

Spaniodontella Andrussow in Goloubiatnikow, 1902 – a critical survey of use and validity of the genus, and its relationship to the genus *Alveinus* Conrad, 1865 (Mollusca, Bivalvia: Glossoidea, Kelliellidae)

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Ever since its introduction the genus *Spaniodon* Reuss, 1867 (a preoccupied name replaced by *Spaniodontella* Andrussow in Goloubiatnikow, 1902) has been the subject of discussions and misinterpretations concerning its nomenclatural and systematical status. Originally described from the Middle Miocene (Middle Badenian, Wieliczian) of Poland the type species, *S. nitida* Reuss, 1867, also is a common bivalve in several Oligocene and Miocene assemblages of the North Sea and Aquitaine basins, as well as in Miocene assemblages of the Central Paratethys. The various, and frequently conflicting, opinions were reason for us to have a closer look at the literature to evaluate the different concepts. Ultimately we had to agree with Harris's (1920), Glibert & van de Poel's (1966) and Zhgenti's (1976b) decision that the genus *Alveinus* Conrad, 1865, introduced from the North American Eocene, indeed is a senior synonym of *Spaniodon*/*Spaniodontella*. The genus *Davidaschvilia* Merklin, 1950 (type species *Spaniodontella intermedia* Andrussow in Bajarunas, 1910), introduced for Middle Miocene (Karaganian) species in the eastern Paratethys, differs only slightly from *Alveinus* and should be retained in the same family Kelliellidae as *Alveinus*. The genus *Lutetia* Deshayes, 1860 differs in construction of the hinge and placement of the ligament, and should be placed in the separate family Lutetiidae Zhgenti, 1976. For *Spaniodontella gentilis* (Eichwald, 1851) and related species from the Ponto-Caspian Miocene a new genus *Zhgentiana* is introduced, tentatively placed in Lutetiidae.

KEY WORDS: *Spaniodon*, *Spaniodontella*, *Alveinus*, *Lutetia*, *Davidaschvilia*, *Kelliella*, new genus, Miocene, North Sea Basin, Aquitaine Basin, Paratethys, Ponto-Caspian area, nomenclature, systematics.

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Резюме на русском

Spaniodontella Andrussow in Goloubiatnikow, 1902: критический обзор использования рода, его валидность и отношение к роду *Alveinus* Conrad 1865 (Mollusca, Bivalvia: Glossoidea, Kelliellidae)

Сразу после установления род *Spaniodon* Reuss, 1867 (преокупированное название, замещенное на *Spaniodontella* Andrussow in Goloubiatnikow, 1902) стал предметом обсуждения и неправильного толкования его номенклатурного и систематического статуса. Первоначально описанный из среднего Миоцена Польши (Бадениан) типовой вид, *S. nitida* Reuss, 1867, оказался также широко распространенным во многих Олигоценых и Миоценовых комплексах Северного моря, Вены и Аквитанских бассейнов. Разнообразные и часто взаимоисключающие мнения побудили нас внимательно просмотреть литературу и изучить

имеющиеся концепции. В результате мы согласились с мнением Харриса (Harris, 1920), Глиберта и ван де Пула (Glibert & van de Poel, 1966) и Жгенти (1976b) о том, что род *Alveinus* Conrad, 1865, установленный в Еоцене Северной Америки, является старшим синонимом *Spaniodontella*. Род *Davidaschvilia* Мерклин, 1950 (типовой вид *Spaniodontella intermedia* Andrussow in Vajargunas, 1910), предложенный для видов Понто-Каспийского региона среднего Миоцена, только слегка отличается от рода *Alveinus* и следует рассматриваться в том же семействе, что и *Alveinus*, Kelliellidae. Род *Lutetia* отличается строением связочной полоски и положением лигамента, и поэтому должен быть перемещен в семейство Lutetiidae Жгенти, 1976. Для *Spaniodontella gentilis* (Eichwald, 1851) и родственных видов, описанных из той же области, вводится новый род *Zhgentiana*, который до получения дополнительной информации о положении лигамента помещен в семейство Lutetiidae.

Introduction

The small bivalve species *Spaniodon nitidus* Reuss, 1867 (Fig. 1), originally described from Miocene (Middle Badenian, Wieliczian) salt deposits of Wieliczka in Poland, is also reported as a not uncommon occurrence in Oligocene and Miocene sediments of the North Sea Basin. The first observation for this basin, just a few years after the introduction of the species, was recorded by Wibel & Gottsche (1876, p. 104) from Langenfelde (Hamburg, Germany) and from the so-called 'Holsteiner Gestein' thereby referring to occurrences in the Vienna Basin Miocene as well. Three years later, Wiechmann (1879, p. 3) recorded *Spaniodon* for the first time from erratic boulders of Oligocene (Chattian) age, of the so-called 'Sternberger Gestein'.

The many different opinions, concepts and interpretations concerning this species and its genus assignment were reason for us to have a critical look at the literature of the foregoing 150 years and conclude on its correct name and systematic position.

History of *Spaniodon-Spaniodontella* and its type species

Already in 1865, Stur, based on specimens collected in Holubica from the Late Badenian deposits of the Volhynian-Podolian region in Ukraine, refers on page 280 to 'ein kaum eine halbe Linie im Durchmesser messender Zweischaler, den Herr Letocha zwischen Circe und Lutecia stellt' [a bivalve with a diameter of just under a half line (= about 1,1 mm) which Mr Letocha places between *Circe* and *Lutecia*].

Reuss (1867, p. 135) introduced a new, monotypic genus and new species, as *Spaniodon nitidus*, from Miocene (Middle Badenian. Wieliczian) salt deposits near Wieliczka in Poland, including in his description the minute bivalves already reported in Stur (1865). Reuss, however, was not aware of the fact that the name *Spaniodon* was preoccupied for a fossil fish (Clupeidae) by Pictet (1850, p. 33). Initially this went unnoticed, and the species was repeatedly cited with the name *Spaniodon nitidus*.

It took 35 years after its introduction before a replacement name *Spaniodontella* was designated by Andrussow¹ (in Goloubiatnikow, 1902). In this paper (in Russian) a rather hidden sentence on p. 210, based on an unpublished manuscript of Andrussow, reads: 'Между темъ ранѣе Реусса Пикте далъ это названіе для одной мѣловой рыбы; поэтому Н.И. Андрусовъ предлагаетъ новое названіе для *Spaniodon* – *Spaniodontella*'. Elena A. Jagt-Yazykova kindly translated this as 'Meanwhile, earlier than Reuss, Pictet gave this name to a Cretaceous fish; that is why N.I. Andrussow proposed a new name for *Spaniodon* – *Spaniodontella*'. This makes it clear that the name *Spaniodontella* Andrussow in Goloubiatnikow, 1902 is a replacement name (*nomen novum*) for *Spanio-*

¹ For transcription of Cyrillic texts we apply the 'Modified Library of Congress'-system' (<http://www.mml.cam.ac.uk/slavonic/courses/ugrad/transonline-1.pdf>), except for authors' names that also occur in transcribed form in publications, usually in abstracts. For instance, the name Андрусов would be 'Andrusov' according to the mentioned ML system, but is spelled 'Andrussow' by the author himself in various papers. The name Голубятников is given as Goloubiatnikow in the French summary of his 1902 paper (p. 228). We use the preference of authors.

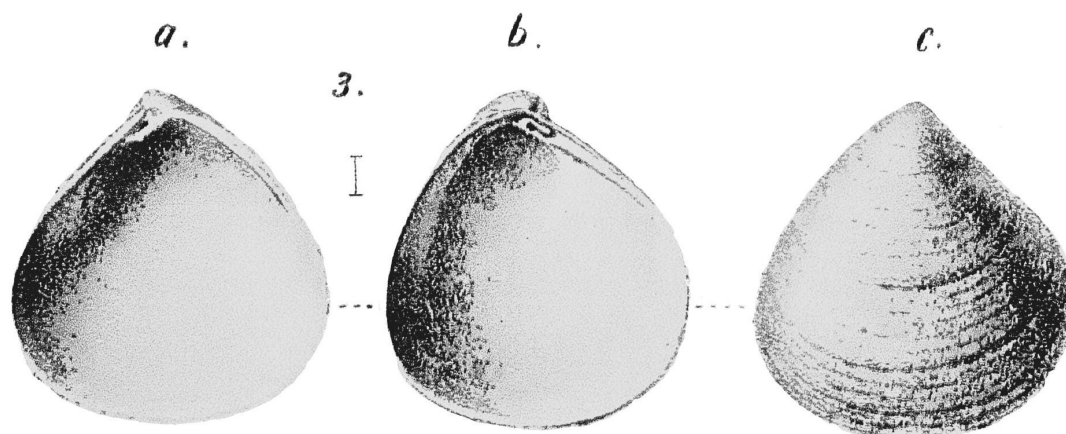


Figure 1. Original illustrations of *Spaniodon nitidus* Reuss (1867, pl. 8, fig. 3a-c), indicated height of the shell: 3 mm. Wieliczka (Poland), Badenian (Middle Miocene); 3a and c: right valve, 3b: left valve.

don Reuss, 1867 non Pictet, 1850. In Nomenclator Zoologicus (Neave, 1939-1996) the publication date is incorrectly stated to be 1912. In the same year Andrussov (1902, pp. 20, 116, 119) himself was still using the names *Spaniodon* and ‘*Spaniodon*-Schichten’.

ICZN art. 67.8 (typification of replacement name) rules that both a preoccupied name and its replacement name per definition have the same type species. Almost all subsequent authors, however, as for instance Friedberg (1934, p. 129, footnote), Davidaschvili (1934, p. 28), Merklin (1950, pp. 69-70), Korobkov (1954, p. 94); Glibert & van de Poel (1966, p. 22) ignored the fact that consequently both *Spaniodon* Reuss and *Spaniodontella* Andrussov in Goloubiatnikow have the same type species, namely *Spaniodon nitidus* Reuss, 1867.

The correct type species of *Spaniodontella* was finally given by Keen in Moore (1969, p. N653), but even after that time authors like Zhgenti (1976a, p. 23) and, based on Merklin (1950), Studencka (1986, pp. 88-89), Studencka *et al.* (1998, p. 411) and Neveeskaya *et al.* (2013, p. 411) continued, incorrectly, to consider *Astarte pulchella* Baily (1858, p. 146, pl. 9, fig. 10a-c), described from the Miocene of the Crimea peninsula, as the type species of *Spaniodontella*. Furthermore, as an extra complication, the name *Astarte pulchella* is preoccupied by *Astarte pulchella* Jonas in Philippi (1845, p. 60, pl. *Astarte* 1, fig. 12; Recent, Greenland) = *Venus montagui* Dillwyn (1817, p. 167) = replacement name for *Venus compressa* Montagu (1808, p. 43, pl. 26, fig. 1) non Linné (1771, p. 546). Erroneously, Hoernes (1859, p. 115) included *Astarte pulchella* Baily in the synonyms of ‘*Tapes gregaria* Partsch’, now treated as *Polititapes tricuspis* (Eichwald, 1829, p. 282, pl. 4, fig. 15) (see Neubauer *et al.*, 2013), which is a venerid species with a clear pallial sinus, absent in Baily’s species.

Accepting another type species for *Spaniodontella* leads to erroneous conclusions, as is repeatedly demonstrated in later literature, e.g. by Friedberg (1933b, p. 235), who wrote: ‘*Es ist auch nicht richtig, dass die Autoren immer von Spaniodontella nitida Reuss sprechen, statt von Spaniodon nitidus, denn Spaniodontella ist eine ganz andere Gattung als der von Reuss beschriebene Spaniodon*’ [= It is also incorrect that authors always refer to *Spaniodontella nitida*, instead of *Spaniodon nitidus*, as *Spaniodontella* is a completely different genus than *Spaniodon*, as described by Reuss]. This is further made clear by Friedberg (1934, p. 129, footnote) where the author declares to accept ‘*Sp. (Venus) gentilis* Eichw.’ as type species of *Spaniodontella*.

In the same paper referred to above Goloubiatnikow (1902) included, apart from *S. nitidus* Reuss, another eleven species, indicated either as *Spaniodon* or as *Spaniodontella*. From the various literature sources it is evident that species considered to belong to *Spaniodontella* developed especially in the Ponto-Caspian area during the Karaganian (Middle Miocene)², probably under the influence of a reduced salinity, into several species that were com-

monly applied in biostratigraphy and led to the indication ‘*Spaniodon*-Schichten’ (e.g. Toula, 1890) or ‘*Spaniodontella*-Beds’ in various later works, and ‘*Spaniodontella gentilis* Biozone’ (Popov *et al.*, 2004).

Ossipov (1932) gave descriptions and illustrations of several of these species from the Karaganian deposits, thereby validating a number of Andrussov’s *nomina nuda*: *Spaniodontella pulchella* (Baily), *S. tapesoides* ‘Andrus.’, *S. umbonata* ‘Andrus.’, *S. opisthodon* ‘Andrus.’, *S. opisthodon* ‘Andrus.’ var. *squamigera* ‘Andrus.’, *S. gentilis* Eichw. [sic] and *S. andrussovi* Toula [sic].

An overview of all these species, however, soon reveals characteristics, especially in hinge structures and size, that can hardly be included in one and the same genus. This was first realised by Davidaschvili (1934), who summarised his observations on these bivalves in a paper entirely devoted to the development of *Spaniodontella*. He concluded that *Spaniodontella* developed from the genus *Lutetia* into an early ‘primitive’ group (*S. nitida* in a wide sense) during the Chokrakian (Middle Miocene) of the Ponto-Caspian region, whereas during the Karaganian (‘*Spaniodontella*-Beds’) and Konkian several species exist with larger shells and far more strongly developed cardinal teeth. The author also compared the North American Eocene genus *Alveinus*, but concluded that, although related to *Lutetia*, it represents a separate lineage.

The same author summarised his ideas (Davidaschvili, 1937, p. 590) by writing, when discussing *Oncophora*: ‘*The case is largely similar to that of Spaniodontella, whose ancestors have been long totally unknown and whose phylogeny may now be in my opinion traced through the Burdigalian ‘Lutetia’ burdigalensis group and Oligocene lutetiae up to the Lutetia parisiensis group of the Eocene. In this case also the original marine forms are much smaller than the brackish water forms of the Karaganian (or Spaniodon) horizon.*’

Following Davidaschvili’s observations Merklin (1950, p. 69) formalised the subdivision of *Spaniodontella* by introducing the taxon *Davidaschvilia* (type species by original designation *Spaniodontella intermedia* ‘Andrussov’; for illustration see Fig 2 herein, and Merklin & Neveeskaya, 1955, pl. 23, figs 12-15), but considered it a subgenus of *Lutetia*. Apart from the type species Merklin included *Spaniodontella nitida* and *S. sokolovi* Sinzov, 1903 in his new subgenus. These are all species belonging to Davidaschvili’s ‘primitive’ group’, characterised by small size and much weaker dentition of the hinge than the larger sized species from the Karaganian, for which Merklin retained the genus *Spaniodontella* with *S. pulchella* as type species. Surprisingly, Merklin & Neveeskaja (1955, p. 84) neither mentioned the genus *Lutetia* nor *Davidaschvilia* and included the type species of the latter again in *Spaniodontella*, just stating in a footnote that it is very close to *Lutetia*.

² For stratigraphical position of the eastern Paratethys regional stages (Tarkhanian, Chokrakian, Karaganian and/or Konkian) from which *Spaniodon* eq. *Spaniodontella* was recorded in literature see Popov *et al.* (2004).

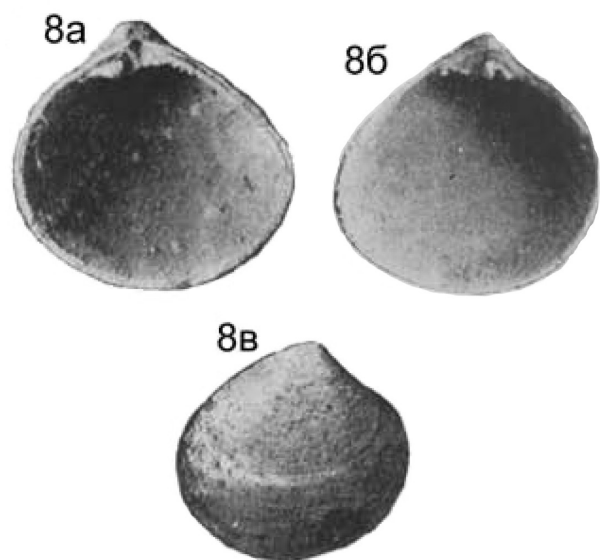


Figure 2. Type species of *Davidaschvilia* Merklin, 1950 (= *Spaniodontella intermedia* Andrussov in Bajarunas, 1910). Illustration from Neveeskaya *et al.* (2013, figs 148-8. Indicated shell height 3 mm; 8a and 8B: right valves, 8b: left valve.

Bodylevsky *et al.* (1960, p. 118) listed both *Lutetia* and *Spaniodontella* for the Ponto-Caspian Miocene. As examples they illustrated *Lutetia intermedia* (pl. 26, figs 12-14) and *Spaniodontella gentilis* Eichwald (figs 167-168; pl. 26, figs 15-17). The latter taxon is considered a synonym of *Astarte pulchella* by some authors. They mentioned the genus *Alveinus* as related, but not occurring in the U.S.S.R.

Glibert & van de Poel (1966, p. 22) were the first, without any discussion, to formally apply the genus *Alveinus* Conrad, 1865 for European species, and included in that genus *Spaniodon nitidus*, with *Lutetia girondica* Cossman & Peyrot, 1912 as a synonym, and *Kellyella (Lutetia) rotunda* Sorgenfrei, 1958. In the same genus *Alveinus* these authors included both *Davidaschvilia* and *Spaniodontella* as subgenera. Contrary to earlier authors they did not consider *Venus gentilis* Eichwald to be a synonym of *Astarte pulchella* Baily.

Zelinskaya *et al.* (1968, p. 186) considered *Spaniodon* a synonym of *Lutetia*, listing *L. intermedia* (Andrussov) Bajarunas, 1910 (pl. 51, figs 14, 15), *L. nitida* (Reuss, 1867) and *L. sokolovi* (Sinzov, 1903). Further these authors recognised the genus *Spaniodontella* 'Andrussov, 1902', with type species '*Venus gentilis* Eichwald, 1851 (*Astarte pulchella* Baily, 1858)', in which they list the species *S. andrussovi* (Toula, 1890); *S. gentilis* (Eichwald, 1851) (pl. 51, figs 16, 17) (with *Astarte pulchella*, *Cyrena barbotii* Stuckenberg, 1873, *S. major* Andrussov, 1885 and *S. opisthodon* [sic] Andrussov in Ossipov, 1932 as synonyms), *S. tapesoides* Andrussov in Ossipov, 1932 and *S. umbonata* Andrussov in Ossipov, 1932.

In 1969 Keen *in Moore* (p. N653) assigned *Spaniodon-*

tella as a subgenus to *Lutetia* and treated *Davidaschvilia* as a synonym of the former. As discussed below we do not agree with these points of view.

Zhgenti (1976a) followed Merklin in considering *Davidaschvilia* a subgenus of *Lutetia*, including the same three species *Spaniodontella intermedia*, *S. nitida* and *S. sokolovi*, and adding *Spaniodontella minima* Bagdasarjan & Zhgenti, 1962 as a subspecies of *S. intermedia*.

We have no specimens of *Davidaschvilia intermedia* available, but based on illustrations in the literature and on the hinge formula as given by Studencka (1986, p. 89) we note clear differences in the hinge construction of *Lutetia* and the *Spaniodontella* type species *S. nitida* (compare Fig. 2 with Figs 1 and 4a-b).

In the *Davidaschvilia intermedia* left valve tooth 2 is clearly subdivided in an anterior and posterior branch, together forming a v-shape, with a short anterior branch. A posterior lateral is absent or weakly developed, an anterior lateral is lacking or coincides with the dorsal margin. In the right valve tooth 1 is much shorter and tubercular. Zhgenti (1976a, p. 18) described the ligament for the type species *D. intermedia* as internal: 'ямка для внутренней связки' (= fossa for internal ligament) with which we agree, considering the various available illustrations. We conclude on a rather close relationship of *Spaniodontella*, as typified by *S. nitida*, and the *Davidaschvilia* type species, both differing basically from *Lutetia* by the position of the ligament. This also means that we do not consider either *Spaniodontella* or *Davidaschvilia* to be a subgenus of *Lutetia*, as done by Keen *in Moore* (1969). We consider the differences in size and hinge structure of the type species of *Davidaschvilia* to be large enough to retain it as a separate genus in Kelliellidae, but realise that a more detailed study of actual specimens (which we do not have available) and their variability might result in a different conclusion, such as subgenus status or even in synonymy of both genera.

Zhgenti (1976a) accepted the genus *Spaniodontella* with (incorrect) type species *S. pulchella*, considering '*Cyrena barbotii*' [sic] Stuckenberg, 1873 and *Spaniodon major* Andrussov, 1885, as synonyms. Further species included in *Spaniodontella* by her are *S. umbonata* Andrussov, 1931, *S. tapesoides* Andrussov, 1932, *S. opisthodon* Andrussov, 1932 and *S. ersaconensis* Zhgenti, 1976a. All these species differ from the *Spaniodontella* type species *S. nitida*, as well as from *Davidaschvilia*, by different hinge structures including massive cardinal teeth and shell heights to over 10 mm (see also the various illustrations in Zhgenti, 1976a, pls 1-24).

For this latter group of species (= *Spaniodontella sensu* Merklin, 1950 and Zhgenti, 1976a *non* Andrussov in Goloubiatnikow, 1902) no valid genus is available. Below we introduce *Zhgentiana* gen. nov., with type species *Venus gentilis* Eichwald, 1851.

For still other forms that used to be included in *Spaniodontella*, Zhgenti (1961, p. 43; redescribed 1976a, p. 33) had already introduced the genus *Savanella* with type species *Spaniodon andrussovi* Toula (1890, p. 383, pl. 7,

fig. 6) (misspelled *andrussovi*) from the Karaganian deposits of the Varna vicinity in Bulgaria, and in this context introduced the subspecies *Savanella andrussovi* [sic] *laevis* Zhgenti, 1976a and *S. andrussovi* [sic] *elongata* Zhgenti, 1976a.

In a little known paper Zhgenti (1976b) reconsidered her opinion on *Spaniodontella sokolovi* and transferred that species to the genus *Alveinus*. Apparently she made this decision independently, not referring to Glibert & van de Poel (1966), but only to Dall (1900) and Harris (1920). This also explains her erroneous idea that the genus *Alveinus* Conrad was 'hitherto unknown in Europe'. In the same genus she also included *Spaniodon nitidus* and correctly declared *Spaniodon* Reuss and *Alveinus* Conrad to be synonyms. We do indeed agree with this point of view, as discussed below in the paragraph 'Genus assignment'.

Additional important notes on this group of species were given by Studencka (1986, p. 89). She also criticised Keen's decision concerning the *Davidaschvilia* taxon, but arrived at the erroneous conclusion that '.... *S. nitidus* Reuss cannot be treated as the type species of *Spaniodontella* and hence, it cannot be placed into the genus *Lutetia*'. The first part of that statement does not make sense of course, as *S. nitida* is the type species per definition. Its possible assignment to *Lutetia* will be discussed below. Also she agrees with Glibert & van de Poel (1966) that the hinge structure of *S. nitida* 'is entirely consistent' with that of the genus *Alveinus*.

Studencka *et al.* (1998, p. 319) in their discussion of the species indicated as *Alveinus nitidus* (Reuss, 1867) repeated Studencka's (1986) view concerning *Davidaschvilia*, correctly stating that Reuss' *nitidus* cannot be treated as the type species, which in fact is an 'open door' statement, as type species of that genus is *Spaniodontella intermedia* by original designation of Merklin, 1950. They do not, however, comment on Studencka's (1986) opinion that *S. nitida* also cannot be the type species of *Spaniodontella*, apparently so as they now include that species in the genus *Alveinus*. In their distribution table (pp. 306-307) they refer to the occurrence of that species in the Badenian (Langhian/early Serravallian) of the Central Paratethys and in the Konkian of the Eastern Paratethys.

In their voluminous book on the phanerozoic bivalves of Russia and surrounding countries Nevevskaya *et al.* (2013, pp. 409-411) discussed the same group of taxa. These authors included both *Davidaschvilia* and *Spaniodontella* as subgenera of *Lutetia*. In a footnote on p. 411 they discuss the validity of the name *Spaniodontella*, arriving at the conclusion that Goloubiatnikow (1902) is the correct author. However, they still considered '*Astarte pulchella* Baily, 1858 (= *Venus gentilis* Eichwald, 1850 [sic])' as the type species of *Spaniodontella*. They do not refer to any Russian species of *Alveinus*, but give its distribution as: Eocene-Miocene Europe, North America. Middle Miocene Ukraine, Turkmenistan. In Russia: Middle Miocene of Central (Konka) Ciscaucasia. Recent: Japan Sea, S. Kuril Islands.

Genus assignment

Apart from *Spaniodon* and/or *Spaniodontella* the species discussed herein, *Spaniodon nitidus*, has been included, in the course of time, in various other (sub)genera, such as *Lutetia*, *Davidaschvilia*, *Kellyella* (= *Kelliella*) or *Alveinus*. We analyse these assignments below.

Lutetia

The genus *Lutetia* Deshayes (1860, p. 787, type species *L. parisiensis* Deshayes, 1860, p. 789, pl. 16bis, figs 34-37, by subsequent designation of Stoliczka (1871, p. 279) was introduced for two species, *L. parisiensis* and *L. umbonata* Deshayes (1860, p. 789, pl. 59, figs 12-14) from the Paris Basin Eocene. Deshayes furthermore referred to unnamed species occurring 'dans le bassin de la Gironde ou d'autres localités du même âge' (= in the Gironde Basin or other localities of the same age). Fischer (1887, p. 1024, text-fig. 771) gave clear illustrations of the hinge of the type species (copied herein as Fig. 3c-d).

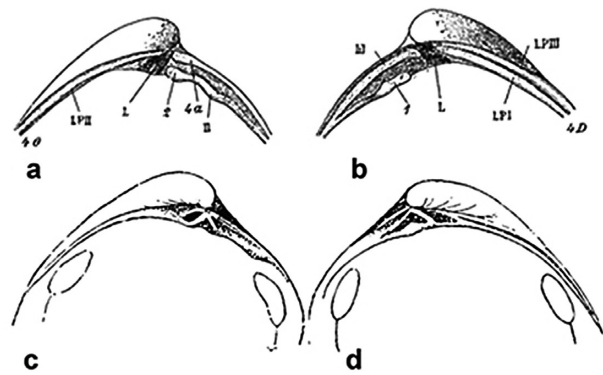


Figure 3. Hinges of '*Lutetia*', later named *Lutetia girondica* by Cossmann & Peyrot, 1912 (a-b: after Bernard, 1895, fig. 21), and *Lutetia parisiensis* (c-d; after Fischer, 1887, fig. 771).

Also Bernard (1895, p. 139, text-fig. 21) gave a description and several illustrations of the *Lutetia* hinge (e.g. Fig. 3a-b herein), inclusive of several ontogenetic developmental stages. But contrary to Fischer (1887) he unfortunately based his observations not on the type species, but on material from the Early Miocene (Burdigalian) of Dax (Aquitaine Basin, France).

The species from Dax studied by Bernard was later described as *Lutetia girondica* Cossmann & Peyrot (1912, p. 229, pl. 26, figs 16-19) (a name based on an unpublished collection name of Benoist). The same authors also examined specimens of '*Spaniodon nitidum*' [sic] ('*specimens authentiques*') and, based on Bernard's description, concluded on the synonymy of the genera *Lutetia* Deshayes and *Spaniodon* Reuss ('*ce Genre est absolument identique à Lutetia*'). Therefore they applied the genus *Lutetia* for their Miocene material, as it has priority over *Spaniodon*. But they furthermore concluded that later

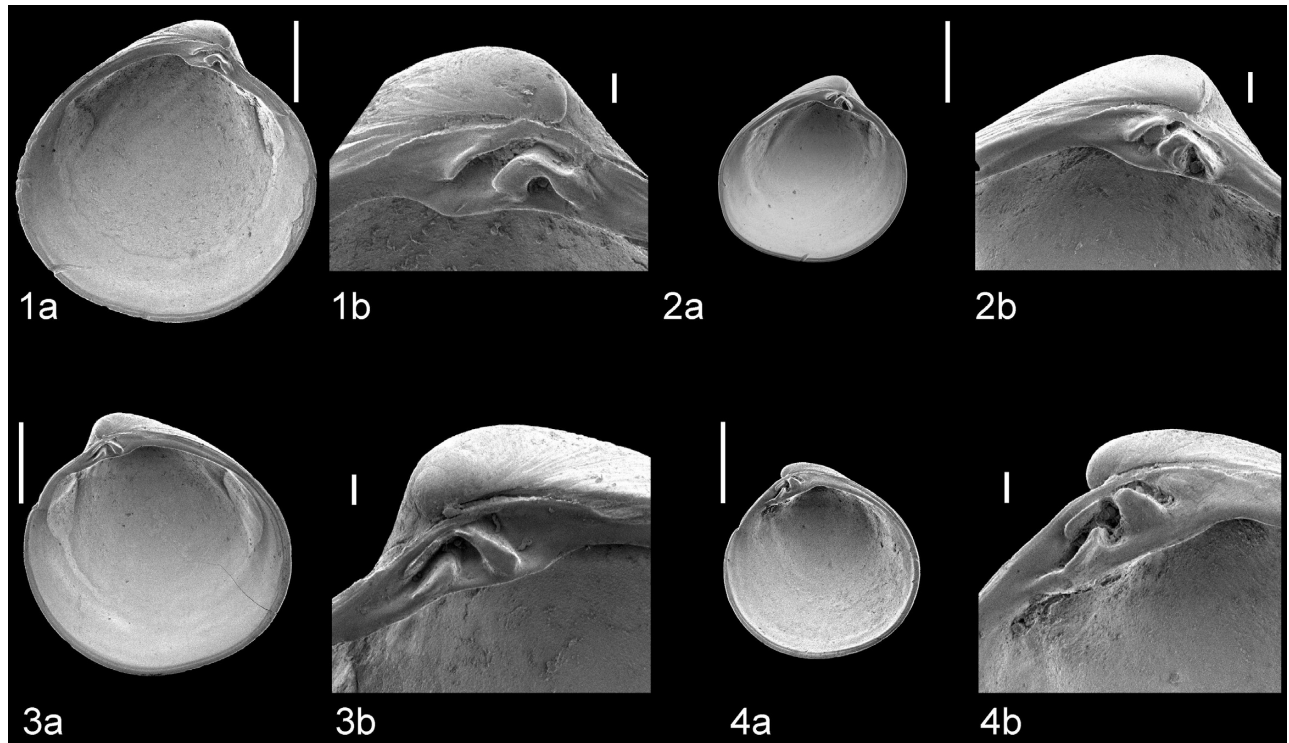


Figure 4a. *Lutetia parisiensis* Deshayes, 1860, from Daméry, Paris Basin, France; 1-2: left valves, 3-4: right valves. RGM.220489a. SEM images made by Renate Helwerda. Bar represents 1 mm for complete valves and 100 μm for hinges.

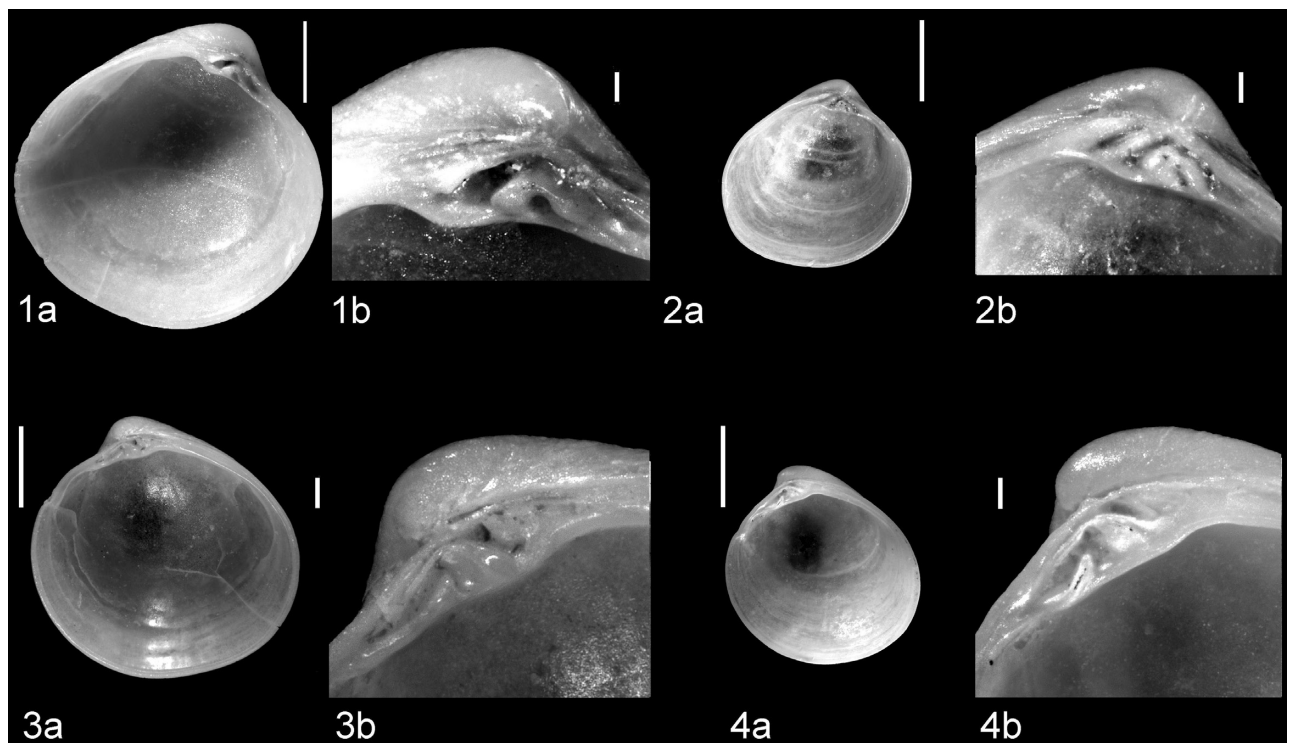


Figure 4b. Same specimens as in Fig. 4a, in digital stacked photography, by Petra Sonius and Eduard de Vogel. Bar represents 1 mm for complete valves and 100 μm for hinges.

Miocene species indicated with the genus name *Spaniodontella* differ greatly in hinge construction from ‘*Lutetia*’, illustrating the hinge of ‘*Spaniodontella Barboti* [sic] Andrzejowski.’ in their text figure 118 as an example.

Although accepted by many later authors (e.g. Friedberg, 1934, p. 129; Anderson, 1964, p. 165; Nordsieck, 1972, p. 35; Jakubowski & Musiał, 1977, 1979; Schultz, 2005, p. 833) Cossmann & Peyrot’s conclusion was erroneous of course, as the ‘*Lutetia*’ studied by Bernard was not the type species, but the species later described as *L. girondica*, which is generally (e.g., Kautsky, 1939, p. 637; Glibert & van de Poel, 1966, p. 22; Anderson, 1964, p. 165; Schultz, 2005, p. 833; Cahuzac *et al.* 2012, p. 392) considered to be a junior synonym of *Spaniodon nitidus*. So in fact Cossmann & Peyrot compared different specimens of the same species: no wonder they found them to be identical.

On Cossmann & Peyrot’s authority, however, this erroneous conclusion has greatly influenced later nomenclature, almost until the present day (see the list of synonyms, below), in spite of the fact that the differences between Bernard’s ‘*Lutetia*’ and the Paris Basin species were already convincingly indicated by Harris (1920, p. 5).

These differences in hinge structure were already evident from a comparison of illustrations in Fischer (1887, fig. 771) and those of Bernard (reproduced herein Fig. 3). We illustrate (Fig 5a-b) specimens of *Lutetia parisiensis* from the Lutetian of the Paris Basin, as well as type specimens of *S. nitida* from Wieliczka housed in the Vienna museum (Fig. 10) and several specimens (Pls 1-2) from other locations, among which two Polish localities, Nawodzice and Korytnica, from Dax, the type locality of ‘*Lutetia girondica*’, and from one locality (Winterswijk, Miste) in the North Sea Basin, demonstrating these differences once more. The two genera cannot be considered to be synonyms. This is furthermore demonstrated by the fact that in *Lutetia* the ligament is external (Glibert & van de Poel, 1966, p. 20; Keen *in* Moore, 1969, p. N653; R. Jansen, 1979, p. 120; Welle, 1993, p. 102), which makes a close relationship of these genera quite unlikely. Adding to the confusion, Kautsky (1939, p. 587) wrote that the ligament in *Lutetia* is internal, but his opinion seems to be based on Bernard’s 1895 observations, and therefore not on *Lutetia* but on *Spaniodontella*.

Davidaschvili (1934, pp. 28-29, abstract) differed also of opinion with Cossmann & Peyrot and considered the Miocene occurrences of *Spaniodontella* from Poland and southern France, although closely related to *Lutetia*, to represent a ‘primitive’ group of the genus *Spaniodontella* that developed into several further species during the Miocene of the Ponto-Caspian region, in deposits commonly indicated as ‘*Spaniodon*- or *Spaniodontella*-Beds’ (compare e.g. Zhizhchenko, 1936, pp. 65-68; 1959, pp. 205-212).

Davidaschvilia

Merklin (1950, p. 69) agreed with Davidaschvili’s ideas and introduced *Davidaschvilia* as a subgenus of *Lute-*

tia for the ‘primitive’ group of *Spaniodon*, designating ‘*Lutetia intermedia* Andrus.’ as its type species. Korobkov (1954, pl. 10, figs 11-13) also used the combination *Lutetia (Davidaschvilia) nitida* and considered *Spaniodontella* a separate genus, incorrectly mentioning *Astarte pulchella* Bailly, 1858 as its type species. *Spaniodontella nitida* was included by Merklin in the genus *Davidaschvilia* but it fits better in the genus *Alveinus* by its smaller size and weakly developed cardinal teeth. Glibert & van de Poel (1966, p. 22) included *Davidaschvilia* as a subgenus in *Alveinus*, next to *Spaniodontella*, but Keen *in* Moore (1969, p. N653) considered *Davidaschvilia* a synonym of *Spaniodontella*. *Davidaschvilia* was still accepted as a subgenus of *Lutetia* by Radionova *et al.* (2011, p. 37) and Neveeskaya *et al.*, (2013, p. 411). Some authors also considered *Davidaschvilia* to be a subgenus of *Spaniodontella*, e.g. Görür *et al.*, (2000, p. 255), who used the combination *Spaniodontella (Davidaschvilia) intermedia*’ for occurrences on the Black Sea coast of Turkey. The spelling ‘*Davitaschvilia*’ is incorrect, based on straight transliteration of the name Давиташвили. In the original paper (Merklin, 1950) the name is spelled *Davidaschvilia*, agreeing with the spelling of the name on the bi-lingual title page of Davidaschvili’s 1934 publication, the transliteration used by the author himself is Davidaschvili (hence *Davidaschvilia*).

Kellyella (= *Kelliella*)

From the Miocene Arnum Formation in Denmark Sorgenfrei (1958, pp. 86-87) introduced two species, indicated as *Kellyella (Lutetia) rotunda* and *K. (L.) patera*, the first of which seems to be closely related or even identical with *Spaniodontella nitida*. The author himself already admitted that it is closely related to ‘*Lutetia girondica*’ and possibly represents juvenile stages of that species. The two taxa were synonymised with *S. nitida* by Anderson (1964, p. 165) and Wienrich (1999, p. 251) indeed, but Glibert & van de Poel (1966, p. 22) considered one of Sorgenfrei’s 1958 taxa (*rotunda*) to be a separate species referred to as *Alveinus (s.s.) rotundus*. We agree with Moths *et al.* (2010, p. 26) that Sorgenfrei’s *K. (L.) patera* is a juvenile representative of *Timoclea*. The spelling Kellyellidae is based on *Kellyella* Fischer, 1887, an unjustified emendation of *Kelliella* Sars (1870, p. 201). Interesting is furthermore that Studencka (1987) introduced the species *Kelliella barbara* from the Middle Miocene (Late Badenian) of Nawodzice (Poland), the same locality from where we illustrate (Pls 1-2) Reuss’s species. Although her illustrations of the hinge are difficult to interpret, differences compared to *S. nitida* are present, especially so in the left valve in which the 2a-tooth has a sigmoid shape.

Alveinus

Glibert & van de Poel (1966, p. 22) followed Harris (1920) and included *Spaniodon nitidus* in the genus *Alveinus*,

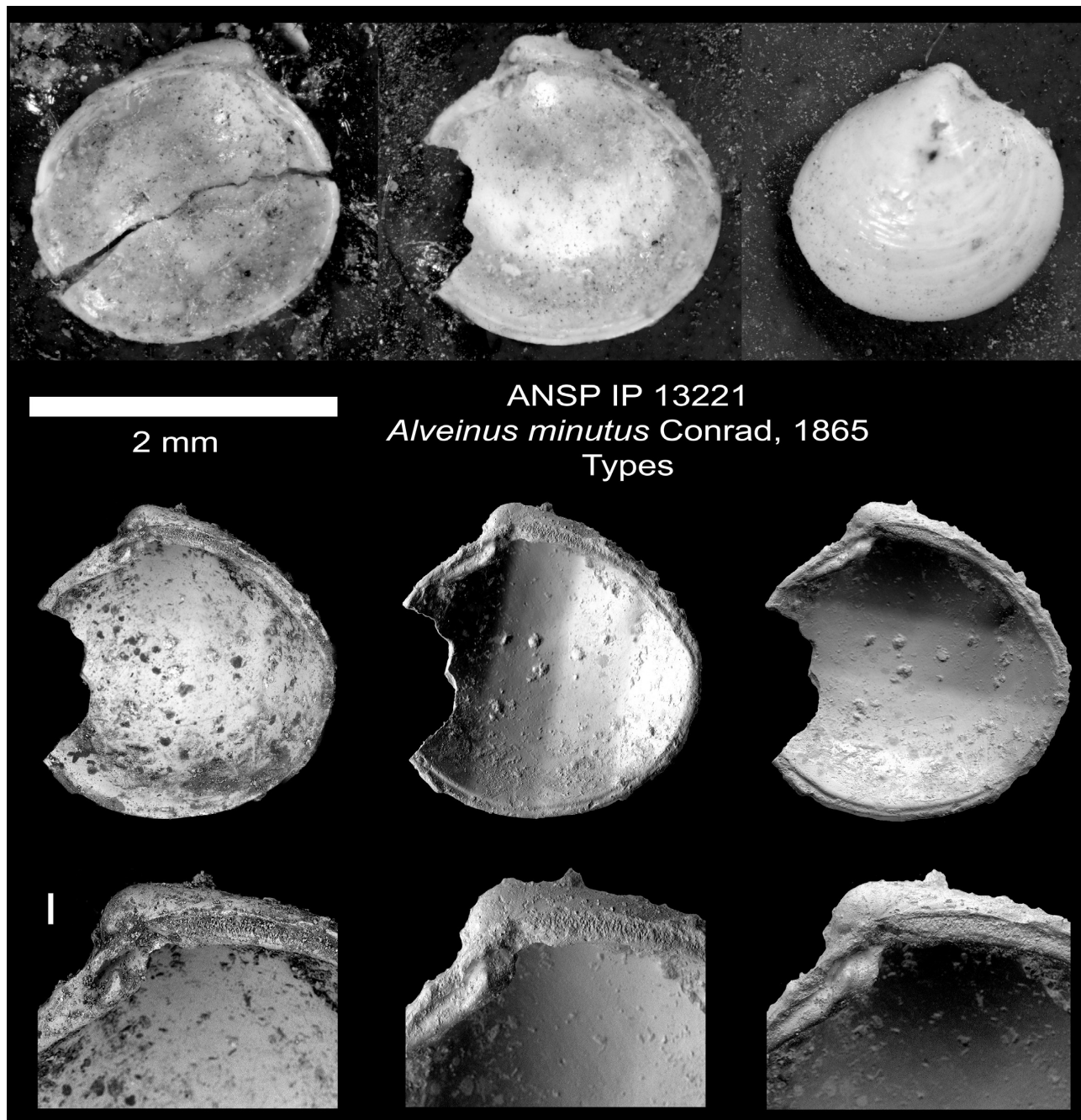


Figure 5. *Alveinus minutus* Conrad, 1865b. The three available syntypes glued on cardboard strip. Collection ANSP nr. 13221, from the Eocene of Enterprise, Mississippi (USA) as indicated by Conrad, but presumably from the Lower Jackson Group (late Eocene) of Garland's Creek in Clarke County, Miss., according to Dall (1900, p. 1166) and Palmer & Brann (1965, p. 27). Upper row: digital photographs; other figures SEM images of the middle specimen in three modes: normal (two sensors) and topographic (left sensor only/right sensor only). Images: courtesy of Paul Callomon (ANSP). Bar represents 100 μm for the hinges.

which they considered a senior synonym of *Spaniodon* Reuss, 1867 and even introduced a new family Alveinidae. This name, however, is not available because it was introduced without any description (Bouchet & Rocroi (2010, p. 16). Independently, Zhgenti (1976b) reached the same conclusion concerning the synonymy of these two genera.

The monotypic genus *Alveinus* Conrad (1865b, p. 138,

pl. 10, fig. 2) was described from late Eocene deposits in Mississippi, USA. In his 'Catalogue' (Conrad, 1865a) a taxon was listed as *Alveinus parva* (p. 10), but in his description of species (Conrad, 1865b) the species is named *Alveinus minuta*. Although the genus name is masculine, Conrad applied a feminine form for both names. The name *A. parva*, as occurring in the 'Catalogue', is rectified in an additional 'Corrections and additions ...' on the

final (unnumbered) pages of the third issue of the 1865 volume of the American Journal of Conchology, but the incorrect spelling of the name *A. minuta* remained unnoticed and was only emended in 1900 by Dall. Conrad's description is very insufficient and the accompanying illustration is (at least in our digital copy of the paper) no more than a small grey spot on the plate and only shows the exterior of a right valve; the interior and hinge are not figured. Three syntypic specimens are housed in the Academy of Natural Sciences of Philadelphia, and Dr Paul Callomon of that institute was so kind to send us several images (Fig. 5), that unfortunately demonstrate their present poor condition, the left valve broken and its hinge covered in glue.

Cossmann (1893, p. 13), after comparing the hinge structure of *Alveinus* with that of *Lutetia*, concluded on their identity and considered *Alveinus* a junior synonym of *Lutetia* Deshayes, 1860.

Alveinus was not discussed by Fischer (1887) or by Bernard (1895), but Dall (1900, p. 1166) criticised Conrad's work in unmistakable wording ('slipshod methods, or want of method'), also pointing to a probable erroneous location (see caption of Fig. 5) of the type sample. He gave clear descriptions of especially the hinges of *Lutetia* and *Alveinus* and observed sufficient differences to keep the two apart. The same author (p. 1175), however, considered *Spaniodon nitidus* to be closely related to the genus *Aligena* Lea (1843, p. 163, type species *A. striata* Lea, 1843, by subsequent designation of Dall, 1900, p. 1175). Harris (1920, p. 110 ff, text-fig. 5; reproduced as Fig. 6 herein; pl. 17, figs 11-13) agreed with Dall and clearly differentiated the two genera *Alveinus* and *Lutetia*.

Keen in Moore (1969, p. N653, fig. E130-11a-c, copied from Harris, 1920) listed *Alveinus* and *Lutetia* as separate genera, but treated *Spaniodontella* as a subgenus of *Lutetia*. The latter concept was followed e.g. by Jakubowski & Musiał (1977, 1979), Oliver & Zuschin (2001, p. 6), Nevesskaya et al., (2006, p. 347) and Nevesskaya et al. (2013, p. 411).

Studencka (1986, p. 88), Studencka et al. (1998, pp. 306, 307, 319), Popa (2001, p. 63), Moreno et al. (2003, p.168), Zuschin et al. (2007, p. 291) and Studencka & Jasionowski (2011, p. 97) followed Glibert & van de Poel in applying the genus *Alveinus* (misspelled as *Alvenius* by Studencka, 1986, p. 89 and as *Alveidus* by Moreno et

al., 2003, p. 168) for the Miocene species. Keen in Moore (1969, p. N653) considered *Alveinus* a separate genus in the Kelliellidae, next to *Lutetia*, distributed in the Eocene-Miocene of Europe and northern America, but did not acknowledge Glibert & van de Poel's 1966 family Alveinidae. The genus *Alveinus* is accepted in WoRMS (Sartori, 2015) for two Recent species and was also assigned therein to the Kelliellidae. In spite of being used already for European Miocene species ever since 1966 western European authors in general continued using the genera *Spaniodontella* or *Lutetia*, see the list of synonyms for *Alveinus nitidus* below.

Family assignment

There is hardly any agreement among authors to which family *Spaniodontella* or *Alveinus* should be assigned:

Alveinidae: Glibert & van de Poel (1966) (*nomen nudum*). Erycinidae: Reuss (1867); Stoliczka (1871); Fischer (1887). Erycinidae, Chlamydoconchinae: Thiele (1934, p. 875), where *Spaniodon* Reuss, 1867, is considered (based on Dall, 1900, see above?) a synonym of *Aligena* Lea (1845, p. 163, in the family Mactridae), nowadays (Bouchet, 2015) assigned to the family Lasaeidae.

Kelliellidae: Vokes (1967); Keen in Moore (1969); Jakubowski & Musiał (1977); R. Janssen (1979); Jakubowski & Musiał (1979); Vokes (1980); A.W. Janssen (1984); Studencka (1986); Dulai (1996); Studencka et al. (1998); Moreno et al. (2003); Schultz (2005); Moths et al. (2010).

Kellyellidae: Bernard (1895); Cossmann & Peyrot (1912); Friedberg (1934), Zhizhchenko (1936); Friedberg (1938); Korobkov (1954); Sorgenfrei (1958); Zhizhchenko (1959); Anderson, (1959).

Lutetiidae: Davidaschvili (1970); Zhgenti (1976a, b); Nevesskaya et al. (2013)

Neoleptonidae: Kautsky (1939); Csepregy Meznerics (1950); Merklin & Nevesskaya (1955); Anderson (1964); Zelinskaya et al. (1968); Jakubowski (1972).

We agree with most authors that *Alveinus* fits best in Kelliellidae. In Fig. 7 we present SEM images of the type species of *Kelliella*, which is *K. abyssicola* Sars, 1870 (original designation), from the Trondheim Fjord, which is in its type area (= Norwegian coast). *Kelliella abyss-*

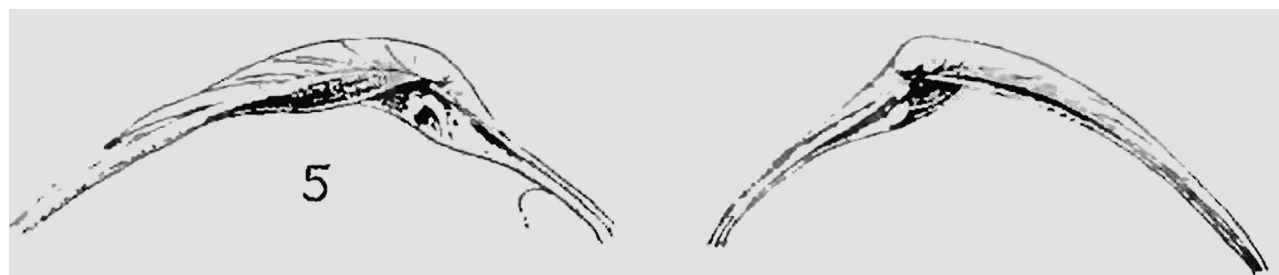


Figure 6. Hinges of *Alveinus minutus* Conrad, 1865b, from the Jackson Group, Jackson, Louisiana (USA). Enlarged after Harris (1920, fig. 5), left and right valves.

sicola is a junior synonym of *K. miliaris* Philippi, 1844 as discussed by R. Janssen & Krylova (2012, p. 91). SEM images in the last mentioned paper indeed resemble our Norwegian shells closely, but here we prefer to illustrate specimens from the original type area. The hinge of *K. miliaris* differs from *Alveinus* especially by the sigmoid shape of the 2a-tooth. Although the ligament in *Kelliella* is external and internal in *Alveinus* both agree with the family diagnosis (Keen in Moore, 1969, p. N651) and we find in the general arrangement of the hinges sufficient reason to maintain *Alveinus* in the Kelliellidae. We consider Alveinidae an (invalid) junior synonym of Kelliellidae.

The (real!) genus *Lutetia*, however, displays a very different hinge structure. As discussed in a convincing way by

Dall (1900) and Harris (1920) we find these differences of such magnitude that we cannot maintain *Lutetia* in the Kelliellidae.

Davidaschvili (1970, p. 25) suggested a separate family ‘Лютетии’ (Lutetiids) for the genera *Lutetia*, *Spaniodontella* and *Davidaschvilia*, the vernacular name of which was validated as Lutetiidae by Zhgenti (1976a, p. 17). We suggest maintaining *Davidaschvilia* Merklin, 1950 as an independent genus in the Kelliellidae as well. This might be different for the group of species here indicated as ‘*Spaniodontella sensu* Merklin, 1950 - Zhgenti, 1976a non Andrussov in Goloubiatnikow, 1902’, for which we introduce (see below) a new genus *Zhgentiana*. We have no material available to obtain a fair impression of the position of the ligament, so possibly they should be included in Lutetiidae.

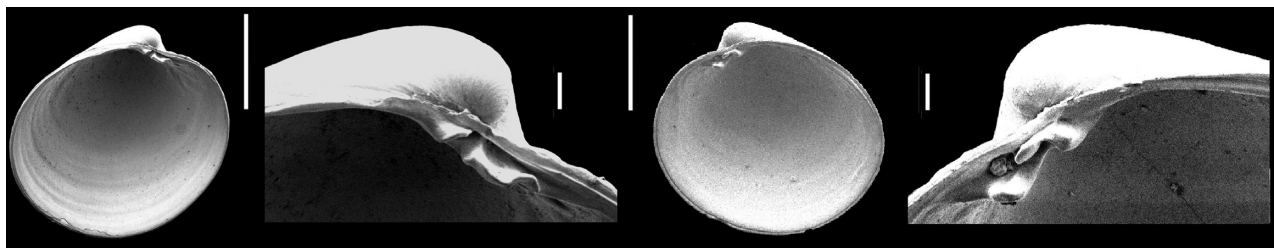


Figure 7. *Kelliella miliaris* Philippi, 1844, Norway, Trondheim Fjord, depth 150 m, July 1974, ex coll. B. Zoder (Recent), RMNH. MOL.338213. Bar represents 1 mm for valves, 100 μ m for the hinges. SEM images by Renate Helwerda.

Conclusions

1. *Spaniodontella* Andrussov in Goloubiatnikow, 1902 is a replacement name for *Spaniodon* Reuss, 1867 non Pictet, 1850.
2. Type species of *Spaniodontella* is *Spaniodon nitidus* Reuss, 1867 (typification of replacement name), ICZN art. 67.8.
3. *Alveinus* Conrad, 1865 is a senior subjective synonym of *Spaniodontella*. Its type species is *A. minutus* Conrad, 1865 by subsequent designation of Stoliczka, 1871.
4. The genus *Alveinus* belongs to the Kelliellidae.
5. The genus *Lutetia* Deshayes, 1860 should not be arranged in Kelliellidae, but in a separate family Lutetiidae Zhgenti, 1976a.
6. *Davidaschvilia*, for the time being, is considered a separate genus in Kelliellidae.
7. Bernard's (1895) description of ‘*Lutetia*’ does not discuss a species of that genus, but contrarily refers to the *Spaniodontella* type species, *S. nitida*.
8. No valid genus name is available for ‘*Spaniodontella sensu* Merklin (1950) and Zhgenti (1976a) non Andrussov in Goloubiatnikow (1902). Therefore we introduce *Zhgentiana* gen. nov. (see below).
9. The name *Astarte pulchella* Baily, 1858 is preoccupied by *Astarte pulchella* Jonas in Philippi, 1845 and a replacement name is mandatory. As one or more taxa in the same group might be synonymous with *Astarte pulchella* Baily (which we cannot decide because of lack of material) we refrain from introducing a new name, leaving this matter open to further research.

Note – One could argue that the name *A. pulchella* Baily should be maintained for reasons of ‘prevailing usage’, but saving the younger homonym would only be possible if both conditions of Article 23.9.1 ICZN would be fulfilled at the same time. This is, however, not the case, because *Astarte pulchella* Jonas was applied after 1899 at least twice as a valid name, viz. by Dall (1903, p. 942) and Poirier (1954, p. 157), which means that the senior homonym should be retained and a new name is needed for the junior homonym.

Introduction of a new genus

Zhgentiana gen. nov.

- | | |
|-------|-----------------------------------------------------------------------------------------------|
| 1902 | <i>Spaniodontella sensu</i> Andrussov in Goloubiatnikow (<i>partim</i>). |
| 1950 | <i>Spaniodontella sensu</i> Merklin (<i>partim</i> , non Andrussov in Goloubiatnikow, 1902). |
| 1976a | <i>Spaniodontella sensu</i> Zhgenti, 1976 (non Andrussov in Goloubiatnikow, 1902). |

Type species – *Venus gentilis* Eichwald, 1851 (Figs 8, 9a). Karaganian (= early Serravallian) of the Ustjurt plateau, Kazakhstan.

Etymology – The genus is named after Елена Мириановна Жгенти (Elena Mirianovna Zhgenti) in recognition of her contributions to the Ponto-Caspian Neogene mollusc faunas. *Zhgentiana* gender feminine.

Diagnosis – Shell circular to somewhat higher than wide, with slightly protruding, prosogyrous umbones, external surface with more or less strongly developed concentric ornament. Inner margin smooth, pallial line entire. Hinge plate strongly developed with cardinal 2a in left valve massive and tubercular, cardinal 2b insignificant, anterior lateral AII weak and margin parallel. In the right valve lateral AIII coinciding with anterior dorsal margin, cardinal 3b massive, tubercular, 3a narrow and much weaker, directed backwards, ligamental area wide, situated behind cardinal teeth and margin parallel (compare Fig. 8). Shell height to *c.* 15 mm.

Discussion – The genus *Zhgentiana* gen. nov. is introduced here for *Spaniodontella* as understood by Merklin (1950) and Zhgenti (1976a). That genus, however, had been incorrectly interpreted, as a result of accepting an incorrect type species. Instead of applying *S. nitida*, which is the type species according to ICZN ruling, authors had either chosen *Astarte pulchella* Baily, 1858 or *Venus gentilis* Eichwald, 1851 as type species. Merklin (1950) already excluded a group of smaller species with weak dentition of the hinge in the genus *Davidaschvilia*, with type species *Lutetia intermedia* (Andrussow in Bajarunas, 1910) and Zhgenti (1961) erected the genus *Savanella*, with type species *Spaniodon andrussowi* Toulou, 1890 for much larger species with heavy hinges and strongly protruding umbones. Species accepted by both authors in the restricted genus *Spaniodontella* are: *S. barbotii* (Stuckenberg, 1873), *S. crassidens* Andrussow in Goloubiatnikow, 1902, *S. ersaconensis* Zhgenti, 1976a, *S. gentilis* (Eichwald, 1851), *S. major* Andrussow, 1885 (*nomen nudum*), *S. opisthodon* Andrussow in Ossipov, 1932, *S. opisthodon squamigera* Andrussow in Ossipov, 1932, *S. pulchella* (Baily, 1858), *S. rubassensis* Goloubiatnikow, 1902, *S. tapesoides* Andrussow in Ossipov, 1932 and *S. umbonata* Andrussow in Ossipov, 1932. Several of these taxa have been synonymised in the course of time by various authors, e.g. *S. major*, introduced by Andrussow, 1885 without description was already synonymised by the same author in 1887 with *S. barbotii*. We do not have specimens available and for the time being we therefore prefer to refrain from opinions in this respect.

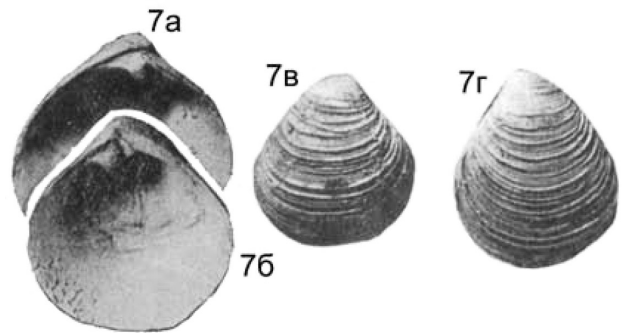


Figure 8. *Zhgentiana gentilis* (Eichwald, 1851) [after Neveeskaya, 2013, fig. 149-7, as *Lutetia (Spaniodontella) gentilis*], indicated height 12,5 mm (Miocene, Karaganian, Mangyshlak (W. Kazakhstan).

We hesitated about the choice of the *Zhgentiana* type species as either *Venus gentilis* Eichwald, 1851 or *Astarte pulchella* Baily, 1858 could be candidates. We opted for *Venus gentilis* as it is very well illustrated and clearly responds to the general concept of this group of species by its ‘massive’ cardinal teeth and dimensions. Although these two species are treated as synonyms by several previous authors we can hardly believe that they are really conspecific. We reproduce (Fig. 9a) the original illustrations of Eichwald (1851) [see also the drawing in Davidaschvili (1949, fig. 257)] for *V. gentilis* and of Baily (1858, pl. 9, fig. 10a-c) for *Astarte pulchella* (Fig. 9b).

Synonymy of *Alveinus nitidus* (Reuss, 1867)

Figs 1, 10; Plates 1-2

Type locality – Wieliczka, Poland; ‘Salzthon und Steinsalz’, Middle Miocene (Middle Badenian; Wieliczian regional substage of the Central Paratethys; about 13.8-13.4 Ma = early Serravallian, based on the dating of the Badenian Salinity Crisis by de Leeuw *et al.*, 2010).

Type material – Naturhistorisches Museum Wien, Vienna, Austria, 2/2 specimens (left and right valve, Fig. 10, lectotype and paralectotype (herein designated): NHM

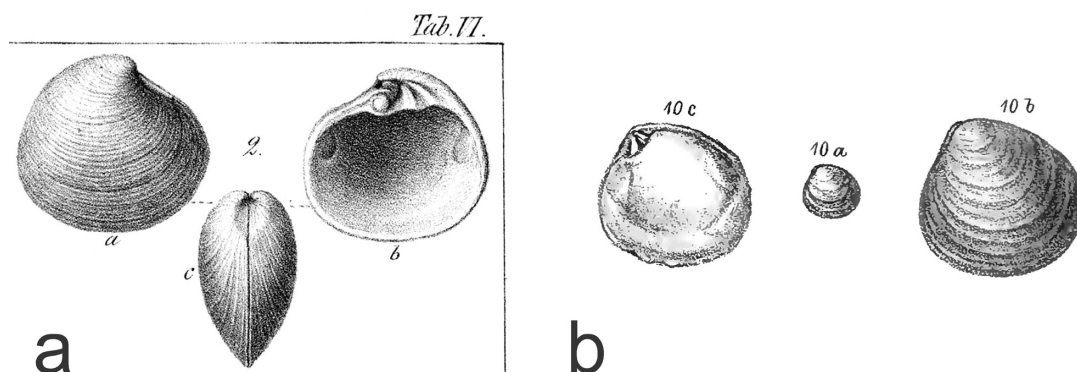


Figure 9a-b. Original illustrations of a: *Venus gentilis* Eichwald (1851, pl. 6, fig. 2a-c), length indicated as 5''' = 12,7 mm), and b: *Astarte pulchella* Baily (1858, pl. 9, fig. 10a-c, indicated size ¼ of an inch = 6.35 mm), both Ustyurt (Kazakhstan/Uzbekistan).

Wien 1867/VII (Schultz, 2005, p. 834 considered this to be the holotype, but Reuss mentioned several specimens).

Stratigraphic range in the North Sea Basin – Early Oligocene (Rupelian) to Late Miocene ('Sylvian' = Late Tortonian). Other representatives of the genus *Alveinus* have not been recognised so far in the North Sea Basin. The similar *Lutetia ovalis* von Koenen, 1893 from the Latdorfian (earliest Rupelian) seems to belong to *Lutetia* (see Welle, 1997) indeed.

- 1865 'Acephale zwischen *Circe* und *Lutecia*' [sic] – Stur, p. 280.
- *1867 *Spaniodon nitidus* Reuss, p. 135, pl. 8, fig. 3a-c; non Pictet (1850, p. 33) (Pisces).
- 1871 *Spaniodon nitidus* Rss – Stoliczka, p. 264.
- 1871 *Spaniodon nitidum* [sic] Reuss – Fuchs & Karrer, p. [47]113.
- 1871 *Spaniodon nitidus* Reuss – Fuchs & Karrer, p. [48]114.
- 1875 *Spaniodon nitidus* Reuss – Neumayr & Paul, p. 17.
- 1876 *Spaniodon nitidus* Reuss – Wibel & Gottsche, p. 104.
- 1879 *Spaniodon nitidus* Reuss – Wiechmann, p. 3.
- ?1884 *Lutetia burdigalensis* Desh. – Cossmann & Lambert, p. 94 (*nomen nudum*, non Deshayes).
- 1889 *Spaniodon nitidus* Rss. – Gottsche, p. 151.
- 1892 *Spaniodon nitidus* Rss – Kinkel, pp. 404, 407.
- 1895 *Lutetia* sp. – Bernard, p. 139, fig. 21.
- 1899 *Spaniodon nitidus* Reuss – Sokolov, p. 9, pl. 1, figs 4-8.
- 1900 *Spaniodon nitidus* Reuss – Dall, p. 1119.
- 1902 *Sp. nitidus* Reuss – Goloubiatnikow, p. 201.
- 1912 *Lutetia girondica* Benoist 'in coll.' Cossmann & Peyrot, p. 229, pl. 26, figs 16-19.
- 1915 *Spaniodon nitidus* Reuss - Gripp, p. 19.
- 1920 *Lutetia girondica* Ben. – Harris, p. 110, fig. 3.
- 1920 '*Lutetia burdigalensis* Desh.' – Harris, p. 111, fig. 4 (*nomen nudum*, non Deshayes).
- 1933a *Spaniodon nitidus* Reuss – Friedberg, p. 54.
- 1933b *Spaniodon nitidus* Reuss – Friedberg, pp. 209, 215, 216, 221, 227, 235.
- 1933b *Lutetia nitida* Reuss [sic] – Friedberg, p. 227.
- 1933b *Spaniodontella nitida* Reuss [sic] – Friedberg, pp. 227, 235.
- 1934 *Spaniodon nitidus* Reuss – Davidaschvili, p. 22.
- 1934 '*Lutetia*' *burdigalensis* Desh., '*Spaniodon*' *nitidus* Reuss – Davidaschvili, p. 28.
- 1934 *Lutetia nitida* Reuss [sic] – Friedberg, p. 129, text-fig. 17, pl. 21, figs 9-11.
- 1938 *Lutetia nitida* Reuss [sic] – Friedberg, p. 39.
- 1939 *Lutetia nitida* Reuss [sic] - Kautsky, pp. 586-588, 634-637, pl. 22, figs 23-26.
- 1946 *Lutetia nitida* Reuss [sic] – Sieber, p. 113.
- 1950 *Lutetia nitida* Reuss [sic] – Csepregy Meznierics, p. 75, pl. 5, figs 1-2.
- 1953 *Lutetia nitida* (Rss.) – Sieber, p. 191.
- 1954 *Lutetia* (*Davidaschvilia*) *nitida* Reuss [sic] – Kobrov, pl. 10, figs 11-13 (copied from Friedberg, 1934).
- 1956 *Kellyella rotunda* Sorgenfrei – Rasmussen, p. 41 (*nomen nudum*).
- 1958 *Kellyella* (*Lutetia*) *rotunda* Sorgenfrei, p. 86, pl. 10, fig. 32a-e.
- non 1958 *Kellyella* (*Lutetia*) *patera* Sorgenfrei, p. 87, pl. 11, fig. 33a-b [= *Timoclea patera* (Sorgenfrei, 1958)].
- 1959 *Lutetia nitida* (Reuss 1867) – Anderson, p. 119, pl. 16, fig. 1a-c.
- 1964 *Lutetia nitida* (Reuss 1867) – Anderson, p. 165.
- 1966 *Alveinus* (*s.s.*) *nitidus* (Reuss, 1867) – Glibert & van de Poel, p. 22.
- 1968 *Kellyella rotunda* Sorgenfrei 1958 – Rasmussen, p. 55.
- 1968 *Lutetia nitida* (Reuss, 1867) – Zelinskaya *et al.*, pp. 186-187.
- 1969 *Lutetia* (*Spaniodontella*) *nitida* (Reuss, 1867) – Keen in Moore, p. N653, text-fig. E130-2a, b.
- 1970 *Lutetia nitida* (Reuss) – Bałuk, tab. 1, pl. 5, fig. 1.
- 1972 *Lutetia rotunda* (Sorgenfrei, 1958) – Nordsieck, p. 35, pl. 7, fig. 49 (2 figs).
- 1972 *Lutetia* (*Spaniodontella*) *nitida* (Reuss, 1867) – A.W. Janssen, p. 8.
- ?1972 *Lasaea mioborealis* Nordsieck, p. 35, pl. 7, fig. 48 (2 figs).
- 1972 *Lutetia nitida* (Reuss, 1867) – Jakubowski, pp. 94-101, text-fig. 23, pl. 8, figs 1-35.
- 1976a *Lutetia nitida* Reuss – Zhgenti, pp. 7, 8, 10, 18 (as *Lutetia nitidus* on p. 18).
- 1976a *Spaniodon nitidus* Reuss – Zhgenti, pp. 7, 8, 10, 75.

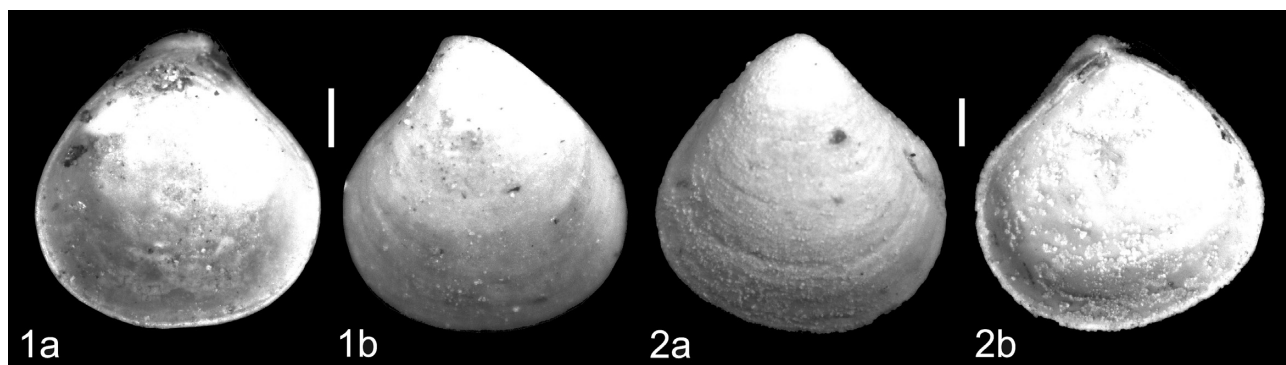


Figure 10. Lectotype (1a-b) and paralectotype (2a-b) of *Alveinus nitidus* (Reuss, 1867). Naturhistorisches Museum, Vienna, registration nr NHM Wien 1867/VII. Photographs courtesy of Mathias Harzhauser. Bar represents 1 mm.

- 1976b *Alveinus nitidus* (Reuss) (= *Spaniodon nitidus* Reuss) – Zhgenti, p. 507.
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- 1977 *Lutetia (Spaniodontella) nitida* (Reuss, 1867) – Jakubowski in Jakubowski & Musiał, p. 104, pl. 11, figs 9-10.
- 1979 *Lutetia (Spaniodontella) nitida* (Reuss, 1867) - Jakubowski in Jakubowski & Musiał, p.59, pl.4, figs 5-10.
- 1979 *Spaniodontella nitida* (Reuss 1867) – R. Janssen, p. 120.
- 1983 *Spaniodontella nitida* (Reuss, 1867) – Janse & Janssen, p. 119.
- 1984 *Spaniodontella nitida* (Reuss, 1867) – A.W. Janssen, p. 96, pl. 36, figs 2a-b, 3a-b.
- 1986 *Alveinus nitidus* (Reuss) – Studencka, p. 88, pl. 13, figs 18a-b, 19a-b.
- 1989 *Spaniodontella nitida* (Reuss, 1867) – Moths, p. 110, pl. 4, fig. 21.
- 1991 *Spaniodontella nitida* (Reuss, 1867) – Müller & Welle, p. 172, pl. 2, figs 5-6.
- 1996 *Lutetia (Spaniodontella) nitida* Reuss 1867 [sic] – Dulai, p. 41.
- 1996 *Spaniodontella nitida* – Spiegler & Gürs, p. 141.
- 1997 *Spaniodontella nitida* (Reuss, 1857 [sic]) – Welle, p. 75, pl. 11, figs 3-4, pl. 16, figs 4-5.
- 1998 *Alveinus nitidus* (Reuss) – Studencka *et al.*, p. 306, 319.
- 1998 *Spaniodontella nitida* (Reuss, 1867) – Moths *et al.*, p. 18, pl.12, fig. 2a-b.
- 1999 *Spaniodontella nitida* (Reuss, 1867) – Wienrich, p. 251, pl. 38, figs 4a-b, 5.
- 2001 *Alveinus nitidus* (Reuss) – Popa, p. 63.
- 2003 *Alveidus [sic] nitidus* (Reuss) – Moreno *et al.*, p. 168, figs 114-120.
- 2005 *Lutetia (Spaniodontella) nitida* (Reuss, 1867) – Schultz, p. 833 (with additional synonymy).
- 2005 *Spaniodontella nitida* (Reuss, 1867) – Schnetler, p. 80, pl. 2, fig. 15.
- 2008 *Spaniodontella nitida* (Reuss, 1867) – Moths *et al.*, p.89.
- 2010 *Spaniodontella nitida* (Reuss, 1867) – Moths *et al.*, p. 25, pl. 8, figs 10, 11.
- 2011 *Alveinus nitidus* (Reuss) – Studencka & Jasionowski, pp. 97, 101.
- 2012 *Lutetia nitida* (Reuss, 1867) – Cahuzac *et al.*, p. 392.

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Note – Older as well as more recently published literature from eastern Europe (Russia or Georgia *etc.*) was often found to be difficult to obtain or only in exceptional cases to be available from internet sources. Therefore we had to refer to a number of papers as ‘not seen’ below. In many cases we had to cite such papers on the basis of references in other, later publications. For the transliteration of texts in Cyrillic see the footnote on p. 128.

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continued p.142

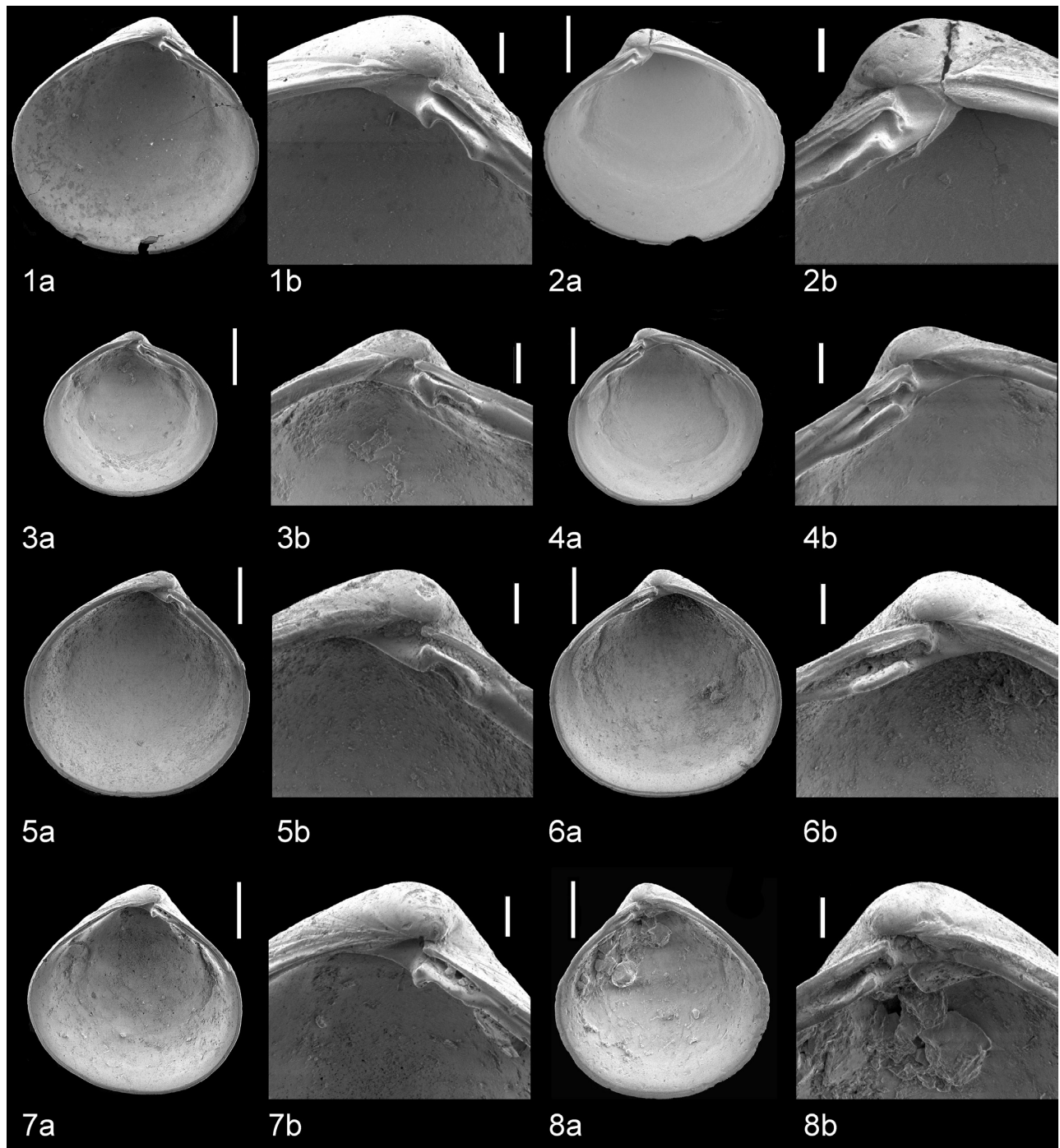


Plate 1.

SEM images of *Alveinus nitidus* (Reuss, 1867).

1-2. Winterswijk, Miste, The Netherlands, Miocene, Late Burdigalian/Langhian, Breda Formation, Aalten Member, RGM.794150.

3-4. Korytnica, Łysa Góra, 20 km S of Kielce, southern slopes of the Holy Cross Mts, Poland, Miocene, Early Badenian, RGM.794151.

5-6. St. Paul-les-Dax, Cabanes, Landes, France, Miocene, Burdigalian, RGM.794152.

7-8. Nawodzice, 60 km SE of Kielce, Poland, Miocene, Late Badenian, RGM.794153.

All leg. A.W. Janssen. Images by Renate Helwerda.

Bars represent 500 μm for valves, 100 μm for hinges.

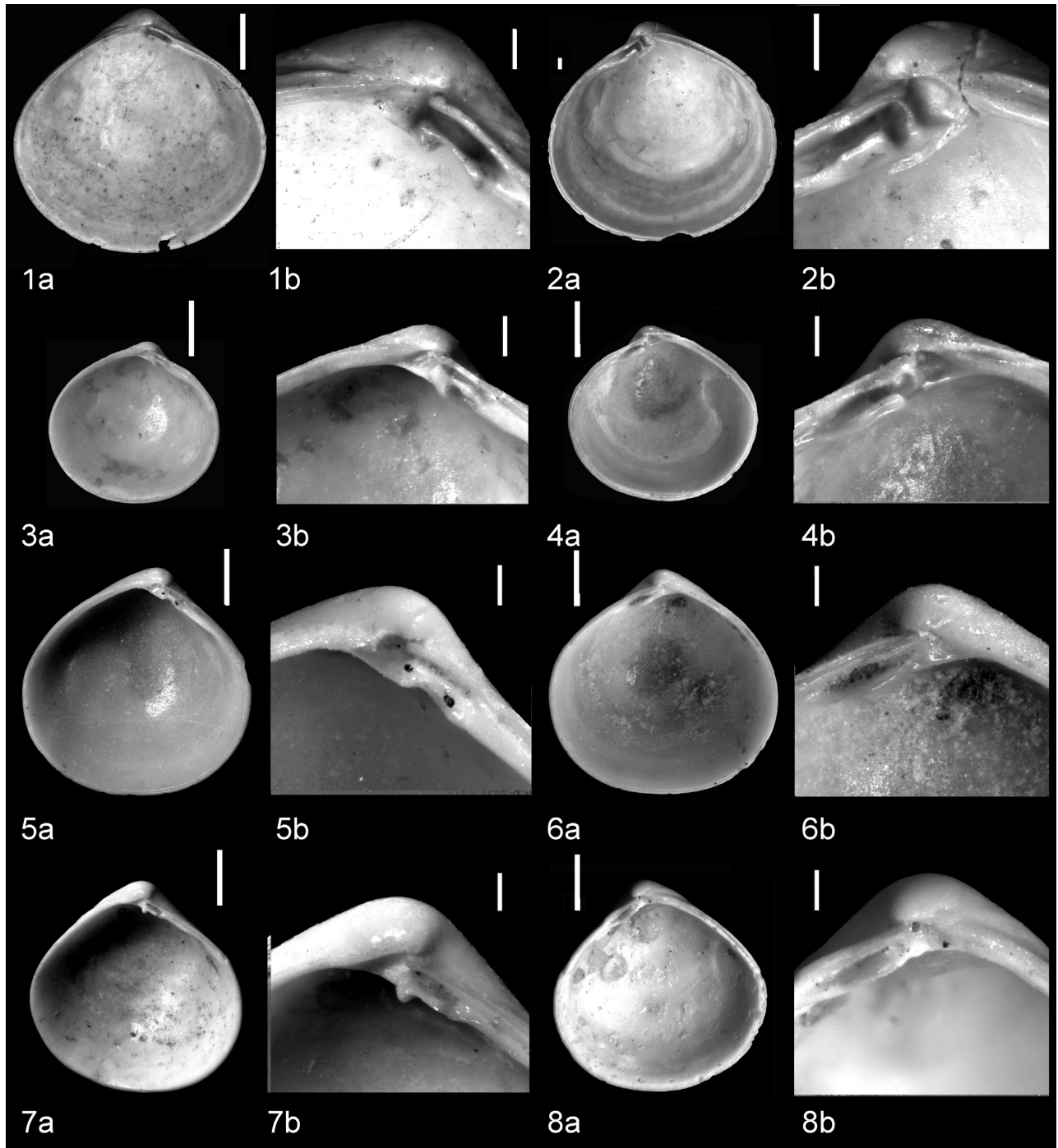


Plate 2.

Same specimens as in Plate 1, in digital stacked photography images.

Photographs by Petra Sonius and Eduard de Vogel.
Bars represent 500 μm for valves, 100 μm for hinges.

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