synonyms of Netschajewia. Netschajewia is definitely known only from its type species and one additional Permian species. It is assigned to the kalenterid subfamily Myoconchinae. The genus Verneuilnodon Fang & Carter, gen. nov. (subfamily Healeyinae Hautmann, 2008, reduced in rank herein from family Healeyidae) is proposed for Permian Mytilus (Modiola) pallasi de Verneuil, 1845, as restricted herein. The new Permian species, Kasimlara? antiqua (subfamily Healeyinae) is proposed. The wide circulation of Chavan’s (1969) republication of Newell’s (1957) erroneous type designation for Netschajewia means that modern references to this genus should be reevaluated.

INTRODUCTION

Licharev1 (1925, p. 149) introduced Netschajewia as a replacement name for Modiolodon Netschajew, 1894, a name preoccupied by Modiolodon Ulrich (1894a). La Rocque and Newell (1969, p. N397) regarded Ulrich’s Modiolodon as a member of the family Modiomorphidae S. A. Miller, 1877, but the phylogenetic analysis of early Bivalvia by Carter, Campbell, and Campbell (2006) placed Ulrich’s Modiolodon in the infraclass Pteriomorpha Beurlen, 1949 in a polytomy with the family Cyrtodontidae Ulrich, 1894b and the Eupteriomorpha Boss, 1982. This is compatible with Pojeta’s (1971, pl. 13, fig. 8) illustration of multiple, nearly horizontal, opisthodetic ligament grooves in Modiolodon oviformis (Ulrich, 1890), which comprise a monovinicular-P ligament as defined by Carter and others (2012). In contrast, Netschajewia has a parvinicular ligament and is a member of the infraclass Heteroconchia Hertwig, 1895, superfamly Kalenteroidea Marwick, 1953.

Netschajew (1894) published Modiolodon as a subgenus of Modiolidopsis Hall, 1847 after March 1, 1894. Licharev (1925) and Pojeta (1971) indicated 1893 as the publication date for Modiolodon Ulrich, 1894a (the date indicated on the title page for Volume 7, Part 2), but the preface to Ulrich’s work (p. xiv) indicates that Part 1, Economic Geology, was issued in 1893, whereas the remainder of the text (which includes Modiolodon) was issued in 1894. The exact date in 1894 is unknown, but this probably predates the June 16, 1894 publication date of Ulrich (1894b). According to La Rocque and Newell (1969, p. 397), Modiolodon Netschajew, 1894 was probably published late in 1894.

Newell (1957) designated the type species of Netschajewia as Mytilus pallasi de Verneuil, 1845, but Newell was apparently unaware of Licharev’s (1925) indication that Netschajewia is a replacement name for Modiolodon Netschajew. As a replacement name, Netschajewia should have taken the same type species as designated by La Rocque and Newell (1969a, p. 397) for Modiolidodon Netschajew, i.e., Clidophorus [err. pro Cleidophorus] pallasi oblongus Golovkinsky, 1869.

This article reviews the taxonomic history of Modiolodon Netschajew, 1894, N. netschajewia Licharev, 1925 and closely related

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1The English translation of the Russian name Б. Лихарев has long been in confusion. Б. Лихарев used both Licharew (1925) and Licharev (1939). Newell (1957) used “Licharew” in his list of references, but “Jakolew” in his text. Chavan (1969, p. 545) used “Yakovlev.” For the sake of consistency, we use the spelling “Licharev.”

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taxa in de Verneuil (1845), Golowkinsky (1869), Netschajew (1894), and Licharev (1925, 1939). The history of this nomenclature is summarized in Table 1. It also discusses the close relationship between the family Kalenteridae Marwick, 1953 and the family Healeyidae Hautmann, 2008.

From *Modiolodon* Netschajew, 1894 to *Netschajewia Licharev, 1925*

The history of *Modiolodon* Netschajew, 1894 and *Netschajewia Licharev, 1925* begins with de Verneuil's (1845) publication of his new species *Mytilus (Modiola) pallasi*. De Verneuil's specimens (Fig. 1) are variable in terms of shell length/height and projection of the anteroventral margin. De Verneuil attributed this variation to allometric growth, but Netschajew (1894, p. 238) disagreed, noting that his more elongate *pallasi* specimens do not change shape with increasing size. Netschajew (1894, p. 238) indicated that de Verneuil's least elongate *pallasi* specimen (Fig. 1.7) might belong to his new species *Modiolopsis globosus*, which has an elongate lunule and an escutcheon (Fig. 3.9–3.11). Licharev (1925, p. 123) assigned *Modiolopsis globosa* to *Netschajewia*. Lutkevich and Lobanova (1959, 1960) subsequently designated the lectotype of *Netschajewia (Angarodon) globosa* as Netschajew's (1894, p. 8, fig. 17) (Fig. 3.9). Lutkevich and Lobanova (1959) justified placement of *globosa* in *Netschajewia* on the basis that its growth increments are imbricated. However, the presence of an escutcheon suggests closer affinity with *Stutchburia* Etheridge Jr., 1900. *Stutchburia* resembles *Netschajewia* in having obsolescent cardinal teeth but differs in having an escutcheon and posterior lateral dentition (Chavan, 1969, p. 548).

A subset of de Verneuil (1845) figured specimens of *Mytilus (Modiola) pallasi* are herein designated types for *pallasi* as presently restricted (Fig. 1.1–1.5). The de Verneuil specimen in Fig. 1.6 might represent a less elongate member of this species or an unnamed species. de Verneuil's specimen in Fig. 1.7 designated types for *V. pallasi* (de Verneuil) or unnamed sp. (Fig.1.6 = pl.19, fig. 16i of de Verneuil, 1845).

From *Modiolus* (Lobanova) 1959, 1960) subsequently designated the lectotype of *Netschajewia* (Angarodon) *globosa* as Netschajew's (1894, p. 8, fig. 17) (Fig. 3.9). Lutkevich and Lobanova (1959) justified placement of *globosa* in *Netschajewia* on the basis that its growth increments are imbricated. However, the presence of an escutcheon suggests closer affinity with *Stutchburia* Etheridge Jr., 1900. *Stutchburia* resembles *Netschajewia* in having obsolescent cardinal teeth but differs in having an escutcheon and posterior lateral dentition (Chavan, 1969, p. 548).

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Golowkinsky (1869) named three morphological variations (not written as varieties) of *Mytilus (Modiola) pallasi* based on Permian specimens from western Russia (Table 1). These are *Clidophorus pallasi oblongus*, *Clidophorus pallasi obliquus*, and *Clidophorus pallasi rectangularis* (his Plate 4, fig. 4–13) (Fig. 2). Golowkinsky's assignment of *pallasi* to *Clidophorus* (a misscoping of *Clidophorus* Hall, 1847) was not adopted by subsequent authors. The type species of *Clidophorus*, Late Ordovician *Nuculites planulata* Conrad, 1841 resembles some of de Verneuil's (1845) *pallasi* specimens in its elongate-ovate, posteriorly extended shape, anterior myophoric buttress, and, according to Hall (1847, p. 300), its edentulous

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| de Verneuil, 1845 | Golowkinsky, 1869 | Netschajew, 1894 | Licharev, 1925, 1939 | This paper | Taxonomic position |
|------------------|------------------|-----------------|---------------------|------------|-------------------|
| *Mytilus* (Modiola) *pallasi* de Verneuil (pl. 19, fig. 16a–i, non 16k) | Cleidophorus *pallasi* (de Verneuil) (pl. 4, fig. 4–6) | *Modiolopsis* *pallasi* (de Verneuil) (pl. 19, fig. 16a–i of de Verneuil, 1845; non pl. 8, fig. 1–4 of Netschajew, 1894) | *Netschajewia* (de Verneuil) (1939, pl. 35, fig. 10–11) | *Netschajewia* elongata (Netschajew) (1925, pl. 2, fig. 13–14; pl. 35, fig. 12 of 1939) | *V. pallasi* (de Verneuil) or unnamed sp. (Fig.1.6 = pl.19, fig. 16i of de Verneuil, 1845) |
| *M. (Modiola) pallasi* de Verneuil (pl. 19, fig. 16k, non 16a–i) | *** | *Modiolopsis* *globosus* Netschajew (pl. 8, fig. 16–18) | *Netschajewia* *globosa* (Netschajew) (1925, pl. 2, fig. 13–14; pl. 35, fig. 12 of 1939) | *Stutchburia? globosa* (Netschajew) (Fig.1.7 = pl.19, fig. 16k of de Verneuil, 1845; Fig. 3.9–3.11 = pl. 8, fig. 16–18 of Netschajew, 1894) | *V. pallasi* (de Verneuil) or unnamed sp. (Fig.1.6 = pl.19, fig. 16i of de Verneuil, 1845) |
| *** | *** | *Modiolopsis* *pallasi* (de Verneuil) (pl. 8, fig. 1–4; non pl. 19, fig. 16a–i of de Verneuil, 1845) | *** | *Kasimlara? antiqua* sp. nov. (Fig. 3.3–3.6 = pl. 8, fig. 1–4 of Netschajew, 1894) | Healeyinae |
| *** | *** | *C. pallasi* *obliquus* Golowkinsky (pl. 4, fig. 7–8) | *** | *obliquus* Golowkinsky, 1869 s. s. (genus indet.) (Fig. 2.4–2.5 = pl. 4, fig. 7–8 of Golowkinsky, 1869) | Subfamily indet. |
| *** | *** | *Modiolopsis* *sp. indet.* Netschajew (1894) (pl. 19, fig. 16a–i of de Verneuil, 1845) | *Netschajewia* *elongata* (Netschajew) (1925, pl. 2, fig. 13–14; pl. 35, fig. 12 of 1939) | *Netschajewia* *elongata* (Netschajew) (Fig. 2.7 = pl. 4, fig. 13 of Golowkinsky, 1869) | Healeyinae |
| *** | *** | *C. pallasi* *oblongus* Golowkinsky (pl. 4, fig. 12) | *Modiolopsis* *oblongum* (Golowkinsky) (pl. 8, fig. 9, 15) | *** | Myoconchinae |
| *** | *** | *C. pallasi* *oblongus* Golowkinsky (pl. 4, fig. 12) | *Modiolopsis* *oblongum* (Golowkinsky) (pl. 8, fig. 9, 15) | *** | Myoconchinae |
| *** | *** | *C. pallasi* *rectangularis* Golowkinsky (pl. 4, fig. 9–11) | *Pleurophorina* *simplex* (Keyserling, 1846) (pl. 8, fig. 21; pl. 11, fig. 25) | *Pleurophorina simplex* (Keyserling, 1846) (pl. 2, fig. 1–4) | Unresolved |
| *** | *** | *** | *** | *** | *** |

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*Table 1. Comparison table of Netschawejia Licharev, 1925 and related taxa names identified by Verneuil (1845), Golowkinsky (1869), Netschajew (1894), and Licharev (1925, 1939) and this paper.*
of Cleidophorus. The hinge structure of Nuculites planulata is unknown (see McAlester, 1968, p. 20), but McAlester (1969, p. 233) regarded Cleidophorus as a junior synonym of the nuculoid genus Nuculites Conrad, 1841.

Netschajew (1894) placed two species in his new subgenus Modiolopsis (Modiolodon): Golowkinsky’s (1869) Cleidophorus pallasi oblongus and Netschajew’s new species Modiolopsis (Modiolodon) elongatum (Table 1). Netschajew did not designate a type species for Modiolodon, but La Rocque and Newell (1969, p. 397) designated Cleidophorus pallasi oblongus (Fig. 2.1) as the type by original designation (actually by subsequent designation). Modiolopsis (Modiolodon) (Netschajew, 1894) (herein Netschajewia) and its two original species (oblongum and elongatum) are described in the systematics section below. Netschajewia is assigned to the kalenterid subfamily Myoconchinae Newell, 1957 because of its modioliform shape, parivincular ligament, and the fact that its strong reduction of hinge dentition is approximated in some members of Myoconchinae. Netschajewia differs from other members of Myoconchinae in having two or more minute, short, tabular, vertically stacked, hinge-parallel cardinal teeth and no posterior lateral teeth.

Golowkinsky’s (1869, pl. 4, fig. 4–8, 13) (Fig. 2.2–2.7) Cleidophorus pallasi obliquus has a highly variable lateral profile. Netschajew (1894, p. 228) criticized Golowkinsky’s lumping such a broad range of forms under one name, so he restricted obliquus to exclude Golowkinsky’s (1869) pl. 4, fig. 13 (Fig. 2.7), which Netschajew (1894) renamed Modiolopsis (Modiolodon) elongatum (herein Netschajewia elongata). Netschajew also excluded from obliquus Golowkinsky’s (1869) pl. 4, fig. 4 and 5 (Fig. 2.2, 2.3), which Netschajew assigned to Modiolopsis pallasi, i.e., Modiolopsis (Modiolodon), not Modiolopsis (Modiolodon). Golowkinsky’s (1869) pl. 4, fig. 6 (Fig. 2.6) has a shape similar to pallasi as restricted herein, so we tentatively include it in Verneuilnodon pallasi. The two remaining obliquus specimens in Golowkinsky (1869, pl. 4, fig. 7, 8) (Fig. 2.4, 2.5) have similarly straight dorsal margins and straight or nearly straight ventral margins. However, one specimen (Fig. 2.4) is moderately elongate and dorsoventrally expanded posteriorly, whereas the other (Fig. 2.5) is more elongate and not dorsoventrally expanded posteriorly. Because these might represent
different species, we designate Fig. 2.5, which alone shows the shell sculpture, as lectotype and Fig. 2.4 as paralectotype for *obliquus*.

Unfortunately, the hinge dentition is unknown for *obliquus* so it is not possible to assign it to a genus. In summary, Golowkinsky’s specimens of *Cleidophorus pallasi obliquus* are herein classified as *obliquus* *sensu stricto* (generically indeterminate) (Fig. 2.4–2.5), tentatively (because of a lack of information on hinge structure) *Verneuilodon pallasi* (de Verneuil, 1845) (Fig. 2.2–2.3, 2.6), and *Netschajewia elongata* (Netschajew, 1894) (Fig. 2.7) (Table 1).

Golowkinsky (1869, pl. 4, fig. 9–11) described his *Cleidophorus pallasi rectangularis* (Fig. 2.8–2.10) as dentate, but the hinge structure is not visible in his illustrations. Netschajew (1894, p. 230) and Branson (1948) regarded *rectangularis* as a junior synonym of *Modiola simpla* Keyserling, 1846 (p. 260, pl. 10, fig. 22, pl. 14, fig. 1), the type by monotypy of *Pleurophorina* Licharev (1925, pl. 2, fig. 1–4). Keyserling (1846) did not describe the hinge of *Modiola simpla*, but Netschajew (1894, p. 305–306), who classified this species as *Pleurophorus simplus* (Keyserling), indicated two cardinal teeth and one posterior lateral tooth in each valve. The left valve has a short, thick cardinal tooth and above this a thinner, longer cardinal tooth. The right valve has two lamellar cardinal teeth above a triangular socket, and the cardinal tooth closest to this socket is short, whereas the other cardinal tooth is longer. However, Maslennikov (1935, p. 82) described the hinge dentition of *Modiola*...
Fang and Carter—Permian kalenterid genus Netschajewia 

Netschajewia antiqua — pallen
from the subfamilies Kalenterinae and Myoconchinae. Fang and Morris (1997) regarded Permophorus (Kiel, 2018). Both specimens Modiola by Netscha differs from King's (1848) — to edentulous shells by Modiola — unless differ in being equivalve, in lacking a posterior myophoric ridge. Netschajew's (1894) specimens are herein designated types for Kasimlara? antiqua Fang & Carter n. sp., herein, with the holotype Netschajew's (1894) pl. 8, fig. 1 (Fig. 3.3), and paratypes his pl. 8, fig. 2–4 (Fig. 3.4–3.6). The name antiqua refers to the Permian age of Kasimlara? antiqua relative to Triassic Kasimlara kosuni. Because of the lack of hinge teeth (at least in Kasimlara? antiqua), Kasimlara is tentatively assigned to the edentulous subfamily Healeyinae. 

The type species of Modiolodon Netschajew and Netschajewia Licharev

Licharev (1925) indicated that Netschajewia could be regarded as a replacement name for Modiolodon Netschajew. He wrote (1925, p. 123, translated herein) "I do not consider the separation of Modiolodon from Netschajewia to be rational. In such a case the name Modiolodon proposed by Netschajew could completely replace the name Netschajewia introduced by me, if it had not been eclipsed by Ulrich a year before the publication of Netschajew's monograph for another genus of pelecypods". [Original text “Gegenwärtig mich nur auf den Hinweis dieses engen Zusammenhanges beschränkt, halte ich jedenfalls die Trennung des Modiolodon von Netschajewia nicht für rationell. In solchem Falle könnte die von Netschajew vorgeschlagene Benennung (Modiolodon) vollkommen die von mir eingeführte Bezeichnung Netschajewia ersetzen, wenn dieselbe nicht ein Jahr vor dem Erscheinen der Monographie Netschajew's für die andere Gattung der Pelecypoden [XL, 521] von Ulrich übertroffen worden wäre.”]

Newell (1957) treated Netschajewia as a subgenus of Stutchburiu. Not realizing that Netschajewia had been proposed as a replacement name for Modiolodon Netschajew, Newell designated Mytilus pallasi i.e., Mytilus (Modiola) pallasi de Verneuil, 1845, as the type. This type designation was accepted by Chavan (1969). Newell (1957) was unaware of the restriction of pallasi to edentulous shells by Netschajew (1894) and Licharev (1925, 1939), as evidenced by the fact that he synonymized pallasi with the dentate Pleurophorus modioliformis King, 1884 (i.e., Cardiomorpha modioliformis King, 1848 not 1884). Newell (1957) used an original figure for his Netschajewia cf. modioliformis (Fig. 3.17) instead of one of de Verneuil's (1845) figures for Mytilus (Modiola) pallasi. Unfortunately, Newell's (1957) figure differs from pallasi, as presently defined, in having posterior lateral dentition and a more angular anteroposterior margin. Chavan (1969, p. 545) and Kiel (1981) accepted Newell's (1957) synonymy of pallasi (de Verneuil) and modioliformis (King). Chavan (1969, fig. E44.3) reused Newell's (1957) figure of modioliformis to illustrate the type species of Netschajewia (although Chavan omitted the cf. before modioliformis). Newell's (1955, pl. 5, fig. 1–5) (Fig. 3.12–3.16) illustration of Stutchburiu? modioliformis differs from King’s (1848) modioliformis in lacking an escutcheon. Not surprisingly, Muromzева and Guskov (1984) were reluctant to recognize pallasi and modioliformis as synonyms.
Additionally, Logan (1967, p. 51) expressed doubt about the identity of Newell’s (1955, p. 28, pl. 5, fig. 1–5) Stutchburia modioliformis with King’s (1848) modioliformis, because Newell’s specimens lack a lunule and escutcheon. However, Logan (1967) listed Newell’s (1957) illustration of Netschajewia cf. modioliformis in his synonymy of Stutchburia modioliformis (King, 1848, 1850, p. 180, pl. 14, fig. 18–23) did not describe the hinge of Cardiomorpha modioliformis. It is unclear whether the specimens illustrated by Newell (1955, 1957) and Chavan, 1969, p. 545) are modioliformis King, 1848 or a related species.

Nakazawa and Newell (1968, p. 95) and Manceño, González, and Damborenea (1976) accepted Licharev’s (1925) suggestion that Netschajewia is a replacement name for Modiolidon Netschajew. Doing so gave Netschajewia the same type species as Modiolidon on the principle of typification of a replaced name (ICZN, 1999, Article 67.8), i.e., Cleidoporus pallasi oblongus Golowkinsky, 1869, as designated for Modiolidon Netschajew by LaRocque and Newell (1969, p. N397).

Because Newell (1957) misidentified the type species of Netschajewia, it would be possible to invoke ICZN (1999) Article 70.3, concerning misidentified type species, and replace Newell’s (1957) type designation. However, this step is not necessary because confirmation that Netschajewia is a replacement name for Modiolidon (Netschajew) invalidates Newell’s (1957) type designation. Two later published replacement names for Modiolidon (Netschajew) are now objective junior synonyms of Netschajewia: Ivanovia Astafieva-Urbajits and Astafieva-Urbajits and Ramovš (1978) and Astafia Goncharova, 2013.

**Taxonomic position of Netschajewia and Verneuilnodon**

Chavan (1969, p. 545) assigned Netschajewia to the kalenterid subfamily Kalenteridae Marwick, 1953, but the subfamily Myoconchinae is more appropriate. Kalentera Marwick, 1953 and Myoconcha J. de C. Sowerby, 1824 both have well-developed cardinal and posterior lateral hinge teeth, but the myoconchine genus Stutchburia approaches Netschajewia in having obsolescent cardinal teeth and partially obsolescent posterior lateral teeth (Chavan, 1969, p. 548), the latter teeth being entirely absent in Netschajewia. The presence of cardinal hinge dentition in Netschajewia excludes it from the edentulous subfamily Healeyinae.

Verneuilnodon is assigned to the subfamily Healeyinae instead of Myoconchinae because its hinge is edentulous. Hautmann (2008) included in his new family Healeyidae, Triassic Healeyia Hautmann, 2001; Middle Triassic Joannina Waagen, 1907; and, questionably, Middle Triassic Protopsis Kirtl, 1904 as well as three additional Middle Triassic genera proposed by Stiller and Chen (2006): Leidapooncha, Qingyiopila, and Waissiaowelia. In addition to being edentulous, Verneuilnodon pallasi resembles Late Triassic Healeyia gonoides (Healey, 1908) in terms of its thick, strongly inequilateral shell with low, rounded, strongly anterior umbos; posteriorly downwardly sloping, shallowly sinuate ventral margins; adductor muscle scars positioned close to a more or less lobate anterior shell margin; and anterior myophoric ridge. Verneuilnodon pallasi differs from Healeyia gonoides in being posteriorly ovate instead of subtruncate, in having a broadly convex instead of nearly straight dorso-posterior margin, in having a more rounded umbonal-posteroventral carina, and in lacking a permanent byssal gape. The family Healeyidae is herein reduced in rank to subfamily Healeyinae because Healeyia gonoides is morphologically and ligamentally similar to some Kalenterinae and Myoconchinae and differs from Myoconchinae principally in having a more extreme reduction of the hinge dentition. Hautmann (2008) assigned Healeyidae to the family Modiomorphidae, but Modiomorpha Hall in Hall and Whitfield, 1869, as exemplified by its type species Devonian Modiomorpha concentrica (Conrad, 1838), differs from Healeyia and other members of Kalenteridae in having a wider, flatter, subumbonal hinge plate; cruder cardinal dentition consisting of dorsally reflected, irregular shell lamellae; and a deeper, more strongly growth-lined lunule (Carter, 1990, p. 266). Additionally, Modiomorpha concentrica has a nacreous shell, whereas members of Kalenteridae are internally porcellaneous and non-nacreous (Carter & Tevesz, 1978; Morris, 1978, p. 273; Carter, Lutz, & Tevesz, 1990, p. 391).

**SUMMARY**

Netschajewia Licharev, 1925 is confirmed as a replacement name for the preoccupied Modiolidon Netschajew, 1894 (non Modiolidon Ulrich, 1894a), thereby invalidating Newell’s (1957) designation of a type species for Netschajewia that is different from the type for Modiolidon Netschajew, 1894. The figures that Newell (1957) used to illustrate the type species of Netschajewia (also used by Chavan, 1969) are actually Stutchburia or a closely related, dentate species. Netschajewia is distinguished from other members of Myoconchinae by having two or more minute, vertically stacked, hinge-parallel, tabular cardinal teeth, no additional cardinal teeth, and no posterior lateral teeth. The confusion stemming from Newell’s (1955, 1957) misidentification of the type species of Netschajewia means that subsequent references to this genus need to be reevaluated.

De Verneuil’s (1845) Mytilus ( Modiola) pallasi is herein restricted to its edentulous members, and this pallasi sensu stricto is designated the type species for the new genus Verneuilnodon. The dentate example of de Verneuil’s (1845) Mytilus ( Modiola) pallasi is now Stutchburia globosa (Netschajew, 1894). Verneuilnodon is assigned to the edentulous kalenterid subfamily Healeyinae, herein reduced in rank from family Healeyidae Hautmann, 2008.

The new Permian species Kasimlara antiqua Fang & Carter is proposed for members of Healeyinae with a lateral profile similar to Late Triassic Kasimlara kosuni Kiell, 2018, but with shells equivalent, not curving to the left or right as in K. kosuni, with a myophoric buttress ( absent in K. kosuni), and without a pallial sinus (short and pointed in K. kosuni).

Additional taxonomic actions are summarized as follows: Licharev’s (1925, 1939) Netschajewia pallasi ( de Verneuil, 1845) is subdivided into Verneuilnodon pallasi, Stutchburia globosa, and possibly an unnamed species closely related to Verneuilnodon.
pallasi. Golowkinsky's (1869) Cleidophorus pallasi obliquus is subdivided into obliquus sensu stricto (genus indeterminate), Verneuilodon pallasi (de Verneuil, 1845), and Netschajewia elongata (Netschajew, 1894). Golowkinsky's (1869) Cleidophorus pallasi oblongus is now Netschajewia oblonga (Golowkinsky, 1869), the type species of Netschajewia by the principle of typification of a replacement name for Modiolodon Netschajew, 1894. Golowkinsky's (1869) Cleidophorus pallasi obliquus, as restricted herein, is generically indeterminate. Netschajew's (1894) Modiolopsis pallasi (de Verneuil, 1845) is subdivided into Verneuilodon pallasi (de Verneuil, 1845) and Kasimlara antiqua sp. nov. Netschajew's (1894) Modiolopsis (Modiolodon) elongatum is now Netschajewia elongata (Netschajew, 1894).

SYSTEMATICS

Superfamily Kalenteroidea Marwick, 1953
Family Kalenteridae Marwick, 1953
Subfamily Myoconchinae Newell, 1957
Netschajewia Licharev, 1925
(nom. nov. pro Modiolodon Netschajew, 1894, non Ulrich, 1894a)

Type species.—Cleidophorus [err. pro Cleidophorus] pallasi oblongus Golowkinsky, 1869, by typification of replacement name for Modiolodon Netschajew, 1894, non Modiolodon Ulrich, 1894a, as designated for Modiolodon Netschajew by La Rocque and Newell (1969, p. 397).

Generic diagnosis.—Members of Myoconchinae with two or more minute, short, tabular, vertically stacked, hinge-parallel cardinal teeth and no posterior lateral teeth.

Generic description.—Netschajew (1894, p. 239–240) described Modiolopsis (Modiolodon) (herein Netschajewia) as of considerable size, very thick shelled, straight or slightly curved, very elongate, with strongly impressed anterior adductor muscle scar; pronounced posterior adductor muscle scar; wide, irregular myophoric buttress bordering the anterior adductor scar; anterior pedal retractor muscle scar positioned dorsal to this buttress; simple, strongly impressed, non-sinuate pallial line; umbos almost terminal anterior and not prominent; slightly concave ventral shell margin, and two or more minute, short, tabular, vertically stacked, parallel cardinal teeth. Added herein, no posterior lateral teeth; shells equivale, strongly inequilateral, strongly posteriorly extended, elongate ovate (oblonga) to elongate subtriangular (elongata), and no permanent byssal gape. Sculpture varying from entirely commarginal to also radial. Pallial line well recessed from ventral shell margin. Any concavity of ventral shell margin that might be present (as in elongata, see Netschajew, 1894, pl. 8, fig. 19) very shallow. [Netschajew (1894) illustrated two internal molds of oblongus that reveal the hinge structure (Fig. 3.7–3.8).]

Member species.—The two original species of Modiolopsis (Modiolodon) Netschajew are now called Netschajewia oblonga (Golowkinsky, 1869) and Netschajewia elongata (Netschajew, 1894). Netschajewia oblonga, the type species, can be described as follows, based on Golowkinsky (1869) and Netschajew, 1894: Shells medium size (up to 85 mm long), equivale, moderately to strongly (?) inflated, strongly inequilateral, strongly posteriorly extended; margins not gaping, dorsal and ventral margins only slightly diverging from anterior to posterior; posterior margin slightly more broadly ovate than anterior margin. In lateral profile, shells elliptical, anterior margin narrowly to moderately ovate; anterior part of dorsal margin very short, nearly horizontal or curving downward, probably without a distinct indentation directly anterior to beaks (although this is difficult to evaluate from internal molds); ventral margin very broadly ovate to nearly straight, and nearly horizontal to sloping slightly downward toward posterior, passing smoothly into posterior margin, which is moderately ovate; posterior part of dorsal margin very weakly convex and sloping slightly upward toward posterior, passing smoothly into posterior margin. Presence or absence of lunule and escutcheon unknown. Sculpture of growth lines or ridges and obsolete radial ribs, the latter extending from umbo to posterior margin. Umbonal-posteroventral carina probably not well developed, judging from internal molds. Umbos probably low, not projecting, strongly anterior but not terminally so. Anterior adductor muscle scar rounded, deeply impressed, positioned directly below anterior hinge, close to anterior shell margin. Posterior adductor muscle scar nearly twice as large, subcircular, more shallowly impressed, positioned directly below posterior end of hinge. Anterior pedal retractor muscle scar small, positioned dorsal and adjacent to anterior adductor scar. Short myophoric ridge present along posterior margin of anterior adductor muscle scar, extending posteroventrally from below anterior hinge. Pallial line continuous, deeply impressed, well removed from ventral and posterior shell margins, without sinus. Anterior end of pallial line contacting posteroventral margin of anterior adductor scar; posterior end of pallial line contacting medioposterior margin of posterior adductor scar. Interior shell surface directly proximal to ventral pallial line bulging more or less abruptly outward (laterally) relative to shell directly distal to pallial line. Hinge slightly arched, very short and narrow to moderately wide anterior to beaks, much longer and (possibly?) narrower posterior to beaks (width of posterior hinge difficult to determine from internal molds). Each valve with three minute, short, tabular, vertically stacked, hinge-parallel cardinal teeth and no lateral teeth. Ligament opisthodetic; ligament insertion area not seen, but probably parivincular.

Netschajewia elongata (Netschajew, 1894) resembles Netschajewia oblonga in having minute, short, tabular, vertically stacked, hinge-parallel cardinal teeth, an elongate-ovate shell not curving downward posteriorly, no sinus in the ventral shell margin, a moderately recessed pallial line, and a sculpture of growth lines and a few radial ribs. Both taxa also have a prominent lateral expansion of the shell’s inner surface, directly proximal to the anteroventral pallial line. Netschajewia elongata differs from Netschajewia oblonga in having fewer (only two) cardinal teeth, a flatter shell, a moderately ovate instead of narrowly ovate posterior, and nearly straight instead of convex dorsal and ventral margins. Maslennikov (1935) and Noinsky (1935) referred this species to Stutchburia, apparently assuming the presence of posterior lateral dentition.

Two additional Permian species might be members of Netschajewia. These are Netschajewia (?) sibirica Kulikov, 1967, which lacks posterior lateral dentition, and a specimen cited by Nakazawa and
Newell (1968, p. 95, pl. 11, fig. 5, 6) as *Netschajewia cf. elongata* (Netschajew, 1894). The latter specimen was described as having a right posterior lateral tooth, but this so-called tooth is very short and does not extend far posterior to the umbo, suggesting that it might be a low ligament nympha.

The species that Newell (1957) and Chavan (1969) used to illustrate *Netschajewia*, Newell’s (1957, Fig. 2D) “*Netschajewia cf. modioliformis* (King)” is not a *Netschajewia* because it has a posterior lateral dentition. Newell (1957) used this species to illustrate the type species of *Netschajewia* because Newell (1957, p. 7) regarded “*Plerophorus modioliformis* King, 1884” (actually *Cardiomorpha modioliformis* King, 1848, not 1884) as a synonym of *Mytilus pallasi* de Verneuil, 1845. Complicating this matter, Lutkevich and Lobanova (1959, p. 161) indicated that Netschajew’s (1894, p. 309, pl. 10, fig. 2, 3, 3) “*Cardiomorpha cf. modioliformis*” King is not that species, so they renamed it *Modiola netschajewi* (see Lutkevich & Lobanova, 1959, pl. 32, fig. 10–14). Neither King (1848) nor Netschajew (1894) described the hinge structure of *Cardiomorpha modioliformis*.

The wide circulation of Newell’s (1957) and Chavan’s (1969) misidentification of the type species of *Netschajewia* means that subsequent references to this genus should be reevaluated. For example, Muromzova and Gusakov (1984) reassigned *Netschajewia oblonga* to *Stutchburia*, incorrectly believing that *oblonga* resembles *Stutchburia* in having posterior lateral dentition. Kiel (2018) indicated that his new genus *Terszleria* resembles *Netschajewia* in having posterior hinge teeth, although their absence is now considered to be a hallmark of *Netschajewia*. Several authors have incorrectly assigned posteriorly dentate species to *Netschajewia*. These include Permian *Netschajewia maslennikovi* Lutkevich & Lobanova, 1971 (p. 87, pl. 6, fig. 5–7); Middle Triassic *Netschajewia sviilajensis* Chorowicz & Termier, 1975 (their p. 240, text-fig. 10, pl. 21, fig. 13–15), and a Permian *Netschajewia* sp. in Mancenido, Gonzalez, and Damborenea (1976, p. 90). Sha and Grant-Mackie (1996, p. 434, fig. 3A) reassigned Permian *Stutchburia jianguensis* Liu in Gu & others, 1976, p. 97, pl. 11, fig. 8) to *Netschajewia*, although this species has a divided posterior lateral tooth in the left valve and two posterior lateral teeth in the right valve. The *Netschajewia cf. modioliformis* (King, 1848) in Sha and Grant-Mackie (1996, p. 434, fig. 3B) resembles a bakevellid in terms of its lobate anterior ear delimited posteriorly by a shallow, radial furrow, a depressed posterior wing, and umbos salient above the hinge margin. The surface of the internal mold (their fig. 3B) has vague traces of radiating ridges. This is probably a member of the Permian–Early Triassic bakevellid genus *Towapteria* Nakazawa & Newell, 1968. Other taxa have assigned to *Netschajewia* despite a lack of information on their hinge structure, e.g., Permian *Netschajewia pallasi* var. *kendyrlikensis* Lutkevich & Lobanova, 1960 (p. 182, pl. 2, fig. 14) and Permian *Netschajewia kugolare* Nelzina in Kalmikova & others (1978, p. 19, pl. 1, fig. 16, 19, 20).

Lutkevich and Lobanova (1959, p. 151) did not consider hinge dentition when they differentiated *Netschajewia* from *Stutchburia*, *Myconcha*, and *Permosphorus* on the basis that imbricated growth increments are diagnostic of *Netschajewia*. Consequently, their concept of *Netschajewia* includes some taxa with posterior lateral hinge teeth. Their new species *Netschajewia striata* Lutkevich & Lobanova, 1959 (pl. 32, fig. 4–7) has imbricated growth increments crossed by very narrow, closely spaced radial ribs, but these so-called ribs consist of a dense network of radial pimplies, suggesting that they are actually radial rows of mineralized periostracal granules or spines, a common feature among kalenterids. Lutkevich and Lobanova (1959) did not describe the hinge structure of *striata*, so its placement in *Netschajewia* is certain. Lutkevich and Lobanova (1959, p. 152, pl. 31, fig. 5, 6) reassigned *Stutchburia tschernyschewi* Maslennikov, 1935 to *Netschajewia*, although they indicated that other authors have observed a thickened ridge (posterior lateral tooth?) on its hinge. Finally, Lutkevich and Lobanova (1959) proposed three new varieties of *Netschajewia pallasi*, two of which, *aversa* and *alta*, also have a thickened ridge on their hinge. Their variety *aversa* would be unique in *Netschajewia* for having a slight pallial sinus. The hinge of their third new variety, *Netschajewia pallasi* var. *duplex*, was not described, so its assignment to *Netschajewia* is not confirmed.

**Stratigraphic distribution.**—Permian of western Russia.

### Subfamily Healeyinae Hautman, 2008

*Verneuilodon Fang & Carter, herein gen. nov.*

Figures 1.1–1.5, 2.2–2.3, 2.6, 3.1–3.2

#### Type species.—*Mytilus (Modiola) pallasi* de Verneuil, 1845, as restricted herein to de Verneuil’s (1845) pl. 19, fig. 16a–h (Fig. 1.1–1.5), with Fig. 1.1a–b designated herein as lectotype and Fig. 1.2–1.5 designated as paralectotypes.

The new Permian genus *Verneuilodon* is proposed for *Mytilus (Modiola) pallasi* de Verneuil, 1845, as restricted herein. The genus name honors Philippe-Édouard Pouletier de Verneuil (1805–1873), a pioneer in Paleozoic biostratigraphy. *Nodon* derives from the Greek νωδόν for edentulous, in reference to the absence of hinge teeth.

**Generic (and type species) diagnosis.**—Equivalent members of *Healeyinae* with banana-shaped lateral profile, convex dorsoposterior margin, slightly concave (sinuate) ventral margin, low, rounded umbonal-postervental carina, and no anteroventral byssal gape. Hinge edentulous.

**Generic (and type species) description.**—Shells small (as long as 31 mm), considerably thick, moderately inflated, moderately elongate, strongly inequilateral, strongly posteriorly extended, with dorsal and ventral margins slightly to moderately curving downward posteriorly; no permanent shell gapes. As seen in lateral profile, shells anteriorly narrowly ovate and sometimes anteroventrally lobeate; anterior part of dorsal margin very short, moderately to strongly sloping downward, with slight indentation directly anterior to beaks; ventral margin broadly and shallowly sinuate (concave) and sloping slightly to strongly downward posteriorly; posterior margin generally moderately ovate and slightly higher than anterior margin; posterior part of dorsal margin very broadly arched and passing smoothly into posterior margin. Very low, rounded, umbonal-posterior carina present. Broad, shallow, ventral to anteroventral sulcus present. Very small, rather deep lunule commonly present, but no escutcheon. Sculpture of growth lines and sometimes also 3–5 narrow ribs extending posteriorly from umbo (Fig. 1.3a). Umbo very low, strongly anterior but not
overhanging anterior shell margin. Anterior adductor muscle scar deeply impressed, ovate to subtriangular, positioned directly below anterior end of hinge, close to anterior shell margin, bordered posteriorly by oblique, umbalonal-posteroventral, radial to slightly oblique, myophoric ridge. Other muscle scars unknown. Hinge plate narrow, edentulous, anteriorly slightly arched, posteriorly very broadly arched. Ligament external, opisthodetic, parivincular, with low, slightly submarginal nymphs.

Comparisons.—Of the two genera that Hautmann (2008) assigned without question to his family Healeyidae (herein Healeyinae), the Late Triassic *Healeya* Hautmann, 2008 differs from *Verneuilnodon* in having a triangular instead of banana-like shape, a straighter dorsoposterior margin, a sharper, more prominent umbalonal-posteroventral carina, an escutcheon, and a permanent byssal gape. The second genus, Early? to Middle Triassic *Joannina* Waagen, 1907 differs from *Verneuilnodon* in having a stronger umbalonal-posteroventral carina, a deeper ventral sinus, umbos projecting more dorsally than anteriorly, and an escutcheon. *Kasimlara* Kiel, 2018, which we tentatively include in Healeyinae, differs from *Verneuilnodon* in having a more strongly differentiated anterior shell lobe (at least in larger specimens), narrower, more anteriorly projecting umbos that may overhang the anterior shell margin, and a deeper notch between the umbo and the anterior shell margin. The pallial line is unknown for *Verneuilnodon* and most other genera in Healeyinae, but in *Kasimlara* this varies from non-sinuate (Permian *Kasimlara? antiqua*) to having a small, pointed sinus (Triassic *Kasimlara kosuni*). *Verneuilnodon*, like other members of Healeyinae, is edentulous.

Stratigraphic distribution.—Lower to upper Permian of western Russia.

*Kasimlara? antiqua* Fang & Carter, sp. nov.

Figure 3.3–3.6

Type specimens.—Holotype is Netschajew’s (1894) pl. 8, fig. 1 (Fig. 3.3). Paratypes include Netschajew’s (1894) pl. 8, fig. 2–4 (Fig. 3.4–3.6). Netschajew’s (1894) specimens were deposited in the geology department of Kazan University (now Kazan Federal University), but we have not verified that they are still there.

*Kasimlara? antiqua* is proposed for Netschajew’s (1894) pl. 8, fig. 1–4, which Netschajew (1894) identified as *Modiolopsis pallasi* de Verneuil, i.e., *Mytilus (Modiolus) pallasi* de Verneuil, 1845. The name *antiqua* refers to the ancient age of Permian *Kasimlara? antiqua* relative to the Carnian, Late Triassic *Kasimlara kosuni* Kiel, 2018, the type species of *Kasimlara* Kiel, 2018, by original designation.

Diagnosis.—Members of Healeyinae resembling Late Triassic *Kasimlara kosuni* Kiel, 2018 in terms of shell shape, but differing from that species in being equivalent, less elongate, in having a myophoric ridge, and in lacking a pallial sinus. Smaller specimens differ from larger ones in having a more rectangular shape and a shallower or absent ventral sinus.

Description.—Based largely on Netschajew’s (1894) description and illustration of *Modiolopsis pallasi* de Verneuil (his pl. 8, fig. 1–4) (Fig. 3–6).—Shells small, thickness unknown, moderately to strongly inflated, moderately elongate, strongly inequilateral, strongly posteriorly or slightly to moderately posteroventrally extended; no permanent shell gapes. As seen in lateral profile, shells anteriorly moderately to very strongly lobate; anterior part of dorsal margin very short, strongly sloping or strongly curving downward, with distinct indentation between umbo and anterior margin; larger specimens with ventral margin broadly and deeply sinuate (concave) and sloping strongly downward, but smaller specimens with ventral margin straight to shallowly sinuate and sloping only slightly downward; shells posteriorly moderately to broadly ovate; larger specimens much taller posteriorly than anteriorly, some smaller specimens only slightly taller posteriorly; posterior part of dorsal margin slightly to moderately arched, passing smoothly into posterior margin. Very low, rounded, umbalonal-posterior carina and slight anteroventral sulcus present. Presence or absence of lunule and escutcheon unknown. Sculpture of growth lines without radial ribs. Umbos small, strongly anterior, subterminal, terminal, or overhanging anterior shell margin. Anterior adductor muscle scar deeply impressed, positioned directly below anterior end of hinge, close to anterior shell margin, and bordered posteriorly by narrow, oblique, umbalonal-posteroventral, myophoric ridge. Posterior adductor muscle scar larger, elongate, weakly impressed, positioned directly below posterior end of hinge. Anterior pedal retractor muscle scar subtriangular, positioned at dorsal end of myophoric ridge. Hinge nearly straight to slightly arched, edentulous. Ligament insertion area not observed.

Comparisons.—*Kasimlara antiqua* strong resembles *Kasimlara kosuni* in terms of overall shell shape and in having the umbos sometimes strongly overhanging the anterior shell margin, from which they are separated by a distinct notch. However, *K. antiqua* differs from *K. kosuni* in being equivalent (not curving posteriorly to the left or right), in having a myophoric ridge, and in lacking a pallial sinus (small and pointed in *K. kosuni*).

This new species is questionably assigned to *Kasimlara* because it is unknown whether the type species of *Kasimlara*, *Kasimlara kosuni*, is also edentulous. Netschajew’s (1894) pl. 8, fig. 1b (Fig. 3.3b) shows an elongate, lamellar internal ridge in *Kasimlara? antiqua* below and slightly diverging from the hinge in the right valve, but it is doubtful that this represents a lateral tooth. The posterior lateral tooth in the *Netschajewia* cf. modioliformis illustrated by Newell (1957, fig. 2D) is closer to the hinge and therefore more clearly a dental feature.

*Kasimlara? antiqua* differ from *Verneuilnodon pallasi*, as defined herein, in terms of its more strongly lobate anterior margin, narrower, deeper ventral sinus, more dorsoventrally expanded posterior, and more anteriorly projecting umbos.

Stratigraphic distribution.—Permian of western Russia.

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