The Mesozoic pectinid genera *Velata* and *Eopecten* and their type species (Bivalvia: Pteriomorphia)

Thomas A. Neubauer[1,2,3]*, Baran Karapunar[4], Simon Schneider[5], Winfried Werner[1]

[1]SNSB – Bavarian State Collection for Palaeontology and Geology, Richard-Wagner-Straße 10, 80333 Munich, Germany
[2]Department of Earth and Environmental Sciences, Palaeontology & Geobiology, Ludwig-Maximilians-Universität München, Richard-Wagner-Str. 10, 80333 Munich, Germany
[3]Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, The Netherlands
[4]School of Earth and Environment, University of Leeds, Woodhouse Lane, Leeds LS2 9JT, United Kingdom
[5]CASP, West Building, Madingley Rise, Madingley Road, Cambridge CB3 0UD, United Kingdom

*Corresponding author:
Thomas A. Neubauer, E-mail: neubauer@snsb.de

Abstract

Pectinidae were a speciose and morphologically diverse family in the Mesozoic, representing the most genus-rich family in the Jurassic. Their comparatively high representation in fossil faunas is favoured by their calcitic shells. Together with high levels of morphological variability and a long history of research, this has also caused taxonomic inflation both at genus and species level. Here, we discuss the nomenclatural history of a common group of largely Jurassic pectinids, variably known under the genus names *Velata* QUENSTEDT, 1857, *Eopecten* DOUVILLÉ, 1897, and *Velopecten* PHILIPPI, 1899. Especially *Velata* and *Eopecten* have been used interchangeably as names for the same taxon in the literature of the 20th and 21st centuries. However, the two names are based on the same type species and are thus objective synonyms. Tracing back a long history of incorrect spellings and erroneous assumptions of homonymy, we show that, contrary to the predominant opinion, *Velata* is the valid name. Moreover, our study of type collections and additional material in natural history collections revealed that the type species of *Velata*, *Spondylus tuberculosus* GOLDFUSS, 1835, is a junior subjective synonym of *Velata abjecta* (PHILLIPS, 1829). We designate a lectotype for *Spondylus tuberculosus* and a neotype for *Pecten abjectus*, since the type material of the latter is lost. Finally, we discuss the ecology of the genus and provide a list of species introduced or presently considered to belong in *Velata*, along with information on type region, stratigraphic age, and literature.

Keywords: Pectinidae; Jurassic; nomenclature; synonymy; taxonomy

1 Introduction

The Pectinidae are one of the most speciose families of marine bivalves, with a rich Mesozoic and Cenozoic fossil record. With more than 50 genera they represented the most genus-rich family during the Jurassic (KARAPUNAR et al. 2023). First and foremost, this diversity is the result of an extraordinary radiation during the Mesozoic (WALLER 2006). However, in comparison to many other (predominantly) aragonitic-shelled bivalve groups, Pectinidae have an enhanced preservation potential, owing to their calcitic outer shell layers, which are more resistant to dissolution. As a result, they are particularly well represented in the fossil record, and we may know more about their diversity and evolution than for most other bivalve groups. Several important monographs focus specifically on Mesozoic pectinids (e.g. STAESCHE 1926; DECHASEAUX 1936; DHONDT 1971; ALLASINAZ 1972; DHONDT 1972a; DHONDT 1972b; DHONDT 1973; TAMURA 1973; DHONDT 1975; JOHNSON 1984; ROMANOV 1985; DAMBORENEA 1993; WATERHOUSE 2000; DAMBORENEA 2002; KASUM-ZADE 2003) and in numerous other taxonomic works the group features prominently.

Following a recent databasing effort with a focus on fossil Pectinida, MolluscaBase now hosts the most complete taxonomic and nomenclatural inventory of fossil and extant Pectinidae. As of 10 February 2025, the database includes 1466 accepted fossil species in Pectinidae (MOLLUSCABASE EDS 2025). During the process of indexing Mesozoic pectinid names in MolluscaBase, we encountered a significant nomenclatural issue regarding the validity of the widely used genus name *Eopecten* DOUVILLÉ, 1897. As already noted by PHILIPPI (1899) and several authors thereafter (e.g. ERNST 1923; COX 1928, 1942; ROMANOV 1985; KASUM-ZADE & ROMANOV 1986), *Eopecten* is a junior objective synonym of *Velata* QUENSTEDT, 1857, with the same type species. However, COX (1952) later reinstated *Eopecten*, based on the erroneous assumption of homonymy of *Velata*, and his opinion was adopted by numerous subsequent authors (e.g. HERTLEIN 1969; JOHNSON 1984; HODGES 2022).

This nearly 130-year long history of nomenclatural confusion has led to a mixed usage of both genus names (and several others) in the literature to the present day. Currently, at least 15 Middle Triassic (Ladinian) to early Late Cretaceous (Cenomanian) valid species occurring over large parts of the Northern Hemisphere, the western Tethys, and South America are assigned to *Eopecten* (FISCHER 1969; HERTLEIN 1969; HAYAMI 1975; GU et al. 1976; JOHNSON 1984; DAMBORENEA 1987;

HARPER & PALMER 1993; SZENTE 1996; DAMBORENEA 2002; ABERHAN et al. 2011; NEVESSKAJA et al. 2013; ROS-FRANCH et al. 2014; FÜRSICH & PAN 2014; HODGES 2022). However, taxonomic confusion in this group of pectinids is not restricted to the genus level but also concerns the status of the shared type species of *Velata* and *Eopecten*, *Spondylus tuberculosus* GOLDFUSS, 1835.

In the present study, we detail the taxonomic and nomenclatural history of the genus-level and species-level taxa involved and provide a solution for the various issues encountered. We further provide emended diagnoses for the genus *Velata* and its type species, as well as a list of the species-level taxa that were originally or are presently included in *Velata* or any of its objective synonyms, along with information on spatial and stratigraphic distribution.

2 Material and methods

Specimens studied for this article are held by the Bavarian State Collection for Palaeontology and Geology, Munich, Germany (SNSB-BSPG), the Bonner Institut für Organismische Biologie, Goldfuß-Museum, Bonn, Germany (BIOB-PAL), the Sedgwick Museum of Earth Sciences, University of Cambridge, Cambridge, UK (CAMSM), the University of Tübingen, Paleontological Collection, Tübingen, Germany (GPIT-PV), and the Yorkshire Museum, York, UK.

Photographs of the lectotype of *Spondylus tuberculosus* GOLDFUSS, 1835 (SNSB-BSPG AS VII 640) were made with a Canon EOS 800D DSLR camera. Photographs were stacked to get a throughout focused image using Photoshop CC 2024. Specimens held by the Sedgwick Museum (CAMSMJ.51196, CAMSMJ.51197, CAMSMJ.51198, CAMSMJ.23238) were imaged using a Nikon D7100 DSLR camera, equipped with a Nikon Micro-Nikkor 50 mm macro lens. Specimens were coated with ammonium chloride prior to photographing to enhance the contrast of surface features.

To compile the list of species originally or currently placed in *Velata* or its synonyms, we screened the Jurassic Bivalve Catalogue (a record of 30,852 published and figured bivalve occurrences, mostly from the Jurassic) housed at SNSB-BSPG, online databases (MolluscaBase and Paleobiology Database), and the literature.

3 Systematic palaeontology

Class Bivalvia LINNAEUS, 1758
Infraclass Pteriomorphia BEURLEN, 1944
Order Pectinida GRAY, 1854
Superfamily Pectinoidea RAFINESQUE, 1815
Family Pectinidae RAFINESQUE, 1815

Genus *Velata* QUENSTEDT, 1857

* 1857 *Velata* QUENSTEDT: p. 435.
1897 *Eopecten* DOUVILLÉ: p. 203.
1899 *Pecten* (*Velopecten*) PHILIPPI: p. 600.
1906 *Velatopecten* ROLLIER: p. 745.
1906 *Hinnites* (*Velatopecten*): ROLLIER, p. 747.
? 1930 *Ventalium*: DE GREGORIO, p. 23.

Type species: *Spondylus tuberculosus* GOLDFUSS, 1835 [= *Pecten abjectus* PHILLIPS, 1829, see below], by monotypy; Jurassic, Germany.

Emended diagnosis (modified from JOHNSON 1984)**:** Medium- to large-sized pectinids with a flat, cemented or closely byssally attached right valve and a slightly to markedly inflated left valve. Right valve *Chlamys*-like in outline; anterior auricle large and relatively narrow, with a deep byssal notch, and an active or occluded ctenolium in adulthood; posterior auricle shorter than anterior one, its dorsal and posterior margins meeting at obtuse angles; external shell surface ornamented with radial costae. Outline of left valve often irregular, its shape depending on substrate, with shallow sulcus at transition from disc to anterior auricle. Auricles of left valve poorly delimited; anterior auricle large, with anterior and dorsal margins meeting almost at right angles; posterior auricle smaller, matching that of right valve in size and shape. External shell surface of left valve ornamented with undulating radial costae of up to five orders of strength, crossed by commarginal lirae or growth lines.

Xenomorphic ornament occurring in some specimens. Ligament alivincular-alate, with a triangular resilifer present in both valves.

Nomenclatural remarks: QUENSTEDT (1857) introduced the new genus name *Velata* for *Spondylus tuberculosus* GOLDFUSS, 1835. QUENSTEDT's (1857, p. 435) wording is rather tentative: "Im Hinblick auf das gewaltige Byssusohr könnte man sehr versucht sein, ein besonderes Geschlecht *Velata* daraus zu machen […]. Neuerlich stellt man sie nicht ganz glücklich zum *Hinnites*." which translates to "Considering the enormous byssal auricle one could be tempted to turn it into a particular genus *Velata* [...]. Lately, it is not entirely satisfactorily assigned to *Hinnites*." In the plate captions, he still labelled the species as *Pecten tuberculosus*. However, according to Article 11.5.1 of the International Code of Zoological Nomenclature (ICZN 1999), the conditionally proposed new genus name is available. Along with the generic remarks, QUENSTEDT (1857) also mentioned that *Spondylus tuberculosus* GOLDFUSS, 1835 was a potential junior synonym of *Pecten abjectus* PHILLIPS, 1829.

DOUVILLÉ (1897), in a short note on the systematics of pectinids, introduced the new genus *Eopecten* for "*H.*[*innites*] *tuberculatus* Goldf.", obviously a misspelling of *Spondylus tuberculosus* GOLDFUSS, 1835. Accordingly, *Velata* and *Eopecten* have the same type species, and the latter is a junior objective synonym of the former.

Two years later, PHILIPPI (1899) introduced the subgenus *Pecten* (*Velopecten*) to mitigate the similarity of the genus-group names *Velata* QUENSTEDT, 1857 and *Velates* MONTFORT, 1810, the latter representing a genus in the gastropod family Neritidae [„Mit dem Namen *Velopecten* will ich durchaus nichts neues schaffen, sondern lediglich Quenstedt's *Velata* zweckmässig verändern" which translates to "With the name *Velopecten* I intend not to create anything new, by all means, but only to modify Quenstedt's *Velata* appropriately]; *Velopecten* PHILIPPI, 1899 is therefore an unjustified emendation. Although Philippi was aware of DOUVILLÉ's name *Eopecten* for the same group (PHILIPPI 1899, p. 600), he considered *Velopecten* to have priority because he attributed the authorship of the amended name to QUENSTEDT. *Velopecten* was later used by WAAGEN (1907), GOETEL (1917), MATSUMOTO (1930), KOBAYASHI (1931), STAESCHE (1932), and KIPARISOVA (1938), variably as a subgenus of *Pecten* or as a full genus, for the descriptions of new (partly Cenozoic) species, all of which are now placed in other genera (see e.g. NAKAZAWA 1952; ALLASINAZ 1972; SINELNIKOVA 1975; DOMINICI et al. 2024).

Velatopecten, as used by ROLLIER (1906), was later referred to as a "*nomen vanum*" (empty name) by several authors (HERTLEIN 1969; JOHNSON 1984; HODGES 2022) and is not an available name. Rollier did not provide an authorship or discuss the name, and it is to be regarded as an incorrect subsequent spelling of *Velopecten*.

ROLLIER (1915) considered *Velata*, *Velopecten*, and *Eopecten* as synonymous with *Prospondylus* ZIMMERMANN, 1886. Although *Velata* would take precedence, he claimed that it would be an adjective in its feminine declension that, for undisclosed reasons, could not be used as genus name and had to be rejected. ROLLIER's (1915) synonymy was adopted by GILLET (1924–1925, p. 54) without discussion, but was rejected by later workers because of differences in the hinge, which is of pectinid-type in *Eopecten/Velata* and of aviculopectinid/pterioid-type in *Prospondylus* (e.g. COX 1952, p. 28). *Prospondylus* now is the type genus of its own valid family, Prospondylidae PCHELINTSEV, 1960 (see e.g. HAUTMANN 2001; CARTER et al. 2011).

STAESCHE (1926, p. 113–114) followed the argumentation of PHILIPPI (1899) and used the name *Velopecten*. He also stated that the name *Eopecten* would insinuate an incorrect ancestry of pectinids, being another reason to abandon the name.

ERNST (1923) and shortly later COX (1928) were the first to recognize PHILIPPI's (1899) mistake; COX (1928) stated that "[u]nder the existing rules of nomenclature *Velates* MONTFORT, 1810, does not rule out *Velata*; Philippi's emendation is therefore unnecessary." In following works, COX (1931, 1942), ARKELL (1931a, b), STAESCHE (1931), and COX & ARKELL (1948) used *Velata* as a valid genus name (see also discussion in ARKELL 1931b, footnote on p. 119).

STAESCHE (1932) used the combination "*Velopecten* (*Velata*)" in the description of a new species from northern India, but did not discuss the genus-level names. Supposedly, this manuscript had been written before STAESCHE's (1931) contribution but was published later.

DECHASEAUX (1936, p. 8, 99) did not discuss the nomenclatural problems but apparently followed ARKELL (1931b) and listed *Eopecten*, *Velopecten*, and *Prospondylus* sensu ROLLIER (1915) in the synonymy of *Velata* (which she indicated to be a subgenus but treated like a full genus throughout the work).

KIPARISOVA (1938, p. 243) described several new taxa in *Pecten* (*Velopecten*); the other genus names were not mentioned or discussed.

The main step backward, leading to the present state of confusion, was made by COX (1952, p. 26), who rejected his previous assessment and reverted to using

Eopecten, considering *Velata* QUENSTEDT as a junior homonym of "*Velata* Griffith, in Cuvier, 1934" [sic] (*recte* GRIFFITH & PIDGEON 1834). However, GRIFFITH & PIDGEON (1834, p. 64) had used this name as "*Velata*, Montf.", in the same taxonomic context as Montfort (1810), without discussing the spelling. According to ICZN Art. 33.2.1, *Velata* of GRIFFITH & PIDGEON (1834, p. 64) is therefore an incorrect subsequent spelling of *Velates* MONTFORT, 1810 and not a subsequent emendation, hence not a separately available name.

COX' (1952) assessment was later followed by HAYAMI (1957), TAMURA (1959), FISCHER (1969), and, most momentously, the Treatise on Invertebrate Paleontology (HERTLEIN 1969, p. 373), which propagated the use of *Eopecten* by numerous authors until today (e.g. YAMANI 1975, GU et al. 1976, HAYAMI 1975, JOHNSON 1984, HARPER & PALMER 1993, SZENTE 1996, DAMBORENEA 1987, 2002, ABERHAN et al. 2011, NEVESSKAJA et al. 2013, FÜRSICH & PAN 2014, ROS-FRANCH et al. 2014, HODGES 2022).

In contrast, ROMANOV (1985, p. 101–102), and KASUM-ZADE & ROMANOV (1986, p. 12) noted the incorrect assumption of homonymy and used *Velata* as the correct genus name. They listed 14 species of *Velata* from Jurassic deposits of Moldova, Crimea, the Caucasus, and Central Asia (see also KASUM-ZADE 2003), but did not consider JOHNSON's (1984) revision of Jurassic pectinids, where he had synonymised several of these species.

Subsequently, SHURYGIN & LUTIKOV (1991) summarized the historic usage of the genus names *Velata* and *Eopecten* in the Russian literature and also discussed the unjustified emendation by PHILIPPI (1899), as well as the incorrectly purported homonymy of *Velata* and *Velates* (SHURYGIN & LUTIKOV 1991, p. 51–52, 72–73). They stated that the byssal notch in the right valve of *Spondylus tuberculosus*, which served as the basis for the introduction of the genus *Velata* by QUENSTEDT, is not visible in the drawing of GOLDFUSS (1833–1841). They concluded that "[a]pparently, different taxa were described under the names *Spondylus tuberculosus* (= *Hinnites tuberculatus* after DOUVILLÉ, 1897) and *Pecten tuberculosus* [QUENSTEDT, 1857]" (translated from Russian). Accordingly, they considered *Pecten tuberculosus* QUENSTEDT, 1857 as a taxon distinct from *Spondylus tuberculosus* GOLDFUSS, 1835 and designated *P. tuberculosus* QUENSTEDT, 1857 as the type species of *Velata*, referring to the ICZN edition of "1966" (actually 1964) (SHURYGIN & LUTIKOV 1991, p. 73). However, at the date of publication of their study, the third edition of the ICZN (1985) was already in use. In any case, according to both the second (1964) and

third (1985) editions, cases of misidentified type species are to be referred to the Commission to designate the type species (ICZN 1964, p. 73; ICZN 1985, p. 137; see ICZN 1999, Art. 70.3 for the current version). As a result, SHURYGIN & LUTIKOV's (1991) type designation is invalid. Although the works by KASUM-ZADE & ROMANOV (1986) and SHURYGIN & LUTIKOV (1991) were cited subsequently (e.g. ABERHAN 1998; ROS-FRANCH et al. 2014), the nomenclatural discussions therein apparently remained unnoticed.

Summarizing the findings detailed above, the valid name for the genus in question is *Velata* QUENSTEDT, 1857. *Eopecten* DOUVILLÉ, 1897 is a junior objective synonym of *Velata*, and *Velopecten* PHILIPPI, 1899 is an unjustified emendation of the latter.

DAMBORENEA (1987, p. 198) tentatively included *Ventalium* DE GREGORIO, 1930 in the synonymy of *Eopecten* (see also ROS-FRANCH et al. 2014, p. 174). DE GREGORIO's drawing of the type and only species, *Ventalium insigne* DE GREGORIO, 1930 from the Jurassic of Sicily, depicts a fragmentary specimen, where only parts of the disc are preserved. As in *Velata*, the disc is ornamented with numerous costae, apparently of two orders of strength. Yet, there is no indication of undulating costae or irregular growth, which would be common for *Velata*, and the drawing is undiagnostic. Having not studied the type material, we follow DAMBORENEA (1987) and retain *Ventalium* in tentative synonymy of *Velata*.

Taxonomic remarks: Establishing the phylogenetic relationships of *Velata* is beyond the scope of this study, but its taxonomic assignment needs justification. Critically, left valves of *Velata* are much more common than right ones in the fossil record (e.g., JOHNSON 1984; HARPER & PALMER 1993), and the internal features of both valves are often obstructed by matrix; thus, a full set of characters is rarely at hand. For our own study, we had no specimens available where the inside of the shells is exposed. However, as demonstrated here (see Figures 2 and 3), both GOLDFUSS (1835) and QUENSTEDT (1857) had articulated specimens of *Velata* at their disposal, and various subsequent authors studied well preserved material, where left and right valves clearly belong to the same species.

The hinge and ligament of several species of *Velata* were illustrated by DECHASEAUX (1936: pl. 8, fig. 14), COX (1942: pl. 4, figs 1–3), FÜRSICH & WERNER (1989: pl. 13, figs 7–9) and SHURYGIN & LUTIKOV (1991: pl. 15, figs 7b, 8). All of these

show alivincular ligaments situated below the hinge rotation axis. This condition was termed alivincular-internal by NEWELL & BOYD (1987) and alivincular-alate by HAUTMANN (2004), and is considered an autapomorphy of the Pectinoidea (WALLER 2006). The presence of a ctenolium in the type species of *Velata* is barely visible in GOLDFUSS' (1835) material (Fig. 2E), but was well illustrated by QUENSTEDT (1857; Fig. 3C), and, as an autapomorphy of the Pectinidae (WALLER 2006), serves for confident family placement. Note that the poor state of GOLDFUSS' (1835) specimen, together with his confusion of left and right valves, prompted SHURYGIN & LUTIKOV (1991) to doubt that QUENSTEDT (1857) had dealt with the same species.

A cementing life style has been shown to occur in various pectinid lineages (e.g. *Velata*, *Hinnites* DEFRANCE, 1821, *Talochlamys* IREDALE, 1929, *Austrohinnites* BEU & DARRAGH, 2001) and some genera, as currently defined, contain cementing as well as byssate species. Attachment is invariably with the right valve, and *Talochlamys* and *Austrohinnites* are distinguished by their microsculpture, which is absent in *Hinnites* and *Velata*. As discussed by YONGE (1951) and WALLER (2006), the high, deeply incised resilifer occurring in *Hinnites* is a result of cementation, where growth requires the ventral migration of the hinge system. A similarly deeply incised resilifer occurs in Kimmeridgian *Velata obliqua* (FÜRSICH & WERNER, 1989) from Portugal, and the tendency to develop this feature is seen in other species where hinge details are known and has been discussed by COX (1942).

It could thus be argued that *Velata* is simply a Mesozoic representative of *Hinnites* – which in turn was somewhat provocatively termed as 'essentially a *Chlamys* that becomes permanently cemented to a hard substrate' by WALLER (2006: 331). However, the widespread and prolonged occurrence of *Velata* during the Mesozoic, its demise at around the Early–Late Cretaceous transition, and the first occurrence of true *Hinnites* in the Neogene (*Hinnites crispus* BROCCHI, 1814) strongly suggest that these genera represent separate lineages. This is further supported by the observation that several species of *Velata* remained byssate during lifetime. Nonetheless, the precise phylogenetic relationships of these taxa (including the position of Mesozoic *Chlamys*) require further research.

Species included: We collated 80 species-group names that were proposed or are currently placed in the genus *Velata* or its synonyms (*Eopecten*, *Velopecten*). This list includes species presently considered junior synonyms. The stratigraphically oldest

species is the Ladinian *Pecten flagellum* STOPPANI, 1858, which was tentatively assigned to *Eopecten* by DAMBORENEA (2002, p. 61) (see also ROS-FRANCH et al. 2014, p. 102). The next oldest species are *Velata maizurensis* NAKAZAWA, 1952 and *Velata sumeriensis* KOBAYASHI & ICHIKAWA, 1949, both from the Carnian of Japan (HAYAMI 1975). The geologically youngest representatives are *Prospondylus* (*Velopecten*) *madagascariensis* COLLIGNON, 1950 from the Albian of Madagascar, a species that has not been discussed in the literature since its description, and *Hinnites studeri* PICTET & ROUX, 1853 from the Albian/Cenomanian of France (compare HARPER & PALMER 1993).

Supplementary Table 1 lists all species that were originally placed in *Velata* or its synonyms or are assigned to these genera according to the latest published opinion. With the exception of the names treated below, this is an uncritical list, provided to serve future research, and does not attempt a revision of all taxa listed.

We are currently aware of 210 illustrated Jurassic occurrences of *Velata*, which are included under the names *Eopecten* (110), *Velata* (79) and *Velopecten* (20) in the Jurassic Bivalve Catalogue housed at the SNSB-BSPG. Most of the 84 occurrences of *Hinnites* in the catalogue may also refer to *Velata*.

Velata abjecta (PHILLIPS, 1829)

Figs 1A–D, 2A–E

* 1829	*Pecten abjectus* PHILLIPS: p. 129, 151, 156, pl. 9, fig. 37.
1835	*Pecten abjectus* – PHILLIPS: p. 101, 123, 128, pl. 9, fig. 37.
v 1835	*Spondylus tuberculosus* GOLDFUSS: p. 93, pl. 105, fig. 2a, b.
v 1855	*Hinnites abjectus* (Phillips) – MORRIS & LYCETT: p. 125, 131, pl. 9, fig. 7, pl. 14, fig. 3.
non 1857	*Pecten tuberculosus Gingensis* QUENSTEDT: p. 379, pl. 51, fig. 4.
1857	*Pecten tuberculosus* – QUENSTEDT: p. 434, pl. 59, figs 9, 10.
1866	*Pecten tuberculosus* – QUENSTEDT: pl. 52, fig. 17.
1863	*Hinnites gradus*, Bean. sp. – LYCETT: p. 35, pl. 33, fig. 10, 10a.
1883	*Hinnites abjectus* (Phill.?) Morris & Lycett – DE LORIOL & SCHARDT: p. 72, pl. 10, figs 12, 13.
1897	*Hinnites tuberculatus* [sic] Goldf. – DOUVILLÉ: p. 203.

? 1900 *Velopecten abjectus* Phill. sp. – MÜLLER: p. 530, fig. 40.

? 1905 *Velopecten tuberculosus* Gldf. sp. – BENECKE: p. 114, pl. 4, figs 1–4.

1910 *Eopecten gradus* (Bean) – LISSAJOUS: p. 351, pl. 9, fig. 13.

1910 *Eopecten abjectus* (Phillips) – LISSAJOUS: p. 351, pl. 9, fig. 14.

1911 *Hinnites abjectus* Phil. – FUCINI: p. 11, pl. 1, fig. 3.

? 1915 *Eopecten abjectus* (Phillips) – PARIS & RICHARDSON: p. 530.

1915 *H.*[*innites*] (*P.*[*rospondylus*]) *abjectus* Phill. – ROLLIER: p. 454.

v 1915 *H.*[*innites*] (*P.*[*rospondylus*]) *Morrisi* sp. nov. ROLLIER: p. 455.

? 1923 *Eopecten gradus* (Bean) – LISSAJOUS: p. 157.

? 1923 *Eopecten tuberculosus* (Goldfuss) – LISSAJOUS: p. 157.

? 1923 *Velopecten abjectus* Morr. et Lyc. sp. – TRAUTH: p. 208.

1926 *Velopecten abjectus* (Phillips) – STAESCHE: p. 119.

? 1930 *Velata abjecta* (Phill.; Müller) – WEIR: p. 88, pl. 9, figs 7, 8.

? 1934 *Velata abjecta* Phill. – KRACH: p. 567, pl. 12, figs 16, 20.

? 1934 *Velata hartzi* n. sp. – ROSENKRANTZ: p. 42, pl. 8, fig. 1 (unavailable according to ICZN Art. 13.1, no description).

? 1936 *Velata abjecta* (Phillips) – DECHASEAUX: p. 68.

? 1936 *Velata gradus* (Bean) – DECHASEAUX: p. 69.

1938 *Velopecten abjectus* Phil. – KUHN: p. 147, pl. 1, fig. 15.

? 1938 *Velata abjecta* (Phillips?; Müller) – WEIR: p. 50, pl. 3, figs 22, 23.

1942 *Velata abjecta* (Phillips) – COX: p. 119, pl. 4, figs 2, 3.

1948 *Velata gradus* (Lycett) – COX & ARKELL: p. 15.

? 1956 *Velata hartzi* n. sp. ROSENKRANTZ: p. 79, figs 1–7.

? 1960 *Eopecten abjectus* (Phillips) – JOUBERT: p. 15, 62, pl. 7, fig. 7.

1962 *Eopecten abjectus* (Phillips) – COX et al.: p. 72, pl. 14, fig. 5.

non 1969 *Eopecten abjectus* Phillips 1829 – BARBULESCU & GRĂDINARU: p. 89, pl. 3, fig. 2.

1969 *Eopecten gradus* (Bean MS., Lycett) – FISCHER: p. 90, pl. 9, fig. 18a, b.

1984 *Eopecten abjectus* (Phillips 1829) – JOHNSON: p. 158, pl. 6, figs 1, 3, 5, 6, 8, 9.

1984 *Eopecten spondyloides* (Roemer 1836) – JOHNSON: p. 155 [partim, only concerning synonymy of *Spondylus tuberculosus* GOLDFUSS, 1835 and *Hinnites abjectus* of MORRIS & LYCETT 1855, here designated as neotype of *Pecten abjectus*].

? 1990 *Eopecten abjecta* (Phillips 1829) – ETTER: pl. 3, fig. 15.

1994 *Eopecten abjectus* (Phillips 1829) – ABERHAN: p. 40, pl. 20, figs 1, 2, 4, 7, pl. 21, figs 1, 5.

? 1995 *Eopecten abjectus* (Phillips, 1829) – JAITLY et al.: p. 197, pl. 20, fig. 2.

2005 *Eopecten abjectus* (Phillips) – HAAS & WEIS: p. 41, unnumbered fig.

Emended diagnosis: Large species of *Velata* (up to 150 mm high) with poorly to moderately inflated left valve, ornamented with numerous, progressively intercalated costae occurring at three to four orders of strength at a time in adults. New costae reach the strength of primary costae rather quickly during ontogeny. Costae generally more uneven in strength in central part of disc, where two or three primary costae are markedly to extremely more prominent than the rest.

Type and figured material: Neotype of *Pecten abjectus* PHILLIPS, 1829, designated herein: CAMSMJ.23238, left valve from Whitwell-on-the-Hill, Howardian Hills, North Yorkshire; Lebberston Member, Cloughton Formation; *Hyperlioceras discites* ammonite zone, lower Bajocian (Fig. 1C). Lectotype of *Spondylus tuberculosus* GOLDFUSS, 1835 (pl. 105, fig. 2a, b), designated herein: SNSB-BSPG AS VII 640, specimen with articulated valves from Wasseralfingen, Baden-Württemberg, Germany; Sengenthal Formation; *Stephanoceras humphriesianum* ammonite zone, lower Bajocian (Fig. 2D, E). Paralectotype of *Spondylus tuberculosus* GOLDFUSS, 1835, designated herein: BIOB-PAL-Goldfuss-643, left valve from Aalen, Baden-Württemberg, Germany; Sengenthal Formation; *Stephanoceras humphriesianum* ammonite zone, lower Bajocian (Fig. 2A–C). Original of *Pecten tuberculosus* as figured by QUENSTEDT (1857: pl. 59, fig. 9; 1866: pl. 52, fig. 17): GPIT-PV-51465, specimen with articulated valves from Hohenkarpfen hill south of Spaichingen, Baden-Württemberg, Germany; Gosheim Formation; *Stephanoceras humphriesianum* ammonite zone, lower Bajocian. Original of *Pecten tuberculosus* as figured by QUENSTEDT (1857: pl. 59, fig. 10): GPIT-PV-51464, from Wasseralfingen, Baden-Württemberg, Germany; Sengenthal Formation; *Stephanoceras humphriesianum* ammonite zone, lower Bajocian.

Type locality, type stratum and studied material: When PHILLIPS (1829) erected *Pecten abjectus*, he did not select a type specimen, nor did he provide a description,

type locality or stratum, and he only figured one specimen of his new species (pl. 9, fig. 37). Unfortunately, the type series, including the figured specimen, is lost (*fide* JOHNSON 1984). Our own inquiries at the museums at York, London, Oxford, Bristol and Cambridge also were fruitless. We thus regard it as prudent to designate a neotype, ideally from the same locality and stratum where PHILLIPS' (1829) figured specimen was collected.

This locality and stratum can be reconstructed as follows. Plate 9, figure 37 is referred to several times in PHILLIPS' (1829) text: on page 129, in the context of the 'Coralline Oolite', with Malton and Oxon mentioned as localities; on page 151, in the context of the 'Gray Limestone, or Bath Oolite', with Whitwell as locality mentioned; and on page 156, in the context of the 'Inferior Oolite', with Glaizedale mentioned. However, the captions for plate 9 indicate only the 'Bath Oolite, or Great Oolite' as the stratum of the specimens figured. Combining the information from the text and the plate caption, it is obvious that the specimen figured by PHILLIPS (1829, 1835: pl. 9, fig. 37) was from the only locality mentioned in the context of the 'Bath Oolite', Whitwell-on-the-Hill in the Howardian Hills, approximately 18 km northeast of York, North Yorkshire (54.0834 N, -0.8969 E, WGS1984 datum; not to be confused with Whitwell ~25 km SW of Middlesborough, also North Yorkshire).

ARKELL (1931a: 439) came to the same conclusion and remarked that the type specimen of *Pecten abjectus* originated from the Bajocian *Hyperlioceras discites* ammonite zone at Whitwell. It should be noted that PHILLIPS' (1829) figured specimen is a syntype, not the holotype, given that he evidently assigned specimens from several localities to his new species.

The 'Whitwell Oolite', cropping out at Whitwell-on-the-Hill, also known as the 'Millepore Bed/Oolite/Series', is now assigned to the Lebberston Member of the Cloughton Formation (BGS Lexicon of Named Rock Units 2024). The 'Bath Oolite', which PHILLIPS (1829) compared to these beds, is late Bathonian in age, and thus younger than the strata occurring at Whitwell-on-the-Hill.

We closely examined four specimens from Whitwell-on-the-Hill, curated at the Sedgwick Museum, Cambridge, UK. Specimen CAMSMJ.23238 is the original of plate 14, figure 3 of MORRIS & LYCETT (1855), from the 'Whitwell Limestone'. Specimens CAMSMJ.51196 to CAMSMJ.51198, from the 'Millepore Series' or 'Millepore Oolite', have not been figured or referenced before. Furthermore, we received photographs of ten additional specimens from Whitwell, held by the

Yorkshire Museum at York, UK. All of the studied specimens are left valves, and we consider these specimens as belonging to a single species, representing *Pecten abjectus* PHILLIPS, 1829.

Description: The specimens from Whitwell are between approximately 25 and 80 mm long and are generally slightly longer than high or of nearly equal dimensions. All specimens are rather poorly inflated. The auricles, while present in the sense of angular shoulders to the shell, are not distinguished as such, and the transition to the disc is gradual. The anterior auricle is significantly larger than the posterior one and its anterior and dorsal margins almost meet at right angles. The posterior auricle is more rounded and its dorsal margin is sloping, meeting the posterior margin at obtuse angles.

The left valves are ornamented with undulating radial costae of variable strength, which become inserted progressively during ontogeny and gain rather quickly in strength during ontogeny. In none of the specimens from Sedgwick Museum, the juvenile shell portion is particularly well preserved, and the earliest approximate count can be taken at a height of around 10 mm, where 18 to possibly 20 costae are present; these are termed primary costae here for practical considerations, although they may still have been inserted initially at different times. All radial elements are termed costae here, given that all of them would eventually raise to greater strength with growth, and all were considered for the following maximum counts. At its maximum height of approximately 60 mm, specimen CAMSMJ.23238, which is selected as the neotype of *Pecten abjectus* herein, has more than 130 costae (Fig. 1C). Specimen CAMSMJ.51197 has approximately 140 costae at a height of approximately 55 mm (Fig. 1D). Specimen CAMSMJ.51196 is particularly densely ornamented, including numerous very fine costae, some of which are rather faint; it has approximately 190 radial elements at a height of approximately 46 mm (Fig. 1A). The smallest specimen, CAMSMJ.51198, has approximately 105 costae at a height of approximately 33 mm (Fig. 1B).

In all specimens, later inserted costae raise to the strength of the primary set rather quickly; however, given that new costae are continuously inserted during ontogeny, there are always costae of three to four orders of strength present. Costae are overall more prominent but also more unequal in strength in the central part of the disc, conforming to slightly more than a third of the total shell with respect to its

umbonal angle. Two or three primary costae in the central part of the disc (but not directly adjacent) are distinctly stronger than the rest throughout ontogeny; as an exception, these stronger primary costae are rather poorly expressed in specimen CAMSMJ.51198. All costae are crossed by faint to distinct commarginal growth lines; where these are more distinct, they usually form small nodes at their intersections with the costae. The interior of the shell is unknown in the specimens from Whitwell.

Discussion: It is evident that the drawings of PHILLIPS (1829, 1835) have little in common with the specimens from Whitwell studied herein. However, this is the case with several of PHILLIPS' figures and simply illustrates the necessity to revisit original or topotypic material for taxonomic studies. In light of the considerations on the type locality above, and considering the opinions of previous workers who studied the type material of *P. abjectus* (e.g. COX 1942), we are confident that the specimens from Whitwell represent PHILLIPS' (1829) species. As mentioned, JOHNSON (1984), who gave the latest and most comprehensive account of these Jurassic pectinids, could not trace PHILLIPS' (1829) syntype either. Earlier authors, however, may either have had access to type material, or were otherwise well aware of the material from Whitwell. MORRIS & LYCETT (1855, p. 125) explicitly mention Whitwell, and the specimen figured on their plate 14, figure 3 is from this locality. We thus designate this well-known specimen (CAMSMJ.23238), studied by several subsequent authors, as the neotype of *Pecten abjectus* PHILLIPS, 1829. This specimen is also the holotype of *Hinnites* (*Prospondylus*) *morrisi* ROLLIER, 1915, which thereby becomes a junior objective synonym.

MORRIS & LYCETT (1855) were the first to provide a comprehensive and rather accurate description of *Velata abjecta* (as *Hinnites abjectus*). They mentioned 80 to 100 costae, plus 'more minute costae or lines' in the interstitial spaces, and they stressed the two or three more prominent costae in the central part of the disc as an obvious and distinguishing character. Interestingly, MORRIS & LYCETT (1855) also referred to the 'very rarely seen' right valve of the species, which they described as 'extremely delicate and flattened', ornamented with fine, sometimes indistinct radial lines.

As mentioned above, ARKELL (1931a), while not contributing to the description of the species, remarked that 'the type' of *Pecten abjectus* came from the Bajocian of Whitwell. Moreover, he referred to specimen CAMSMJ.23238, figured by MORRIS &

LYCETT (1855, pl. 14, fig. 3), as a fine example of *V. abjecta*. Interestingly, COX & ARKELL (1948, p. 15) stated that the specimen CAMSMJ.23238 is referrable to *Velata tegulata* (MORRIS & LYCETT, 1853) based on its stratigraphic age because they regarded only *Velata gradus* (LYCETT, 1863) and *V. tegulata* to be present in the Bajocian to Callovian Great Oolite Group.

JOHNSON (1984) deviated from MORRIS & LYCETT's (1855) species concept in three aspects. (1) He considered left valves of *Velata abjecta* as generally more convex than those of other species; this is not observed in the specimens from Whitwell studied here. (2) He remarked that *V. abjecta* had a lower number of costae than its congeners and, as an example, provided a count of 40 costae at a shell height of 53.5 mm from a single specimen. Like other previous authors, JOHNSON (1984) counted more prominent radial elements as costae and treated less prominent ones as striae, but the cut-off between these two categories remains vague. Interestingly, JOHNSON (1984) remarked that specimen CAMSMJ.23238, the here designated neotype, had more numerous costae than *Velata abjecta*, and assigned this specimen to *V. spondyloides* (ROEMER, 1836). Indeed, even when only those costae are counted that reached the primary ones in strength, there are approximately 75. It is evident from his synonymy that JOHNSON (1984) had not seen specimen CAMSMJ.23238, otherwise he would certainly have been intrigued by the three more prominent costae. (3) JOHNSON (1984) only mentioned two prominent costae as diagnostic for *E. abjectus*, not two or three, as MORRIS & LYCETT (1855) did.

The potential synonymy of *Pecten abjectus* PHILLIPS, 1829 and *Spondylus tuberculosus* GOLDFUSS, 1835 was repeatedly discussed (e.g. QUENSTEDT 1857, COX 1942, JOHNSON 1984) but never concluded. Of these authors, only COX (1942) studied the type material of *Pecten abjectus*. GOLDFUSS' material came from Aalen and Wasseralfingen in Baden-Württemberg, southern Germany. In that region, the species is found in lower Bajocian strata of the 'Humphriesianum-Oolite' now assigned to the Sengenthal Formation (pers. commun. GÜNTER SCHWEIGERT, 2024/11). These strata are assigned to the *Stephanoceras humphriesianum* ammonite zone and thus are only slightly younger than the Lebberston Member of Whitwell. Two syntypes of *Spondylus tuberculosus* are preserved. Specimen SNSB-BSPG AS VII 640 (Fig. 2D, E) from Wasseralfingen is the specimen figured by GOLDFUSS (1835, pl. 105, fig. 2a, b) and JOHNSON (1984, pl. 6, fig. 1). This specimen is a syntype, not the holotype by monotypy as assumed by JOHNSON (1984), and is

designated as the lectotype here. The second syntype, BIOB-PAL-Goldfuss-643 from Aalen (Fig. 2A–C), has never been figured before.

GOLDFUSS' (1835) description of the ornament of the specimens is rather accurate, although he confused right and left valves: 'The inflated right [= left] valve is unevenly costate and covered with fine lines in the interspaces. Between two stronger costae are two or three less strong ones, and three to seven lines between the latter, the central one of which is rising above the others. Laterally [posterior and anterior], this alternation is less obvious. Very fine concentric lines cover the entire area, and these, as well as the growth interruptions, lend a wavy-nodose appearance to the costae, particularly the stronger ones. … In one variety, two of the stronger costae rise well above the others and form high wavy bumps; also, the alternation of stronger and weaker costae is less regular.' The left, convex valve of the lectotype (SNSB-BSPG AS VII 640) is much less well preserved than suggested by GOLDFUSS' (1835) rather euphemistic drawing and is partly overgrown by serpulids. It is thus not possible to arrive at a full count of costae along the shell margin, but there are certainly more than 120 based on counting at a height of approximately 95 mm. Although fractured, the two more prominent costae can still be discerned (see arrows in Fig. 2D), and a third one, farther towards the posterior, is also relatively strong. Generally, there are costae of broadly four orders of strength, as already observed by GOLDFUSS. The number of costae in the poorly preserved right valve is lower, around 70 in the middle of the valve, where they can be counted; these costae are much more regular than on the left valve, with only two orders of strength present at any time. The outline shape of the right valve, including the large byssal notch, can barely be guessed from this individual. The second specimen, BIOB-PAL-Goldfuss-643, leaves no doubt as to the two stronger costae, which are extremely high. The specimen as a whole is fragmentary, with approximately 65 radial costae visible in total, at a preserved height of 54 mm; these costae are generally broader and more prominent than in the lectotype. The holotype by monotypy of *Hinnites gradus* LYCETT, 1863, from the Bathonian to Callovian Cornbrash Formation at Scarborough (Yorkshire, UK), shows the same morphology. LYCETT (1863) referred the original description to BEAN (1839), allegedly as "*Pecten gradus*", but the epithet *gradus* was not mentioned in that work, neither in *Pecten* nor any other genus.

QUENSTEDT's (1857, 1866) set of specimens, used to illustrate *Pecten tuberculosus*, and thus to establish *Velata*, is also from the lower Bajocian of Baden-

Württemberg. GPIT-PV-51465 is a specimen with articulated valves from Hohenkarpfen hill south of Spaichingen, attributed to the Gosheim Formation (pers. commun. GÜNTER SCHWEIGERT, 2025/05) (Fig. 3A, C). Its left valve shows three more prominent primary costae and, due to its excellent preservation, perfectly illustrates the difficulty to distinguish between costae and striae (Fig. 3A). Its right valve, which has only partly been freed from matrix sediment, preserves a deep byssal notch and an active ctenolium (Fig. 3C). A second specimen, GPIT-PV-51464, from the type locality, Wasseralfingen, has only the left valve exposed, with two markedly stronger primary costae (Fig. 3B).

We consider *Pecten abjectus* PHILLIPS, 1829, *Spondylus tuberculosus* GOLDFUSS, 1835, and *Hinnites gradus* LYCETT, 1863 as synonyms. Consequently, *Velata abjecta* (PHILLIPS, 1829) is the oldest available name and hence the valid name for the type species of *Velata*. The variability seen in the number of costae on left valves of *Velata abjecta* is considered intraspecific. The studied material from Whitwell already suggests that the more prominent primary costae vary in number from two to three, which is confirmed by the specimens from Germany. These two or three prominent primary costae are the distinguishing characteristic of *Velata abjecta*, which sets it apart from all other species in the genus.

Velata hartzi ROSENKRANTZ, 1956 from the Pliensbachian of Greenland is similar to *Velata abjecta* in having three prominent costae. However, in the type material of *Velata hartzi* the fine costae are not visible, probably due to inadequate preservation. Thus, we tentatively consider *V. hartzi* as a junior synonym of *V. abjecta*.

A similar case of an inequivalved pectinid with strong costae is *Euthymipecten asterianus* (D'ORBIGNY, 1850), the type species of the genus *Euthymipecten* DHONDT & DIENI, 1988, from the Lower Cretaceous of Sardinia. It differs from *Velata* in having the left valve flattened instead of the right one, and it lacks the 2–3 more prominent primary costae.

Distribution: Specimens studied by us derive from the lower Bajocian of Yorkshire (UK) and Baden-Württemberg (Germany). The synonym *H. gradus* was described from Bathonian to Callovian strata of Yorkshire (UK) (LYCETT 1863). Further European records are from the Bajocian of Luxembourg (HAAS & WEIS 2005), France (LISSAJOUS 1910), and Austria (TRAUTH 1923), Bathonian of France (FISCHER 1969) and Sardinia (Italy) (FUCINI 1911), and the Middle Jurassic of Switzerland (ROLLIER

1915). From outside Europe, only Toarcian to Aalenian material from Chile is assigned to this species with certainty (ABERHAN 1994). Pliensbachian material from Greenland (*V. hartzi*) (ROSENKRANTZ 1934, 1956) very likely belongs here. Uncertain records come from the Aalenian of Switzerland (ETTER 1990), Bajocian to Callovian of Kenya (WEIR 1930, 1938; JOUBERT 1960), the Upper Jurassic (?) of Tanzania (MÜLLER 1900), Callovian of India (JAITLY et al. 1995), and the Middle Jurassic of Poland (KRACH 1934). JOHNSON (1984) indicated the earliest record as from the upper Pliensbachian of Yorkshire and considered records from Callovian and Oxfordian strata as questionable.

4 Ecology of *Velata*

The ecology of *Velata* has been discussed repeatedly. It is striking that its right valve, commonly described as fragile, is so rarely preserved. Together with the irregular morphology of the left valve, this has led several authors to the assumption that the right valves were cemented to a substrate during lifetime (e.g. COX 1942; COX 1952; HERTLEIN 1969). Based on 263 shells (of which only nine were right valves), HARPER & PALMER (1993) convincingly documented the cementing habit of *Velata* in later ontogenetic stages. Recently, WEIS et al. (2023, p. 9) reported specimens of *Velata abjecta* attached to shells of the large early Bajocian nautilid *Cenoceras rumelangense* from Luxembourg and Germany.

On the other hand, the *Chlamys*-like morphology of the right valve with a deep byssal notch is remarkable, and the possibility that its ctenolium remained active throughout ontogeny was also discussed (JOHNSON 1984). GOLDFUSS (1835) remarked that the ‘left valve’ [= the right valve] of *Spondylus velatus* was flattened but not cemented to a substrate. QUENSTEDT (1857, 1866) figured an adult right valve of *Pecten tuberculosus* (= *Velata abjecta*) where the active ctenolium is clearly visible, indicating a byssate mode of life (refigured in Fig. 3C here). JOHNSON (1984) maintained that there was no positive evidence for cementation in *Velata*, and the specimens must have been closely attached to the substrate by short byssal threads, given that some specimens were showing xenomorphic sculpture. Moreover, articulated specimens of *Velata* from the Oxfordian of southern Germany present in the collections of SNSB-BSPG show no cementation during adulthood.

In summary, the majority of the known *Velata* right valves do not show evidence of cementing (i.e. attachment scars, preservation attached to a substrate) but possess a deep open byssal notch with an active ctenolium indicating byssal attachment during the entire ontogeny. However, other specimens of *Velata* were found cemented to a substrate, so the genus must be regarded as facultatively cementing in adulthood.

5 Conclusions

After more than 120 years of taxonomic and nomenclatural confusion, we show that *Velata* QUENSTEDT, 1857 is the correct genus name for Mesozoic medium- to large-sized pectinids of *Hinnites*-type morphology, characterised by a flat right valve and a slightly to markedly inflated left valve ornamented with undulating radial costae, often of several orders of strength. The widely used genus name *Eopecten* DOUVILLÉ, 1897 is a junior objective synonym of *Velata*, and *Velopecten* PHILIPPI, 1899 is an unjustified emendation.

Based on investigation of type and topotypic materials we conclude that the type species of *Velata*, *Spondylus tuberculosus* GOLDFUSS, 1835 from the Middle Jurassic (Bajocian) of southern Germany, is a junior synonym of *Velata abjecta* (PHILLIPS, 1829) from broadly coeval strata of northern England. Since the original type material of *Pecten abjectus* PHILLIPS, 1829 is lost, we designate a neotype for this species from the lower Bajocian Cloughton Formation of the original type locality, Whitwell-on-the-Hill (Yorkshire). Furthermore, we designate a lectotype for *Spondylus tuberculosus* GOLDFUSS, 1835. *Velata hartzi* ROSENKRANTZ, 1956 is tentatively included in the synonymy of *Velata abjecta*.

Following a comprehensive survey of the published literature, we present an uncritical list of 80 species-level names originally described or currently placed in *Velata* or its synonyms. Subject to a full revision of the listed species and their occurrences *Velata* has an age range from the Middle Triassic (Ladinian) to the early Late Cretaceous (Cenomanian) and was a common constituent particularly of Jurassic faunas in the Northern Hemisphere, the western Tethys and South America. Based on previous studies and our own observations, *Velata* was facultatively cemented (with a secondarily closed byssal notch) or closely byssally attached (with

an open notch and active ctenolium) in adulthood. Whether cementing versus byssal attachment is a distinguishing character at species level remains to be seen.

Acknowledgements

We are grateful to curators KATIE COLLINS (Natural History Museum London, UK), GEORG HEUMANN (Goldfuß Museum Bonn, Germany), ELIZA HOWLETT and EMMA NICHOLLS (Oxford University Museum of Natural History, UK), SARAH KING (Yorkshire Museum, York, UK), DEBORAH HUTCHINSON (Bristol Museum & Art Gallery, UK), MATT RILEY (Sedgwick Museum of Earth Sciences, UK) and INGMAR WERNEBURG (University of Tübingen) for information on, and assistance with material under their care. ANDREW L. A. JOHNSON (School of Science, University of Derby, UK) is thanked for fruitful discussions, as well as information on type material and regional stratigraphy. GÜNTER SCHWEIGERT (Staatliches Museum für Naturkunde Stuttgart, Germany) provided information on the stratigraphy and ecology of *Velata abjecta* and supplied literature. MANUEL KUNZ kindly provided photographs of the type specimen of *Spondylus tuberculosus* GOLDFUSS stored at Goldfuß Museum Bonn. SUSANA DAMBORENEA (Museo de La Plata, Universidad Nacional de La Plata, Argentina), MICHAEL HAUTMANN (University of Zurich, Switzerland), and KRZYSZTOF HRYNIEWICZ (Polish Academy of Sciences, Warsaw, Poland) provided constructive comments, which greatly improved the manuscript.

References

ABERHAN, M. (1994): Early Jurassic Bivalvia of northern Chile. Part I. Subclasses Palaeotaxodonta, Pteriomorphia, and Isofilibranchia. – Beringeria, **13**: 1–115.

ABERHAN, M. (1998): Early Jurassic Bivalvia of western Canada. Part I. Subclasses Palaeotaxodonta, Pteriomorphia, and Isofilibranchia. – Beringeria, **21**: 57–150.

ABERHAN, M., SCHOLZ, A. & SCHUBERT, S. (2011): Das Ober-Pliensbachium (Domerium) der Herforder Liasmulde. Teil 3: Taxonomie und Paläoökologie der Bivalvia aus der Amaltheenton-Formation (Unterjura) der Herforder Liasmulde. – Geologie und Paläontologie in Westfalen, **80**: 61–109.

ALLASINAZ, A. (1972): Revisione dei Pettinidi Triassici. – Rivista Italiana di Paleontologia e Stratigrafia, **78**(2): 189–428.

ARKELL, W.J. (1931a): Berichtigungen der Identität gewisser jurassischer *Pecten*-Arten. – Centralblatt für Mineralogie, Geologie und Paläontologie. Abteilung B: Geologie und Paläontologie, **1931**: 430–443.

ARKELL, W.J. (1931b): A Monograph of British Corallian Lamellibranchia. Part III. – Monographs of the Palaeontographical Society, **83**: 105–132, pls. 9–12.

BARBULESCU, A. & GRĂDINARU, E. (1969): Studiul faunei de moluşte din formaţiunile Bathonian – Calloviene inferioare din Valea Tichileştilor (Dobrogea Centrală). – Analele Universităţii Bucureşti, Geologie, **18**: 79–115.

BEAN, W. (1839): A Catalogue of the Fossils found in the Cornbrash Limestone of Scarborough; with figures and descriptions of some of the undescribed species. – The Magazine of Natural History, new series, **3**: 57–62.

BENECKE, E.W. (1905): Die Versteinerungen der Eisenerzformation von Deutsch-Lothringen und Luxemburg. – Abhandlungen zur geologischen Spezialkarte von Elsass-Lothringen, Neue Folge, **6**: 1–598.

BEU, A.G. & DARRAGH, T.A. (2001): Revision of southern Australian Cenozoic fossil Pectinidae (Mollusca: Bivalvia). – Proceedings of the Royal Society of Victoria, **113**: 1–205.

BEURLEN, K. (1944): Beiträge zur Stammesgeschichte der Muscheln. – Mathematisch-Naturwissenschaftlichen Abteilung der Bayerischen Akademie der Wissenschaften zu München, Sitzungsberichte, **1944**(1–2): 133–145.

BROCCHI, G. (1814): Conchiologia fossile subapennina con osservazioni geologiche sigli Apennini e sul suolo adiacente. 1–56, I–LXXX, 1–712. Milano (Stamperia Reale).

CARTER, J.G., ALTABA, C.R., ANDERSON, L.C., ARAUJO, R., BIAKOV, A.S., BOGAN, A.E., CAMPBELL, D.C., CAMPBELL, M., CHEN, J.-H., COPE, J.C.W., DELVENE, G., DIJKSTRA, H.H., FANG, Z.-J., GARDNER, R.N., GAVRILOVA, V.A., GONCHAROVA, I.A., HARRIES, P.J., HARTMAN, J.H., HAUTMANN, M., HOEH, W.R., HYLLEBERG, J., JIANG, B.-Y., JOHNSTON, P., KIRKENDALE, L., KLEEMANN, K., KOPPKA, J., KŘÍŽ, J., MACHADO, D., MALCHUS, N., MÁRQUEZ-ALIAGA, A., MASSE, J.-P., MCROBERTS, C.A., MIDDELFART, P.U., MITCHELL, S., NEVESSKAJA, L.A., ÖZER, S., POJETA, J.Jr., POLUBOTKO, I.V., PONS, J.M., POPOV, S., SÁNCHEZ, T., SARTORI, A.F., SCOTT, R.W., SEY, I.I., SIGNORELLI, J.H., SILANTIEV, V.V., SKELTON, P.W., STEUBER, T., WATERHOUSE, J.B., WINGARD, G.L. & YANCEY, T. (2011): A synoptical classification of the Bivalvia (Mollusca). – Paleontological Contributions, **4**: 1–47.

COLLIGNON, M. (1950): Recherches sur les faunes albiennes de Madagascar. IV. L'Albien de Mokaraha (Cercle de Soalala). – Annales géologiques du Service des Mines, **17**: 58–85.

COX, L.R. (1928): The Gastropod and Lamellibranch Molluscs [from the Belemnite Marls of Charmouth]. – Quarterly Journal of the Geological Society of London, **84**(2): 233–245.

COX, L.R. (1931): Zu dem Namen *Velata velata* (Goldfuss). – Centralblatt für Mineralogie, Geologie und Paläontologie. Abteilung B: Geologie und Paläontologie, **1931**: 443–444.

COX, L.R. (1942): Notes on Jurassic Lamellibranchia VIII. On the genus *Velata* Quenstedt. – Proceedings of the Malacological Society of London, **25**(3): 119–124.

COX, L.R. (1952): The Jurassic lamellibranch fauna of Cutch (Kachh). No. 3, Families Pectinidae, Amusiidae, Plicatulidae, Limidae, Ostreidae and Trigoniidae (Supplement). – Memoirs of the Geological Survey of India, Palaeontologia Indica, Series IX, **3**(4): 1–128.

COX, L.R. & ARKELL, W.J. (1948): A survey of the Mollusca from the British Great Oolite Series: primarily a nomenclatorial revision of monographs by Morris & Lycett (1851–55), Lycett (1863) and Blake (1905–07). – Monographs of the Palaeontographical Society: 102(444): i-xiii + 1-48 [1948]; 103(449): xiv-xxiv, 49-105 [1950].

COX, L.R., COSTELL, C.P. & MUIR-WOOD, H.M. (1962): British Mesozoic Fossils. 205 pp.; London (British Museum (Natural History)).

D'ORBIGNY, A. (1850): Prodrome de Paléontologie. Stratigraphique universelle des animaux mollusques et rayonnés faisant suitre au cours élémentaire de paléontologie et de géologie stratigraphique. Deuxième volume. 427 pp.; Paris (Victor Masson).

DAMBORENEA, S.E. (1987): Early Jurassic Bivalvia of Argentina. Part 2: Superfamilies Pteriacea, Buchiacea and part of Pectinacea. – Palaeontographica Abt. A, **119**(4–6): 113–216.

DAMBORENEA, S.E. (1993): Early Jurassic South American pectinaceans and circum-Pacific palaeobiogeography. – Palaeogeography, Palaeoclimatology, Palaeoecology, **100**(1–2): 109–123. doi: 10.1016/0031-0182(93)90036-I

DAMBORENEA, S.E. (2002): Early Jurassic bivalves of Argentina. Part 3: Superfamilies Monotoidea, Pectinoidea, Plicatuloidea and Dimyoidea. – Palaeontographica Abt. A, **265**(1–4): 1–119.

DE GREGORIO, A. (1930): Monografia dei fossili Liassici di Monte San Giuliano conservati nel mio privato gabinetto geologico. – Annales de Géologie et de Paléontologie de Palerme, **53**: 1–57.

DE LORIOL, P. & SCHARDT, H. (1883): Étude paléontologique et stratigraphique des Couches à Mytilus des Alpes Vaudoises. I. Paléontologie. – Mémoires de la Société Paléontologique Suisse, **10**: 1–96.

DECHASEAUX, C. (1936): Pectinidés jurassiques de l'est du Bassin de Paris. – Annales de Paléontologie, **25**: 1–148.

DEFRANCE, J.L.M. (1821): Hinnite (foss.). pp., – In: CUVIER, F. (ed.): Dictionnaire des Sciences Naturelles, **21**: 169–170. Strasbourg (Levrault) & Paris (Le Normant).

DHONDT, A.V. (1971): Systematic revision of *Entolium*, *Propeamussium* (Amusiidae) and *Syncyclonema* (Pectinidae, Bivalvia, Mollusca) of the European boreal Cretaceous. – Bulletin, Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, **47**: 1–95.

DHONDT, A.V. (1972a): Systematic revision of the Chlamydinae (Pectinidae, Bivalvia, Mollusca) of the European Cretaceous. Part 1: *Camptonectes*. – Bulletin, Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, **48**: 1–60.

DHONDT, A.V. (1972b): Systematic revision of the Chlamydinae (Pectinidae, Bivalvia, Mollusca) of the European Cretaceous. Part 2: *Lyropecten*. – Bulletin, Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, **48**(7): 1–81.

DHONDT, A.V. (1973): Systematic revision of the Chlamydinae (Pectinidae, Bivalvia, Mollusca) of the European Cretaceous. Part 3: *Chlamys* and *Mimachlamys*. – Bulletin, Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, **49**(1): 1–134.

DHONDT, A.V. (1975): Systematic revision of the Chlamydinae (Pectinidae, Bivalvia, Mollusca) of the European Cretaceous. Part 4: *Merklinia*. – Bulletin, Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, **51**: 1–36.

DHONDT, A.V. & DIENI, I. (1988): Early Cretaceous bivalves of eastern Sardinia. – Memorie di Scienze Geologiche, **40**: 1–97.

DOMINICI, S., DANISE, S. & TINTORI, A. (2024): A Middle Triassic Cassian-type fauna (Pelsa-Vazzoler Lagerstätte) and the adaptive radiation of the Modern evolutionary fauna. – Papers in Palaeontology, **10**(4): e1579. doi: 10.1002/spp2.1579

DOUVILLÉ, H. (1897): Essai de classification systématique des Pectinidés. – Bulletin de la Société Géologique de France, troisième série, **25**: 202–203.

ERNST, W. (1923): Beiträge zur Paläontologie und Stratigraphie des nordwestdeutschen Jura. IV. Zur Stratigraphie und Fauna des Lias ξ im nordwestlichen Deutschland (Erster Teil). – Palaeontographica, **65**(1–3): 1–96.

ETTER, W. (1990): Paläontologische Untersuchungen im unteren Opalinuston der Nordschweiz. – Inaugural-Dissertation Universität Zürich, 151 pp.

FISCHER, J.-C. (1969): Géologie, paléontologie et paléoécologie du Bathonien au Sud-Ouest du Massif ardennais. – Mémoires du Muséum National d'Histoire Naturelle, Série C, Sciences de la Terre, **20**: 1–319.

FUCINI, A. (1911): Fossili nuovi o interessanti del Batoniano del Sarcidano di Laconi in Sardegna. – Atti della Società toscana di scienze naturali, residente in Pisa. Memorie, **27**: 93–108.

FÜRSICH, F.T. & PAN, Y. (2014): Callovian-Oxfordian (Jurassic) bivalves from the Kamar-e-Mehdi Formation of east-central Iran. – Beringeria, **44**: 3–50.

FÜRSICH, F.T. & WERNER, W. (1989): The Upper Jurassic Bivalvia of Portugal. Part II. Pteriomorphia (Pteroida exclusive Ostreina). – Comunicações dos Serviços Geológicos de Portugal, **74**: 105–164.

GILLET, S. (1924–1925): Études sur les lamellibranches Néocomiens. – Mémoires de la Société Géologique de France, nouvelle série, **3**: 1–339.

GOETEL, M.W. (1917): Die rhätische Stufe und der untere Lias der subtatrischen Zone in der Tatra. – Bulletin international de l'academie des sciences de Cracovie - Classe des sciences mathématiques et naturelles, série A: sciences mathématiques, **1916**: 1–222.

GOLDFUSS, A. (1833–1841): Petrefacta Germaniae tam ea, quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmiae rhenanae servantur quam alia quaecunque in Museis Hoeninghusiano Muensteriano aliisque extant, iconibus et descriptionibus illustrata. Zweiter Theil. i + 1–312 pp., pls. 72–165; Düsseldorf (Arnz & Co.).

GRAY, J.E. (1854): A revision of the arrangement of the families of bivalve shells (Conchifera). – The Annals and Magazine of Natural History, second series, **13**(77): 408–418.

GRIFFITH, E. & PIDGEON, E. (1833–1834): The Mollusca and Radiata. Vol. 12. – In: GRIFFITH, E. (ed.): The Animal Kingdom Arranged in Conformity with Its Organization, by the Baron Cuvier. viii + 601 pp. + 61 pls.; London (Whittaker and Co.).

GU, Z.-W., HUANG, B.-Y., CHEN, C.-Z., WEN, S.-X., MA, Q.-H., LAN, X., XU, J.-T., LIU, L., WANG, S.-M., WANG, D.-Y., QIU, R.-Z., HUANG, Z.-Q., ZHANG, Z.-M., CHEN, J.-H. & WU, P.-L. (1976): The Lamellibranch Fossils of China. 522 pp.; Beijing (Science Press).

HAAS, R. & WEIS, R. (2005): Les bivalves. – In: FAYARD, J.-P., GROSS, N., LAJOURNADE, J.-B., LATHUILIÈRE, B., VAILLY, G. & WEIS, R. (eds.): Fossiles et minéraux de la carrière d'Ottnange-Rumelange. 37–48; Thionville, France (Géolor) et Bous, Louxemburg (AGMP).

HARPER, E.M. & PALMER, T.J. (1993): Middle Jurassic cemented pectinids and the missing valves of *Eopecten*. – Journal of Molluscan Studies, **59**: 63–72.

HAUTMANN, M. (2001): Taxonomy and phylogeny of cementing Triassic bivalves (families Prospondylidae, Plicatulidae, Dimyidae and Ostreidae). – Palaeontology, **44**(2): 339–373.

HAUTMANN, M. (2004): Early Mesozoic evolution of alivincular bivalve ligaments and its implications for the timing of the 'Mesozoic marine revolution'. – Lethaia, **37**: 165–172.

HAYAMI, I. (1957): Liassic *Chlamys*, '*Camptonectes*' and other pectinids from the Kuruma Group in central Japan. – Transactions and Proceedings of the Palaeontological Society of Japan, new series, **28**: 119–127.

HAYAMI, I. (1975): A systematic survey of the Mesozoic Bivalvia from Japan. – University Museum, University of Tokyo, Bulletin, **10**: 1–249.

HERTLEIN, L.G. (1969): Family Pectinidae Rafinesque, 1815. In: Treatise on Invertebrate Paleontology. Part N. Volume 1 (of 3). Mollusca 6. Bivalvia. – In: COX, L.R., NEWELL, N.D., BOYD, D.W., BRANSON, C.C., CASEY, R., CHAVAN, A., COOGAN, A.H., DECHASEAUX, C., FLEMING, C.A., HAAS, F., HERTLEIN, L.G., KAUFFMAN, E.G., KEEN, A.M., LAROCQUE, A., MCALESTER, A.L., MOORE, R.C., NUTTALL, C.P., PERKINS, B.F., PURI, H.S., SMITH, L.A., SOOT-RYEN, T., STENZEL, H.B., TRUEMAN, E.R., TURNER, R.D., WEIR, J. & MOORE, R.C. (eds.). 348–373; Lawrence, Kansas (Geological Society of America and University of Kansas Press).

HODGES, P. (2022): The Early Jurassic Bivalvia from the Hettangian and lower Sinemurian of South-West Britain. Part 4. – Monographs of the Palaeontographical Society, **176**(662): 145–330. doi: 10.1080/02693445.2022.2133204

ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE) (1964): International Code of Zoological Nomenclature. Second edition. 176 pp.; London (International Trust for Zoological Nomenclature).

ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE) (1985): International Code of Zoological Nomenclature. Third edition. 338 pp.; London (International Trust for Zoological Nomenclature).

ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE) (1999): International Code of Zoological Nomenclature. Fourth edition. xxix + 306 pp.; London (International Trust for Zoological Nomenclature).

IREDALE, T. (1929): Mollusca from the continental shelf of eastern Australia. No 2. – Records of the Australian Museum, **17**(4): 157–189.

JAITLY, A.K., FÜRSICH, F.T. & HEINZE, M. (1995): Contributions to the Jurassic of Kachchh, western India. IV. The bivalve fauna. Part I. Subclass Palaeotaxodonta, Pteriomorphia, and Isofilibranchia. – Beringeria, **16**: 147–257.

JOHNSON, A.L.A. (1984): The palaeobiology of the bivalve families Pectinidae and Propeamussiidae in the Jurassic of Europe. – Zitteliana, **11**: 1–235.

JOUBERT, P. (1960): Geology of the Mandera-Damassa Area. – Report of the Geological Survey of Kenya, **48**: 1–65.

KARAPUNAR, B., WERNER, W. & FÜRSICH, F.T. (2023): Were Jurassic oceans a pectinid Sea? – Implications of an initial analysis of the Jurassic Bivalve Catalogue. – Bivalves – Where are we going? Cambridge 5–8 September 2023, Abstracts. Cambridge, p. 61.

KASUM-ZADE, A.A. (2003): Sostoyaniye izuchennosti mezozoyskikh dvustvorchatykh mollyuskov Azerbaydzhana (Otryad Pectinoida: reviziya i sistematika) [Advances in research of Mesozoic bivalve mollusks in Azerbaijan (Order Pectinoida: revision and systematics)]. 112 pp.; Baku (El-ALIiance).

KASUM-ZADE, A.A. & ROMANOV, L.F. (1986): Rod *Velata* Quenstedt, 1858 v yure yuga SSSR [The genus *Velata* Quenstedt, 1858 in the Jurassic of the southern USSR]. – In: Paleontologo-stratigraficheskiye issledovaniya mezozoya i kaynozoya mezhdurech'ya Dnestr-Prut [Paleontological and stratigraphic studies of the Mesozoic and Cenozoic in the Dniester-Prut interfluve]. 11–24; Kishinev (Shtiintsa).

KIPARISOVA, L.P. (1938): Nizhnetriasovyye plastinchatozhabernyye Ussuriyskogo kraya [Lower Triassic lamellibranchs of the Ussuri region]. – Trudy Geologicheskogo Instituta, **7**: 197–311.

KOBAYASHI, T. (1931): Notes on a new occurrence of Ladino-Carnic limestone at Sambosan, Tosa Province, Japan. – Japanese Journal of Geology and Geography, **8**(3–4): 251–258.

KOBAYASHI, T. & ICHIKAWA, K. (1949): *Tosapecten*, gen. nov. and other Upper Triassic Pectinidae from the Sakawa basin in Shikoku, Japan. – Japanese Journal of Geology and Geography, **21**(1–4): 163–176.

KRACH, W. (1934): Przegrzebki (Pectinidae) jury brunatnej okolic Krakowa (Pectinidae du Jura moyen des environs de Cracovie). – Annales de la Société Géologique de la Pologne, **10**: 555–573.

KUHN, O. (1938): Die Fauna des Dogger δ der Frankenalb (Mit Nachträgen zum übrigen Jura). – Nova Acta Leopoldina, neue Folge, **6** (37): 125–170.

LINNAEUS, C. (1758): Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. iv + 824 pp.; Holmiae (Laurentius Salvius).

LISSAJOUS, M. (1910): Jurassique Mâconnais : fossiles caractéristiques. – Bulletin trimestriel de la Société d'histoire naturelle de Mâcon, **3**(11–12): 1–208.

LISSAJOUS, M. (1923): Étude sur la faune du Bathonien des environs de Mâcon. 2e partie. – Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon, **5**(3): 113–286.

LYCETT, J. (1863): Supplementary monograph on the Mollusca from the Stonesfield Slate, Great Oolite, Forest Marble, and Cornbrash. – Monographs of the Palaeontographical Society of London, **15**: 1–129.

MATSUMOTO, H. (1930): On the marine faunae of three fossil zones of the Upper Miocene of Natori District, Province of Rikuzen. – Science reports of the Tohoku Imperial University. 2nd series, Geology, **13**(3): 96–109.

MOLLUSCABASE EDS (2025): MolluscaBase. https://www.molluscabase.org. [Accessed 10 February 2025]

MONTFORT, P.D. de (1810): Conchyliologie systématique et classification méthodique de coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Ouvrage destiné à faciliter l'étude des coquilles, ainsi que leur disposition dans les cabinets d'histoire naturelle. Coquilles univalves, non cloisonnées. Tome second. 676 pp.; Paris (Schoell).

MORRIS, J. & LYCETT, J. (1853–1855): A Monograph of the Mollusca from the Great Oolite, chiefly from Minchinhampton and the coast of Yorkshire. Part II: Bivalves; Part III: Bivalves. – Monographs of the Palaeontographical Society, **7–8**: 7(23): 1-80 [1853]; 8(28): 81-147 [1855; for 1854].

MÜLLER, G. (1900): Versteinerungen des Jura und der Kreide. – In: BORNHARDT, W. (ed.): Zur Oberflächengestaltung und Geologie Deutsch-Ostafrikas. 514–571; Berlin (Dietrich Reimer).

NAKAZAWA, K. (1952): A study on the pelecypod-fauna of the Upper Triassic Nabae group in the northern part of Kyoto Prefecture, Japan. Part 1. Pectinids and limids. – Memoirs of the College of Science, University of Kyoto, Series B, Geology and Mineralogy, **20**(2): 95–106.

NEVESSKAJA, L.A., POPOV, S.V., GONCHAROVA, I.A., GUZHOV, A.V., JANIN, B.T., POLUBOTKO, I.V., BIAKOV, A.S. & GAVRILOVA, V.A. (2013): Dvustvorchatyye mollyuski Rossii i sopredel'nykh stran v fanerozoye. – Trudy Paleontologicheskogo Instituta, **294**: 1–524.

NEWELL, N.D. & BOYD, D.W. (1987): Iteration of ligament structures in pteriomorphian bivalves. – American Museum Novitates, **2875**: 1–11.

PARIS, E.T. & RICHARDSON, L. (1915): Some Inferior-Oolite Pectinidae. – Quarterly Journal of the Geological Society, **71**(1–4): 521–535.

PCHELINTSEV, V. F. (1960): Semeystvo Prospondylidae fam. nov. [Family Prospondylidae fam. nov.]. – In: EBERZIN, A. G. (ed.) Osnovy Paleontologii. Spravochnik dlya paleontologov i geologov SSSR. Mollyuski – Pantsirnyye, Dvustvorchatyye, Lopatonogiye [Basic Paleontology. Reference Book for the Paleontology and Geology of the USSR. Mollusks – Chitons, bivalves, scaphopods]. 86–87; Moskva (Isdastelstvo Akademii Nauk SSSR).

PHILIPPI, E. (1899): Beiträge zur Morphologie und Phylogenie der Lamellibranchier. – Zeitschrift der Deutschen Geologischen Gesellschaft, **50**(4): 597–622.

PHILLIPS, J. (1829): Illustrations of the Geology of Yorkshire; or a description of the strata and organic remains of the Yorkshire Coast. Part 1. 192 pp.; York (Printed for the author).

PHILLIPS, J. (1835): Illustrations of the Geology of Yorkshire; or a Description of the Strata and Organic Remains: accompanied by a geological map, sections and diagrams, and figures of the fossils. Part I. The Yorkshire Coast. Second Edition. 184 pp.; London (J. Murray).

PICTET, F.-J. & ROUX, W. (1847–1853): Description des mollusques fossiles qui se trouvent dans les Grès Verts des environs de Genève. 558 pp., 51 pls.; Genève (Imprimerie de Jules-Gme Fick).

QUENSTEDT, F.A. von (1856–1857): Der Jura. pp. 1–208, pls. 1–24 (July 1856), pp. 209–368, pls. 25–48 (December 1856), pp. 369–576, pls. 49–72 (April 1857), pp. i–vi + 577–842, pls. 73–100 (October 1857); Tübingen (Laupp & Siebeck).

QUENSTEDT, F.A. von (1865–1866). Handbuch der Petrefaktenkunde. Zweite umgearbeitete und vermehrte Auflage. pp. 1–320, pls. 1–24 (1865, second half), pp. 321–640, pls. 25–52, 54–56 (1866, first half), pp. I–VIII, 641–982, pls. 52, 53, 57–86 (1866, second half); Tübingen (Laupp).

RAFINESQUE, C.S. (1815): Analyse de la nature ou tableau de l'univers et des corps organisés. 223 pp.; Palermo (Privately published by author).

ROEMER, F.A. (1835–1836): Die Versteinerungen des norddeutschen Oolithen-Gebirges. 218 pp., 16 pls. [pp. i–vi + 1–74, pls. 1–12 (1835), pp. 75–218, pls. 13–16 (1836)]; Hannover (Hahn).

ROLLIER, L. (1906): Fossile Fauna. – In: KNAPP, C., BOREL, M. & ATTINGER, V. (eds.): Geographisches Lexikon der Schweiz. Vierter Band. Plessur-Schweiz. 737–763; Neunberg (Gebrüder Attinger).

ROLLIER, L. (1911–1917): Fossiles nouveaux ou peu connus des terrains secondaires (mésozoiques) du Jura et de contrées environnantes. – Mémoires de la Société Paléontologique Suisse: 1. partie: 37, pp. 1–32 (1911); 2. partie: 38, pp. 33–148 (1912); 3. partie: 39, pp. 149–318 (1913); 4. partie: 40, pp. 319–344 (1914); 5. partie: 41, pp. 345–500 (1915); 6.+ 7. partie: 42, pp. 501–696 (1917).

ROMANOV, L.F. (1985): Yurskiye pektinoidy yuga SSSR [Jurassic pectinoids from southern USSR]. 231 pp., 30 pls.; Kishinev (Shtiintsa).

ROSENKRANTZ, A. (1934): The Lower Jurassic Rocks of East Greenland. Part I. – Meddelelser om Grønland, **110**(1): 1–122.

ROSENKRANTZ, A. (1956): A Large *Velata* from the Lower Jurassic of East Greenland. – Meddelelser fra Dansk Geologisk Forening, **13**(2): 79–84.

ROS-FRANCH, S., MÁRQUEZ-ALIAGA, A. & DAMBORENEA, S.E. (2014): Comprehensive database on Induan (Lower Triassic) to Sinemurian (Lower Jurassic) marine bivalve genera and their paleobiogeographic record. – Paleontological Contributions, **8**: 1–219. doi: 10.17161/PC.1808.13433

SHURYGIN, B.N. & LUTIKOV, O.A. (1991): Nizhneyurskiye pektinidy severa Aziatskoy chasti SSSR [Lower Jurassic pectinids of the northern Asian parts of the USSR]. – In: Detal'naya stratigrafiya i paleontologiya yury i mela Sibiri [Detailed stratigraphy and paleontology of the Jurassic and Cretaceous of Siberia]. 47–78; Novosibirsk (Nauka).

SINELNIKOVA, V.N. (1975): Mio-pliotsenovyye pektinidy Kamchatki [Mio-Pliocene Pectinidae of Kamchatka]. – Trudy Geologicheskogo Instituta AN SSSR, **229**: 1–142.

STAESCHE, K. von (1926): Die Pectiniden des Schwäbischen Jura. – Geologische und palaeontologische Abhandlungen, neue Folge, **15**: 1–136.

STAESCHE, K. von (1931): Bemerkungen zu einigen jurassischen *Pecten*-Arten. – Centralblatt für Mineralogie, Geologie und Paläontologie. Abteilung B: Geologie und Paläontologie, **1931**: 78–87.

STAESCHE, K. von (1932): Über einige Trias- und Jura-Fossilien aus Nordkaschmir. – In: TRINKLER, E. (ed.): Wissenschaftliche Ergebnisse der Dr. Trinklerschen Zentralasien-Expedition, Band 1, Geographische Forschungen im westlichen Zentralasien und Karakorum-Himalaya. 137–154; Berlin (Verlag Dietrich Reimer).

STOPPANI, A. (1858–1860): Paléontologie Lombarde ou description des fossiles de Lombardie. I. Les pétrifications d'Ésino, ou Description des fossiles appartenant au dépôt triasique supérieur des environs d'Ésino en Lombardie. 151 pp., 31 pls.; Milano (Joseph Bernardoni).

SZENTE, I. (1996): Bivalve ecology in the Pliensbachian (Lower Jurassic) of the Bakony Mts. (Hungary). Description of a new species of *Eopecten*. – Fragmenta Mineralogica et Palaeontologica, **18**: 19–29.

TAMURA, M. (1959): Taxodonta and Isodonta from the Jurassic Soma group in north Japan. – Transactions and Proceedings of the Palaeontological Society of Japan, new series, **36**: 168–180.

TAMURA, M. (1973): Pectinids from Malayan Triassic. – Geology and Palaeontology of Southeast Asia, **13**: 115–131.

TRAUTH, F. (1923): Über eine Doggerfauna aus dem Lainzer Tiergarten bei Wien. – Annalen des Naturhistorischen Museums in Wien, **36**: 167–250.

WAAGEN, L. (1907): Die Lamellibranchiaten der Pachycardientuffe der Seiser Alm nebst vergleichend paläontologischen und phylogenetischen Studien. Als Fortsetzung (II. Teil) zu: A. Bittner, Lamellibranchiaten der alpinen Trias. – Abhandlungen der kaiserlich-königlichen Geologischen Reichsanstalt, **18**: 1–180.

WALLER, T.R. (2006): Phylogeny of families in the Pectinoidea (Mollusca: Bivalvia): importance of the fossil record. – Zoological Journal of the Linnean Society, **148**(3): 313–342.

WATERHOUSE, J.B. (2000): Early Triassic Pectinidina (Mollusca: Bivalvia) from Dolpo and Manang, Nepal Himalaya. – Records of the Canterbury Museum, **14**: 155–186.

WEIR, J. (1930): Mesozoic Brachiopoda and Mollusca from Mombasa. In: McKinnon Wood, M., Reports on geological collections from the coastlands of Kenya Colony. – Monographs of the Geological Department of the Hunterian Museum Glasgow University, **4**: 73–102.

WEIR, J. (1938): The Jurassic Faunas of Kenya, with description of some Brachiopods and Mollusca. In: McKinnon Wood, M., On a second collections of fossils and rocks from Kenya. – Monographs of the Geological Department of the Hunterian Museum Glasgow University, **5**: 17–60.

WEIS, R., SCHWEIGERT, G. & WITTISCHE, J. (2023): A new giant nautilid species from the Middle Jurassic of Luxembourg and Southwest Germany. – Swiss Journal of Palaeontology, **142**(1): 24.

YAMANI, S.-A. (1975): Bivalvenfauna der Korallenkalke von Laisacker bei Neuburg a. d. Donau (Unteres Tithonium, Bayern). – Palaeontographica, Abt. A, **149**: 31–118.

YONGE, C.M. (1951): Observations on *Hinnites multirugosus* (Gale). – University of California Publications in Zoology, **55**: 409–420.

ZIMMERMANN, E.H. (1886): Ein neuer Monomyarier aus dem ostthüringischen Zechstein (*Prospondylus Liebeanus*). – Jahrbuch der Königlich Preussischen Geologischen Landesanstalt und Bergakademie zu Berlin, **6**: 105–118.

Figures

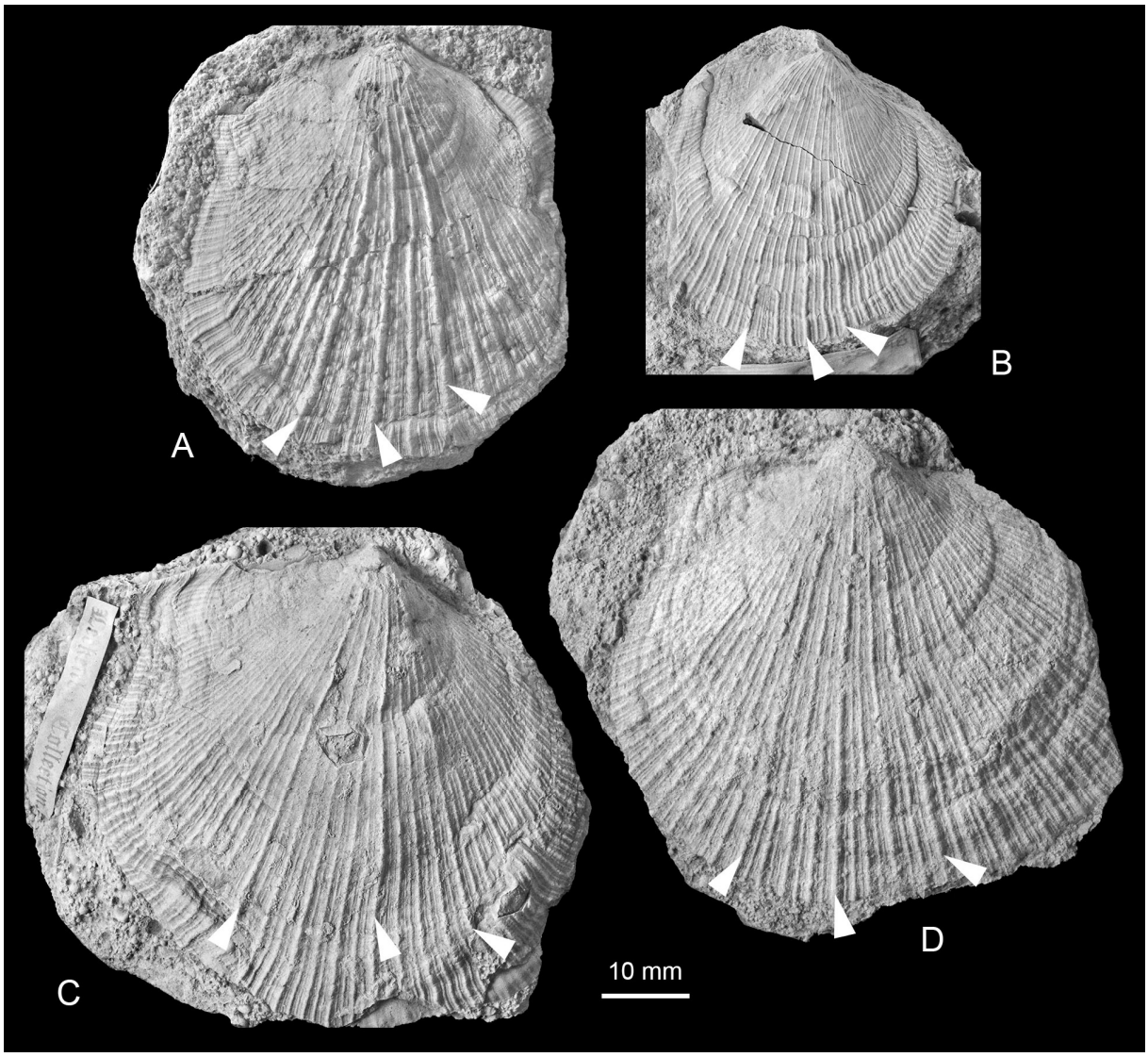

Fig. 1. *Velata abjecta* (PHILLIPS, 1829). Topotypic material from the Lebberston Member of the Cloughton Formation at Whitwell-on-the-Hill, North Yorkshire, UK; *Hyperlioceras discites* ammonite zone, lower Bajocian; all left valves. **A.** Specimen CAMSMJ.51196, with three distinctly more prominent primary costae (arrows). **B.** Specimen CAMSMJ.51198, with three only slightly more prominent primary costae (arrows). **C.** Neotype, CAMSMJ.23238, original of *Hinnites abjectus* (PHILLIPS) in MORRIS & LYCETT (1855: pl. 14, fig. 3), with three distinctly more prominent primary costae (arrows). **D.** Specimen CAMSMJ.51197, with three only slightly more prominent primary costae (arrows).

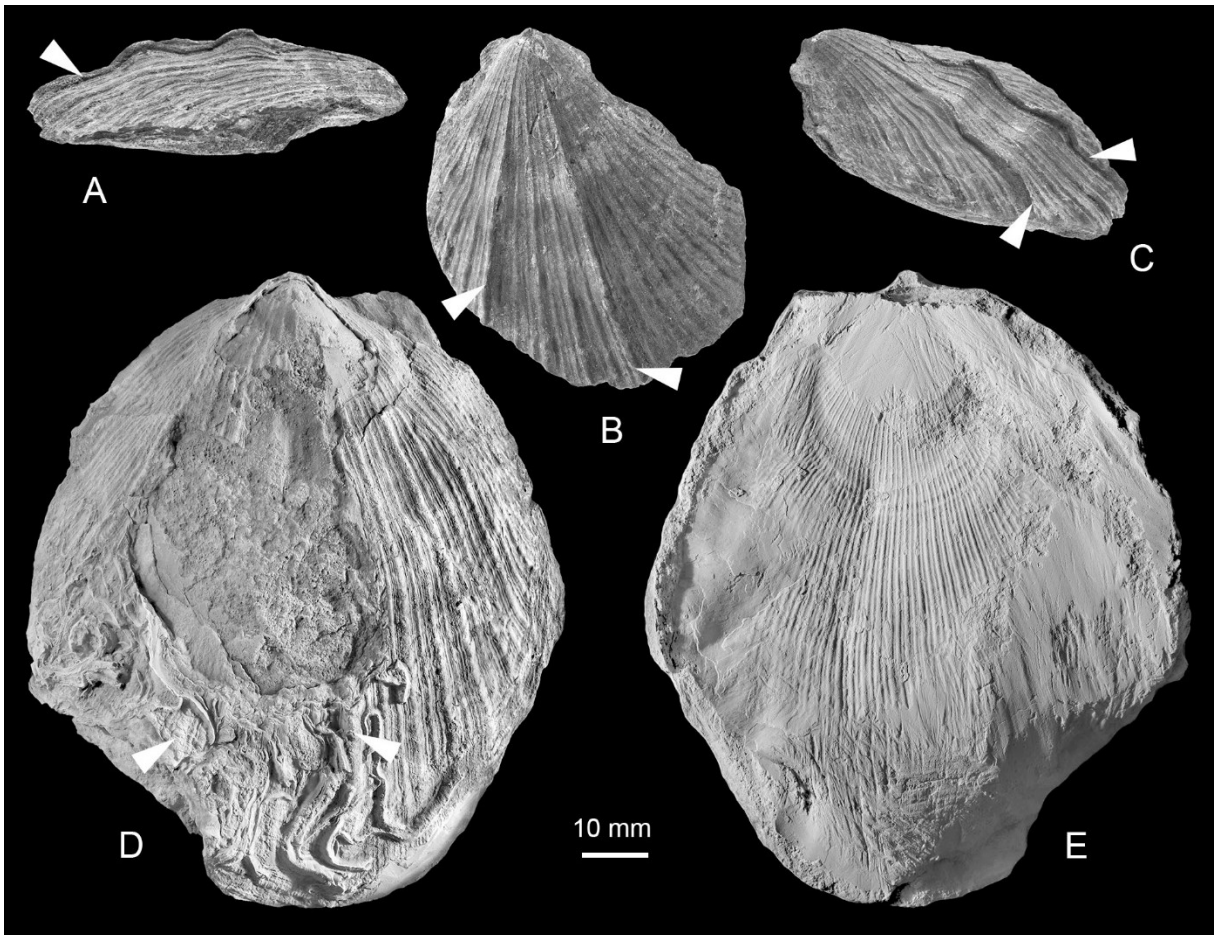

Fig. 2. *Velata abjecta* (PHILLIPS, 1829). Syntypes of *Spondylus tuberculosus* GOLDFUSS, 1835, from the Sengenthal Formation of Baden-Württemberg, Germany; *Stephanoceras humphriesianum* ammonite zone, lower Bajocian. **A–C.** Paralectotype, BIOB-PAL-Goldfuss-643, left valve from Aalen, in posterior (**A**), lateral (**B**) and obliquely anterior (**C**) view (photographs: MANUEL KUNZ, Goldfuß Museum Bonn, Germany). The two prominent first order costae are indicated arrowed. **D, E.** Lectotype, SNSB-BSPG AS VII 640, specimen with articulated valves from Wasseralfingen. **D.** Left valve. The two prominent first order costae are arrowed. **E.** Right valve.

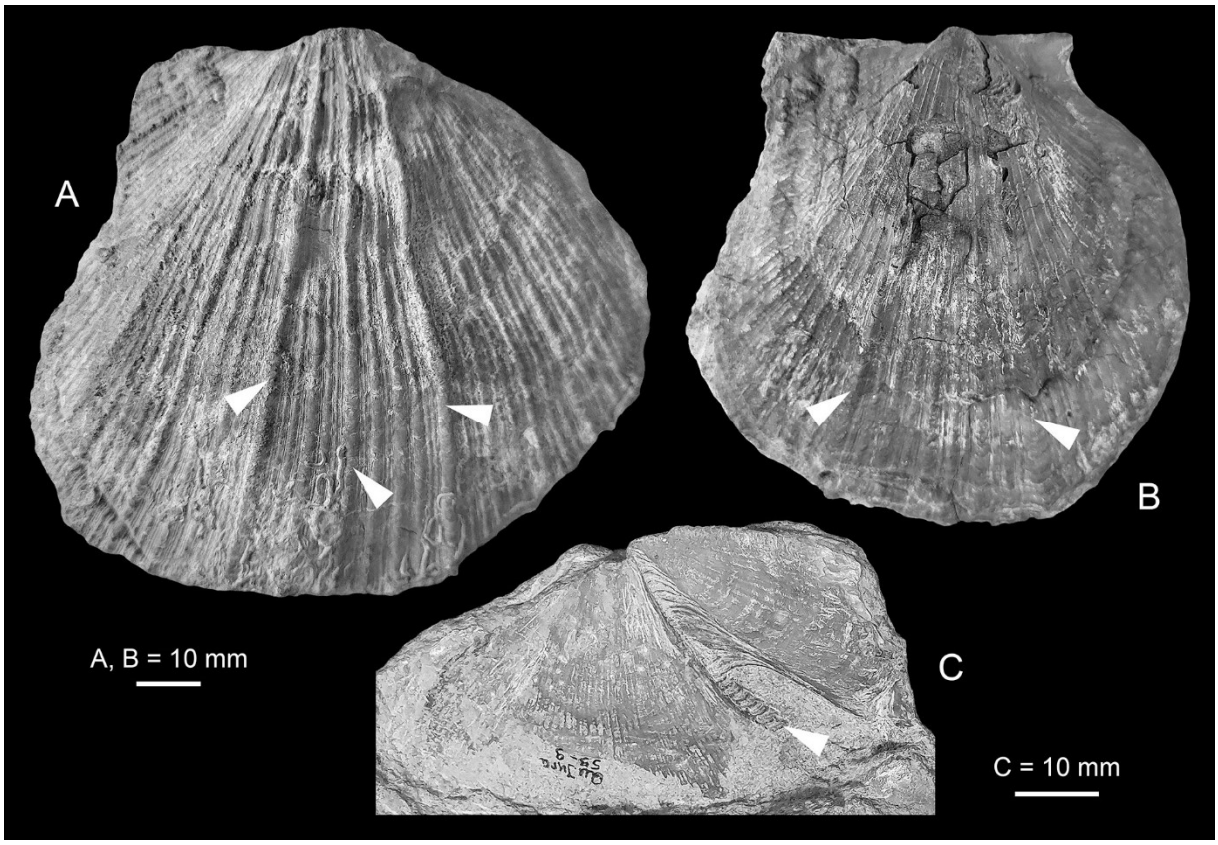

Fig. 3. *Velata abjecta* (PHILLIPS, 1829) from the *Stephanoceras humphriesianum* ammonite zone, lower Bajocian of Baden-Württemberg, Germany. **A, C.** Original of *Pecten tuberculosus* (GOLDFUSS, 1835) as figured by QUENSTEDT (1857: pl. 59, fig. 9, 1866, pl. 52: fig. 17), GPIT-PV-52464, articulated specimen, with posterior auricles missing, from the Gosheim Formation at Hohenkarpfen hill south of Spaichingen. **A.** Left valve. The three prominent first order costae are arrowed. **C.** Top part of right valve from outside, showing the deep byssal notch and active ctenolium (arrowed). **B.** Original of *Pecten tuberculosus* (GOLDFUSS, 1835) as figured by QUENSTEDT (1857: pl. 59, fig. 10), GPIT-PV-52464, left valve from the Sengenthal Formation at Wasseralfingen. The two prominent first order costae are arrowed.

Supplementary material

Table S1. Uncritical list of species-group names that have been originally placed in *Velata* or its synonyms or are assigned to them following the latest literature, including information on the latest published taxonomic status, type region, stratigraphic distribution, and taxonomic sources. Note that this list does not represent a revision of the taxa included. Geographic and stratigraphic data refer only to type material and disregard subsequent changes of a species' taxonomic concept. Additional species mentioned by JOHNSON (1984, p. 150) as potentially belonging to *Eopecten* are excluded here, as is the genus *Ventalium*, which is only tentatively considered a synonym of *Velata*.