

Paleontological Contributions

Number 22

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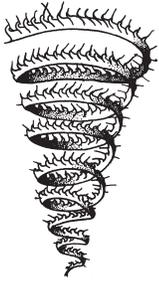


Verneuillodon Fang & Carter, herein *gen. nov.*

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



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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 *Stutchburia* 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, opisthodontic ligament grooves in *Modiolodon oviformis* (Ulrich, 1890), which comprise a monovincular-P ligament as defined by Carter and others (2012). In contrast, *Netschajewia* has a parivincular ligament and is a member of the infraclass Heteroconchia Hertwig, 1895, superfamily Kalenteroidea Marwick, 1953.

Netschajew (1894) published *Modiolodon* as a subgenus of *Modiolopsis* 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 *Modiolodon* Netschajew, i.e., *Clidophorus* [err. pro *Cleidophorus*] *pallasi oblongus* Golowkinsky, 1869.

This article reviews the taxonomic history of *Modiolodon* Netschajew, 1894, *Netschajewia* Licharev, 1925 and closely related

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. N545) used "Yakovlev." For the sake of consistency, we use the spelling "Licharev."

Table 1. Comparison table of *Netschajewia* Licharev, 1925 and related taxa names identified by Verneuil (1845), Golowkinsky (1869), Netschajew (1894), Licharev (1925, 1939) and this paper.

de Verneuil, 1845	Golowkinsky, 1869	Netschajew, 1894	Licharev, 1925, 1939	This paper	Taxonomic position
<i>Mytilus (Modiola) pallasi</i> de Verneuil (pl. 19, fig. 16a–i, non 16k)	<i>Cleidophorus pallasi</i> (de Verneuil) (pl. 4, fig. 4–6)	<i>Modiolopsis pallasi</i> (de Verneuil) (pl. 19, fig. 16a–i of de Verneuil, 1845; non pl. 8, fig. 1–4 of Netschajew, 1894)	<i>Netschajewia</i> (de Verneuil) (1939, pl. 35, fig. 10–11)	<i>Verneuilnodon pallasi</i> (de Verneuil) (Fig. 1.1–1.5 = pl. 19 (16a–h) of de Verneuil, 1845; Fig. 2.2, 2.3, 2.6 = pl. 4, fig. 4–6 of Golowkinsky, 1869; Fig. 3.1–3.2 = pl. 35, fig. 10–11 of Licharev, 1939) <i>V. pallasi</i> (de Verneuil) or unnamed sp. (Fig. 1.6 = pl. 19, fig. 16i of de Verneuil, 1845)	Healeyinae
<i>M. (Modiola) pallasi</i> de Verneuil (pl. 19, fig. 16k, non 16a–i)	---	<i>Modiolopsis globosus</i> Netschajew (pl. 8, fig. 16–18)	<i>Netschajewia globosa</i> (Netschajew) (1925, pl. 2, fig. 13–14; pl. 35, fig. 12 of 1939)	<i>Stutchburia? globosa</i> (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)	Myoconchinae
---	---	<i>Modiolopsis pallasi</i> (de Verneuil) (pl. 8, fig. 1–4; non pl. 19, fig. 16a–i of de Verneuil, 1845)	---	<i>Kasimlara? antiqua</i> sp. nov. (Fig. 3.3–3.6 = pl. 8, fig. 1–4 of Netschajew, 1894)	Healeyinae
---	<i>C. pallasi obliquus</i> Golowkinsky (pl. 4, fig. 7–8)	---	---	<i>obliquus</i> Golowkinsky, 1869 s. s. (genus indet.) (Fig. 2.4–2.5 = pl. 4, fig. 7–8 of Golowkinsky, 1869)	Subfamily indet.
---	<i>C. pallasi obliquus</i> Golowkinsky (pl. 4, fig. 13)	<i>Modiolopsis (Modiolodon) elongatum</i> Netschajew, 1894 (pl. 8, fig. 14, 19)	<i>Netschajewia elongata</i> (Netschajew) (1939, pl. 35, fig. 9)	<i>Netschajewia elongata</i> (Netschajew) (Fig. 2.7 = pl. 4, fig. 13 of Golowkinsky, 1869)	Myoconchinae
---	<i>C. pallasi oblongus</i> Golowkinsky (pl. 4, fig. 12)	<i>Modiolopsis (Modiolodon) oblongum</i> (Golowkinsky) (pl. 8, fig. 9, 15)	---	<i>Netschajewia oblonga</i> (Golowkinsky) (Fig. 2.1 = pl. 4, fig. 12 of Golowkinsky, 1869; Fig. 3.7–3.8 = pl. 8, fig. 9, 15 of Netschajew, 1894)	Myoconchinae
---	<i>C. pallasi rectangularis</i> Golowkinsky (pl. 4, fig. 9–11)	<i>Pleurophorus simplex</i> (Keyserling, 1846) (pl. 8, fig. 21; pl. 11, fig. 25)	<i>Pleurophorina simplex</i> (Keyserling, 1846) (1925, pl. 2, fig. 1–4)	<i>Pleurophorina simpla?</i> (Keyserling, 1846) (Fig. 2.8–2.10 = pl. 4, fig. 9–11 of Golowkinsky, 1869)	unresolved

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, pl. 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 is classified herein as *Stutchburia? globosa* (Netschajew, 1894) (Table 1).

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 *Cleidophorus pallasi oblongus*, *Cleidophorus pallasi obliquus*, and *Cleidophorus pallasi rectangularis* (his Plate 4, fig. 4–13) (Fig. 2). Golowkinsky's assignment of *pallasi* to *Clidophorus* (a misspelling of *Cleidophorus* Hall, 1847) was not adopted by subsequent authors. The type species of *Cleidophorus*, 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

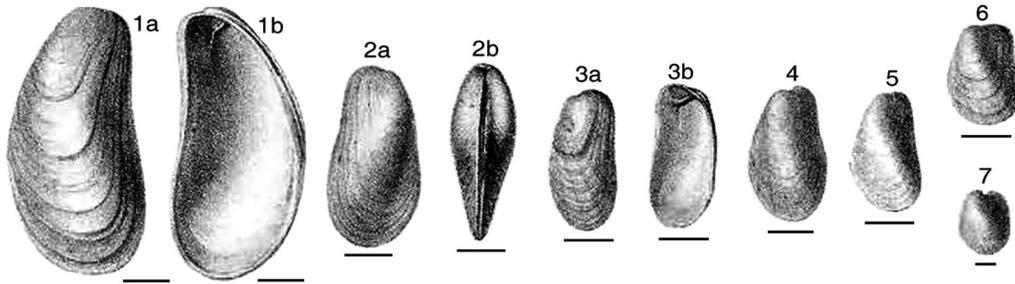


Figure 1. 1–7, de Verneuil's (1845) figures for *Mytilus (Modiola) pallasi* Verneuil (1845, pl. 19, figs. 16a–i, k). 1–5, *Verneuilnodon pallasi* as defined herein: 1, lectotype, exterior and interior views of right valve; 2–5, paralectotypes, 2a, left exterior view, 2b, dorsal view, 3a, right exterior view showing commarginal and traces of posterior radial sculpture, 3b, right interior view; 4, right exterior view; 5, right exterior view. 6, an atypical *Verneuilnodon pallasi* or an unnamed species, right exterior view. 7, specimen indicated by Netschajew (1894) as a possible *Modiolopsis globosus* Netschajew, 1894 (but probably a *Stutchburia*), right exterior view. Scale bars = 5 mm in 1–6, 2 mm in 7.

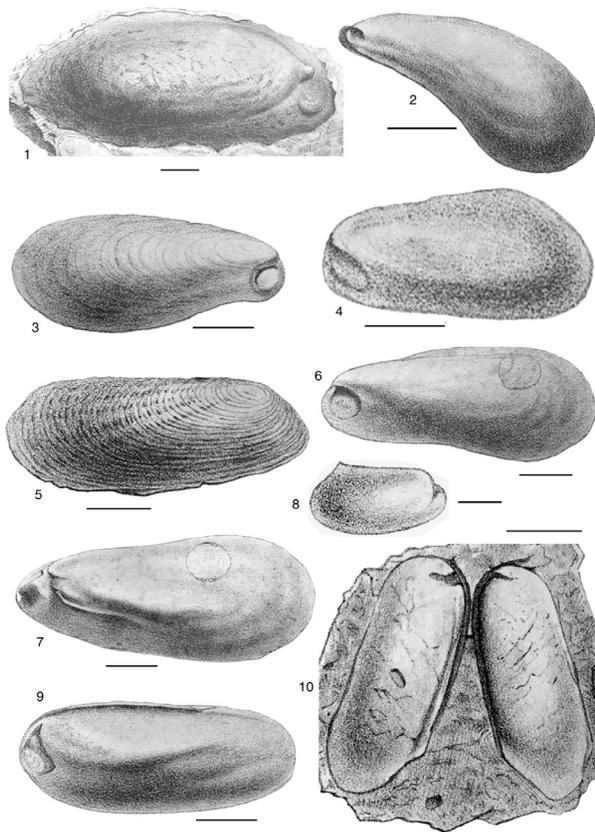


Figure 2. Golowkinsky's (1869, pl. 4, fig. 4–13) three morphological variations of *Cleidophorus pallasi*. 1, *Cleidophorus pallasi obliquus* after Golowkinsky (1869, pl. 4, fig. 12) [=now *Netschajewia oblonga* (Golowkinsky, 1869)]. 2–7, *Cleidophorus pallasi obliquus* after Golowkinsky (1869, pl. 4, fig. 4–8, 13) [2.2, 2.3, and 2.6 are now *Verneuilnodon pallasi*; 2.4 and 2.5 are now the lectotype (2.5) and paralectotype (2.4) of *obliquus* as restricted herein (genus indeterminate); 2.7 is now *Netschajewia elongata* (Netschajew, 1894)]. 8–10, *Cleidophorus pallasi rectangularis* after Golowkinsky (1869, pl. 4, fig. 9–11), possibly a junior synonym of *Pleurophorina simpla* (Keyserling, 1846). Scale bars = 10 mm in 1–3, 5–8, 10; 5 mm in 4, 9.

hinge. However, Golowkinsky (1869) included certain dentate species in his concept of *Cleidophorus*, reflecting his adoption of McCoy's (1855) opinion that the dentate genus *Pleurophorus* King, 1844 (now *Permophorus* Chavan, 1954) is a junior synonym

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 (Modiolopsis)*, 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

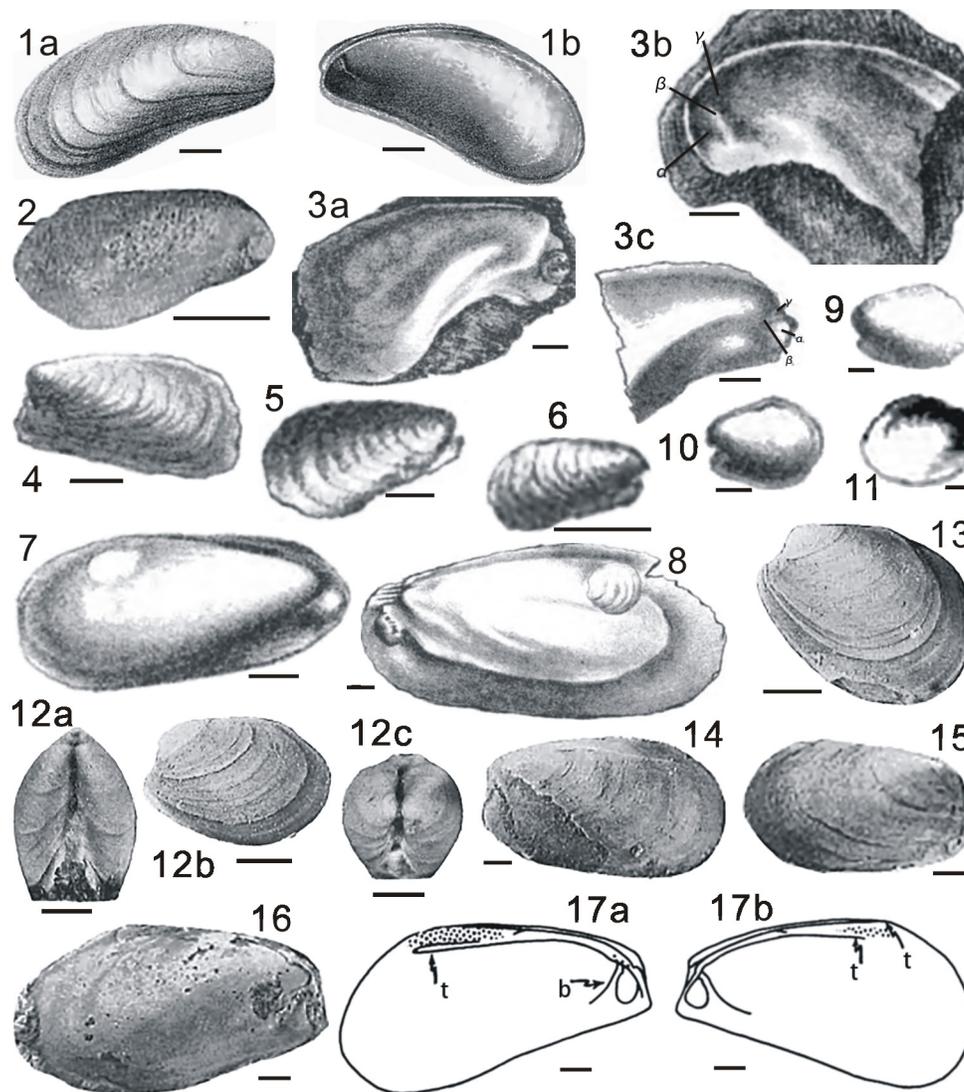


Figure 3. *Netschajewia* and allied taxa. 1–2, “*Netschajewia pallasi* (de Verneuil, 1845)”, after Licharev (1939, pl. 35, fig. 10–11) (=now *Verneuilnodon pallasi*); 1a, right exterior view showing commarginal sculpture; 1b, right interior view (Fig. 3.1 is the same specimen as Fig. 1.1). 2, Right internal mold. 3–6, “*Modiolopsis pallasi* de Verneuil” after Netschajew (1894, pl. 8, fig. 1–4); 3a, 3c, “left” (actually right) internal molds, 3b, plaster cast of 3a, with labels α (anterior adductor muscle scar), β (myophoric ridge) and γ (anterior pedal retractor muscle scar), 3c is labeled as in 3b. 4, Left composite mold. 5, Right composite mold. 6, Right composite mold (3–6 = now *Kasimlara? antiqua*, sp. nov.). 7–8, “*Modiolopsis (Modiolodon) oblongum*” (Golowkinsky, 1869), after Netschajew (1894, pl. 8, fig. 9, 15) (= now *Netschajewia oblonga*); 7, right internal mold; 8, left internal mold. 9–11, “*Modiolopsis globosus*” Netschajew, 1894 (= now *Stutchburia? globosa*), after Netschajew (1894, pl. 8, fig. 16–18); 9, left internal mold of *globosus* lectotype; 10, left internal mold; 11, right internal mold. 12–16, “*Stutchburia? modioliformis*” (King, 1848) after Newell (1955, pl. 5, fig. 1–5); 12, juvenile specimen in posterior dorsal view (12a), left exterior view (12b), and anterior dorsal view (12c). 13, left exterior view; 14, left exterior view showing costellate sculpture; 15, right exterior view; 16, right internal mold. 17, “*Netschajewia cf. modioliformis*” (King, 1848), after Newell (1957, fig. 2D), left (17a) and right (17b) interior views, with myophoric ridge indicated by *b*, hinge teeth indicated by *t*, and tooth sockets shown in stippling (= *Stutchburia modioliformis* (King) in Logan, 1967, p. 51). Scale bars = 5 mm in 1–8, 2 mm in 9–11 and 14–17, 1 mm in 12, 13.

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) *Verneuilnodon 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*

simpla differently, indicating a triangular cardinal socket and one long posterior lateral tooth in the left valve, and one cardinal tooth and possibly a posterior lateral tooth in the right valve. Maslennikov (1935) concluded that the simple cardinal dentition and absence of a lunule and escutcheon exclude *Modiola simpla* from *Pleurophorus* King, 1844 (= *Permophorus* Chavan, 1954). Because of uncertainty in the hinge structure of this species, we accept the conclusion by Morris, Dickins, and Astafieva-Urbajtis (1991, p. 84) that the possibility that *Pleurophorina* is a senior synonym of *Permophorus* remains unsettled. Fang and Morris (1997) regarded *Pleurophorina* as a *nomen dubium* unless *Modiola simpla* becomes properly interpreted.

Mytilus (Modiola) pallasi de Verneuil, 1845, as presently restricted to Fig. 1.1–1.5, Fig. 2.2–2.3, 2.6, and Fig. 3.1–3.2, is designated herein as the type for the new genus *Verneuilnodon* Fang & Carter herein. *Verneuilnodon* and its member species are described in the systematics section below. *Verneuilnodon* differs from *Netschajewia* in having a banana-like instead of elongate-ovate shape, with the posterior dorsal and ventral margins both curving downward posteriorly; in having a broad, shallow ventral sinus; and in lacking hinge teeth. Netschajew (1894, p. 230) confirmed de Verneuil's (1845) description of the hinge of *pallasi* as edentulous. The absence of hinge teeth excludes *Mytilus (Modiola) pallasi* from the subfamilies Kalenterinae and Myoconchinae. We regard *Verneuilnodon* as closely related to the Triassic genus *Healeyia* Hautmann, 2001, which Hautmann (2008) assigned to the family Healeyidae, but which we reduce herein in rank to subfamily Healeyinae in Kalenteridae. *Healeyia gonoides* (Healey, 1908), the generic type species, resembles *Verneuilnodon pallasi* in being strongly inequilateral, thick-shelled, posteriorly expanded, slightly posteroventrally extended, and ventrally broadly and slightly sinuate, with an associated slight sulcus. Both species also have an edentulous, slightly arched hinge, an anterior myophoric buttress, and an opisthodontic, parivincular ligament. *Healeyia gonoides* differs from *Verneuilnodon pallasi* in having a subtriangular instead of banana-like shape, a straighter dorsoposterior margin, a sharply defined instead of rounded umbonal-posteroventral carina, and a permanent byssal gape. *Verneuilnodon* is unique in the Kalenteridae for its combination of a banana-like shape, ventrally curving posterior margins, broad, shallow, ventral sinus, slightly arched edentulous hinge, anterior myophoric buttress, and opisthodontic, parivincular ligament.

A Permian specimen identified as *Modiolopsis pallasi* by Netschajew (1894, pl. 8, fig. 1a–c) (Fig. 3.3) has a shape similar to the holotype of Late Triassic *Kasimlara kosuni* Kiel, 2018 (Kiel, 2018, fig. 4A), the type species of *Kasimlara* Kiel, 2018. Both specimens are strongly posteriorly extended, anteriorly roundly lobate, ventrally nearly straight to deeply concave, posteriorly broadly ovate, and have very low, almost terminally anterior umbos separated from a subadjacent anterior shell lobe by a distinct notch. Both also have a deeply impressed anterior adductor muscle scar positioned on an anterior shell lobe. Two other figures of *Modiolopsis pallasi* in Netschajew (1894, pl. 8, fig. 3–4) (Fig. 3.5–3.6) resemble a paratype of *Kasimlara kosuni* (see Kiel, 2018, fig. 4B), with umbos extending anteriorly beyond the anteroventral shell margin. Plate 8, fig. 2 in Netschajew (1894) (Fig. 3.4) might represent a variation of the Permian species in which the anterior lobe of the shell is

subdued. Netschajew's (1894) specimens lack hinge teeth, but the hinge structure of *Kasimlara kosuni* is unknown. Netschajew's Permian specimens differ from *Kasimlara kosuni* in being equivalve, in lacking a pallial sinus, and in having an anterior myophoric ridge. *Kasimlara kosuni* is slightly inequivalve, with the posterior end of the shell curving indifferently to the left or right; it has a small, pointed pallial sinus; and it lacks a myophoric ridge bordering the anterior adductor muscle scar. Netschajew's (1894, pl. 8, fig. 1–4) 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 beschränkend, 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 *Stutchburia*. 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 angulate anteroventral margin. Chavan (1969, p. 545) and Kiel (2018) 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 *Stutchburia? modioliformis* differs from King's (1848) *modioliformis* in lacking an escutcheon. Not surprisingly, Muromzeva 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). 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 Manceñido, Gonzalez, and Damborenea (1976) accepted Licharev's (1925) suggestion that *Netschajewia* is a replacement name for *Modiolodon* Netschajew. Doing so gave *Netschajewia* the same type species as *Modiolodon* on the principle of typification of a replaced name (ICZN, 1999, Article 67.8), i.e., *Cleidophorus pallasi oblongus* Golowinsky, 1869, as designated for *Modiolodon* 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 *Modiolodon* (Netschajew) invalidates Newell's (1957) type designation. Two later published replacement names for *Modiolodon* (Netschajew) are now objective junior synonyms of *Netschajewia*: *Ivanovia* Astafieva-Urbajtis in Astafieva-Urbajtis and Ramovš (1978) and *Astafia* Goncharova, 2013.

Taxonomic position of *Netschajewia* and *Verneuilnodon*

Chavan (1969, p. 545) assigned *Netschajewia* to the kalenterid subfamily Kalenterinae 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 *Protopis* Kittl, 1904 as well as three additional Middle Triassic genera proposed by Stiller and Chen (2006): *Leidapoconcha*, *Qingyaniola*, and *Waijiaoella*. 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 dorsoposterior 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 porcelaneous 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 *Modiolodon* Netschajew, 1894 (*non Modiolodon* Ulrich, 1894a), thereby invalidating Newell's (1957) designation of a type species for *Netschajewia* that is different from the type for *Modiolodon* 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. *Verneuilnodon* resembles *Healeyia gonoides* (Healey, 1908) in many respects, but differs in having a banana-shaped instead of subtriangular profile; a convex instead of nearly straight dorsoposterior margin; a lower, more rounded umbonal-posteroventral carina; and no byssal gape.

The new Permian species *Kasimlara? antiqua* Fang & Carter is proposed for members of Healeyinae with a lateral profile similar to Late Triassic *Kasimlara kosuni* Kiel, 2018, but with shells equivalve, 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), *Verneuilnodon 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 *Verneuilnodon 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 terminally 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 equivalve, 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), equivalve, 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 obscure 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 roundly ovate, 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 opisthodontic; 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 nymph.

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 pallasii* de Verneuil, 1845. Complicating this matter, Lutkevich and Lobanova (1959, p. 161) indicated that Netschajew's (1894, p. 309, pl. 10, fig. 2, 3, 3¹) Permian "*Cardiomorpha? 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, Muromzeva and Guskov (1984) reassigned *Netschajewia oblonga* to *Stutchburia*, incorrectly believing that *oblonga* resembles *Stutchburia* in having posterior lateral dentition. Kiel (2018) indicated that his new genus *Terzileria* 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 maslennikowi* Lutkevich & Lobanova, 1971 (p. 87, pl. 6, fig. 5–7); Middle Triassic *Netschajewia svilajiensis* Chorowicz & Termier, 1975 (their p. 240, text-fig. 10, pl. 21, fig. 13–15), and a Permian *Netschajewia* sp. in Manceñido, Gonzalez, and Damborenea (1976, p. 90). Sha and Grant-Mackie (1996, p. 434, fig. 3A) reassigned Permian *Stutchburia jiangsuensis* 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 been assigned to *Netschajewia* despite a lack of information on their hinge structure, e.g., Permian *Netschajewia pallasii* var. *kendyrlikensis* Lutkevich & Lobanova, 1960 (p. 182, pl. 2, fig. 14) and Permian *Netschajewia kulogorae* Nelzina in Kalmykova & 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*, *Myoconcha*, and *Permophorus* 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 pimples, 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 tchernyschewi* 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 pallasii*, 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 pallasii* var. *duplex*, was not described, so its assignment to *Netschajewia* is not confirmed.

Stratigraphic distribution.—Permian of western Russia.

Subfamily Healeyinae Hautman, 2008

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

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

Type species.—*Mytilus (Modiola) pallasii* 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 *Verneuilnodon* is proposed for *Mytilus (Modiola) pallasii* de Verneuil, 1845, as restricted herein. The genus name honors Philippe-Édouard Poulletier de Verneuil (1805–1873), a pioneer in Paleozoic biostratigraphy. *Nodon* derives from the Greek νωδός for edentulous, in reference to the absence of hinge teeth.

Generic (and type species) diagnosis.—Equivalve members of Healeyinae with banana-shaped lateral profile, convex dorsoposterior margin, slightly concave (sinuate) ventral margin, low, rounded umbonal-posteroventral 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 lobate; 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). Umbos 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, umbonal-posteroventral, radial to slightly oblique, myophoric ridge. Other muscle scars unknown. Hinge plate narrow, edentulous, anteriorly slightly arched, posteriorly very broadly arched. Ligament external, opisthodontic, 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 *Healeyia* Hautmann, 2008 differs from *Verneuilnodon* in having a triangular instead of banana-like shape, a straighter dorsoposterior margin, a sharper, more prominent umbonal-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 umbonal-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 pallasii* de Verneuil, i.e., *Mytilus (Modiolus) pallasii* 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 equivalve, 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 pallasii* 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, umbonal-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, umbonal-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* strongly 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 equivalve (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 pallasii*, 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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