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On the Vaugoniinae (Trigoniida, Myophorelloidea, Vaugoniidae): their palaeobiogeography and classification

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ABSTRACT

Vaugoniines are a pandemic predominantly Jurassic group of trigoniid bivalves, most diverse in the Tethyan Realm but with a near circum-Pangaeal distribution, unrecorded only from the interior of the supercontinent. They are first reported from the Hettangian of the Oriental Province, seemingly with an origin in Frenguelliellidae close to *Kumatrigonia*, but radiated in the Middle Jurassic of Tethys and declined in the Tithonian, becoming extinct in the Early Cretaceous (Valanginian). Relationships within the group are difficult to assess since flank chevrons vary from V- to U-shaped and curved oblique, some thus approaching myophorellines and orthotrigoniines with which they evolved in parallel. Here 153 species/subspecies/varieties are assigned to the subfamily and distributed among 31 genera, 23 of which are new, as well as two new species. Type species are redescribed, systematics re-assessed and palaeobiogeography outlined.

Key words: Bivalvia, Trigoniida, Myophorelloidea, Vaugoniidae, Vaugoniinae, palaeobiogeography, palaeoecology, systematics, new genera.

INTRODUCTION

The section Ondulées (Undulatae) was one of the first groups of trigoniid bivalves to be discriminated (Agassiz 1840: 9). Perhaps, however, because it was introduced for "a very remarkable small section" (translated), it was soon, as a matter of convenience, subsummed into the Clavellatae (Myophorellidae) (Lycett 1853). It then took ninety years for the group to be separated generically from *Trigonia*, with introduction of the genus *Vaugonia* (Crickmay 1930). Lebküchner (1932) however found it difficult to separate forms with V-shaped flank costae from some with oblique ribs (= *Myophorella*), and so introduced the genus *Clavotrigonia* (type species *Trigonia clavellata* J. Sowerby) to cover those with both these attributes, but this genus is now widely included in the synonymy of *Myophorella* (Poulton 1979, Francis 2000; but see Cooper 1991).

Cox (1950) treated *Vaugonia* as a subgenus of *Myophorella*, but Kobayashi (1954: 68) not only recognized the genus but introduced the subfamily Vaugoniinae for "Trigonal or ovate Trigonians with sinuate, V-shaped or more complicated costae on the disc". Cox (1969: N488), chose not to recognize subfamilies and placed *Vaugonia* in the Trigoniidae, to which he was followed by Reyes & Pérez (1978, 1984). Hayami (1975) however admitted the taxon but relegated it to a tribe within the Myophor-ellinae. Fleming (1987: 33) gave *Vaugonia* "full generic status within Myophor-ellinae … despite Kobayashi's contention that it indicates a distinct and independent branch". Poulton (1979: 21) felt that "The close relationship of

Myophorella and *Vaugonia* is emphasized by the abundance of intermediate forms, but the presence of these forms does not invalidate the taxonomic separation of the genera". Cooper (1991: 11) regarded the Myophorellinae as frenguelllielline descendants, independent of Vaugoniinae, and united the predominantly Jurassic (Fig. 1) Vaugoniinae and the chiefly Cretaceous Quadratotrigoniinae (Cooper 2019) as family Vaugoniidae within the superfamily Myophorelloidea. To this he subsequently added the largely Cretaceous subfamily Orthotrigoniinae (Cooper 2024).

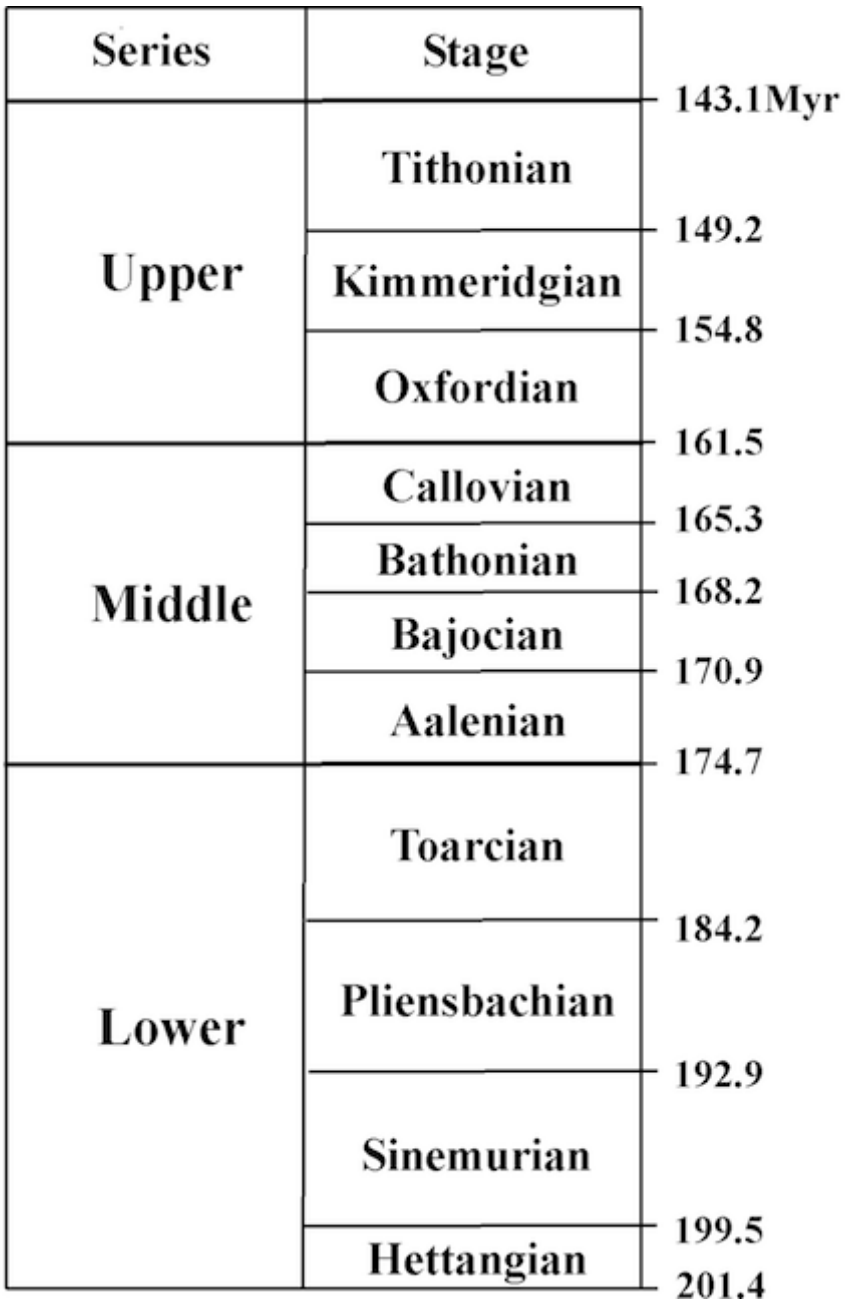

Fig. 1. The Jurassic time scale.

Francis (2000: 255) appreciated that *Vaugonia* was "a large and morphologically complex genus, united by the ubiquitous characteristic of V-shaped tuberculate to non-tuberculate costae on the flank". V-shaped flank costae are, however, plesio-

morphic for the group and by no means ubiquitous. Perspicaciously Echevarría *et al.* (2018: 44) recognized that "a wide variety of species have been included within the genus, which deserves detailed phylogenetic revision" and, as is apparent from this study, a conservative taxonomy has served to mask a significant evolutionary radiation.

With respect to origin, Kobayashi & Mori (1955: 74, unnumbered text-fig. on p.76) suggested "there is every gradation in the development of costae from the *Frenguelliella* to the *Vaugonia* stage through the *Jaworskiella* stage." Echevarría *et al.* (2018, 2021) strongly supported the claim (Kobayashi, 1954) that *Myophorella* and *Vaugonia* belonged to different phyletic lines and, for the Myophorellinae, envisaged the independent lineage *Frenguelliella – Moerickella – Promyophorella – Myophor-ella*.

The side-by-side occurrence of *Hijitrigonia* and *Vaugonia* in the Hettangian of Japan, before the earliest records of either *Frenguelliella* in the Sinemurian or *Jaworskiella* in the Pliensbachian (Peréz *et al.* 2008), points to an older common ancestor for the two lineages. The Frenguelliellinae are first represented by Carnian *Kumagonia* (Tamura 1959), that had been subsumed into *Frenguelliella* (Poulton 1979), which shares with *Hijitrigonia* its shape, very broad lirate area and prominent transversely scaled marginal carina but, most obviously, differs in its fine nontuberculate commarginal flank costellae. According to Poulton (1979: 18), "The morphological and taxonomic separation of *Frenguelliella* from similar and probably ancestral Late Triassic and Early Jurassic *Prosogyrotrigonia* Krombeck is arbitrary, and is based on the prosogyrous umbos, the simple ovate or subcircular outline and the absence of a distinct marginal carina (or edge at the same position) in the type species of *Prosogyrotrigonia.*" Since the writer recognizes the genus *Kumatrigonia* it provides the most likely antecedent for *Vaugonia*, confirming that the latter belongs to a different phyletic line to the Myophorellidae.

PALAEOECOLOGY

Lycett (1874: 75, footnote) reported *T. tripartita* Forbes from the Loch Staffin Shale of Skye "with a *Perna* and an *Ostrea*, and with ten other species, belonging to the fluviatile genera, *Cyrena*, *Potamomya*, *Unio*, *Neritina*, and *Hydrobia*" suggesting an estuarine depositional environment. Anderson & Cox (1948) described *Trigonia staffinensis* from the same Great Estuarine Series in which marine and brack water strata intertongue (Cox 1950). In Japan Hayami (1961: 282) recorded *Vaugonia* "intimately connected with coarse non-bituminous sandy lithology which show littoral and much agitated environment". Poulton & Callomon (1977: 156) suggested however that "The classical marine Bathonian of Britain and north-western Europe was separated from the Arctic seas by a region of deltaic sedimentation in brackish waters whose salinity varied from time to time and place to place. It seems likely that this represented an impenetrable barrier to stenohaline bivalves, such as the Trigoniidae are thought to have been". In Western Europe vaugoniines abound in the Inferior and Great Oolite (Aalenian-Callovian) and Stanley (1977) commented on the frequent association of Jurassic species with oolitic deposits. Palmer (1979) recorded *T. moretoni* Morris & Lycett in clean washed lime sands of the Great Oolite but, since "There is little evidence that trigoniids actually inhabited bars of shifting oolite" (Stanley, 1977: 873), probably they are an allochthonous component washed in from very nearshore, even intertidal, high-energy environments. Stanley (1977, pl. 117,

figs 1-3) figured, however, an articulated *Hijitrigonia* in life position from the Toarcian Peak Shale of Yorkshire, associated with fossil wood, pointing to a low-energy back-barrier (lagoonal) depositional environment. In North America Poulton (1979: 5) observed that "Clastic rocks as coarse as grit grade … contain *Vaugonia* and *Myophorella* species, some of which occur with equal or greater abundance in fine-grained rocks." It seems probable therefore, as implied by their diversity, that vaugoniines were adapted to a variety of very nearshore shallow-marine to estuarine environments and, as with many trigoniids, are particularly abundant in high-energy transgressive marine deposits (Francis 2000).

Like all trigonias, vaugoniines are infaunal burrowers and, contrary to illustrations in the literature, the writer believes the angle of truncation of the respiratory margin is not incidental but an important indicator of burial orientation, broadly coinciding with the sediment-water interface. For *Arkelligonia fischeri* (Bigot 1893, pl. 15, fig. 8) this angle of repose is 20°, for *A. adeli* (Bigot 1893, pl. 13, fig. 5) and *Gerasimovella compta* (Lycett 1874, p. 15, fig. 5) it is 25°, for *Vaugonia veronica* (Poulton 1979, pl.10, fig. 5), *Lissotrigonia doroschini* (Eichwald) (Poulton 1979, pl. 10, fig. 25) and *Vaugoniella vcostata* (Lycett 1874, pl. 15, fig. 1) it is 35°, for *Hijitrigonia literata* (Young & Bird) (Lycett 1874, pl. 14, fig. 1) and *Agassigonia parkinsoni* (Agassiz 1840, pl. 10, fig. 6) it is 45°, for *Morigonia imlayi* (Poulton 1979, pl. 10, fig. 7) 50°, for *Wyomingella poststriata* (Whitfield & Hovey 1906, pl. 48, fig. 6), *Hijitrigonia geniculata* (Kobayashi & Mori 1955, pl. 4, fig. 5) 65°, and for *Pulchelligonia kurri* (Oppel; Lebküchner 1932, pl. 9, fig. 8) it is 72°. As a generality, the smaller the species the steeper its angle of repose within the sediment, a hardly surprising observation since this would impede disinterment by wave action. Of some significance also is the ornament of the area. Delicate lirae and lamellae on this surface would have had functionality only in low-energy environments, whereas growth striae would have prevailed under turbulent high-energy conditions.

Intraspecific variation

There is the presumption of substantial intraspecific variation among vaugoniine species as suggested for *M. niranohamensis* (Kobayashi & Mori 1955), and as illustrated by Choffat (1885) for *Alcobacella lusitanica* (Sharpe). With respect to the latter, however, it should be noted that Choffat's material came from numerous different localities (Santa Cruz, Forts de Telhadouro, environs de Torres Vedras, Boiçâo, Castello Picâo, Maceira, Santa Thiago dos Velhos, Louriciera, Enxara do Bispo, Castello Picâo and Santa Sebastiâo) and is, therefore, a highly mixed sample from different stratigraphical levels, that cannot be accepted as representative of polytypy in a contemporaneous population. On the other hand, with regard to the genus *Hijitrigonia*, Kobayashi & Mori (1955: 84) found it "noteworthy that the surface ornamentation is quite uniform and constant within each of these Japanese species", and Alencáster (1963) commented on the uniformity of ornament within *G. kobayashii*. A similar conformity of ornament is displayed by the syntypes of *W. substriata* (Whitfield & Hovey 1906). Consequently polytypy should not be presumed, especially when based upon material from different localities and disparate stratigraphical horizons. As a result, here, all nominal taxa are treated as valid pending objective population analysis of numerically adequate, stratigraphically tightly constrained topotype samples. In this respect, morphometric analysis of stratigraphically mixed samples, without consideration of "trifling characters" and

phenotype (*cf.* Francis 2000), and the resulting gross lumping of taxa, is regarded as specious.

PALAEOBIOGEOGRAPHY

Vaugoniines have a circum-Pangaeal distribution, longitudinally ranging from the Arctic to Antarctica, with their greatest diversity in the great Tethys Sea and a notable absence from the Ethiopian, Middle East and Australasian provinces (Cooper 2015a). It is important to appreciate, however, that biochore boundaries are labile, and their representation on a map records only a moment in time. The geographical positions of the sedimentary basins in which vaugoniines existed changed with the northward drift of Pangaea during the Jurassic (Fig. 2), and their precise boundaries were in constant flux due to fluctuations in sea level. Vaugoniines prevailed in the Jurassic, with stragglers persisting into the Lower Cretaceous (Valanginian), and existed for a period of about 70 Myr. During this time their dispersal and widespread distribution was facilitated by a succession of transgressive-regressive cycles (Hallam 1978), what Fleming (1987: 16) termed "*the Tethyan Invasion*".

Based on ammonites, Page (2008) distinguished 20 biogeographical provinces and subprovinces during the Jurassic, not all of which are recognizable among the trigoniids. This, however, is unsurprising since it should not be expected that the biochore boundaries of sedentary infaunal burrowers and highly mobile nektonic organisms would coincide precisely. Until reclassification of the trigoniids is complete, the writer retains the trigoniid provinces recognized earlier (Cooper 2015a).

Arctic Province: Cooper (2015a) assigned northern Alaska, the Yukon and the Canadian Arctic archipelago to the Cordilleran Province when, now, together with his Siberian Province, they are incorporated into the Arctic Province (Shurygin *et al.* 2011). It is important to appreciate however that, during the Jurassic, North America (and hence all the attached elements of Pangaea) drifted northwards through about 35° (Fig. 2). It was only by the Late Tithonian that the present-day Arctic archipelago (Bank Island specifically) reached the North Pole. During the Toarcian, southern Alaska lay at 60°N of latitude (Fig. 2) and thus well outside the Arctic Circle at 66°33'N. Poleward of the Arctic Circle, which southern Alaska reached only in the Late Kimmeridgian-Early Tithonian, day and night are each of 6 month duration, with its profound effect on faunas and palaeoecology (Nikitenko *et al.* 2008).

The vaugoniine *athena* Poulton & Callomon (Rosenkranz 1934, 1942, Poulton & Callomon 1977) was discovered in the Bathonian of east Greenland, which lay at about 45°N of latitude at that time, well south of the Arctic Circle, in what Poulton (1979) labelled the Boreal Realm. A marine connection existed between east Greenland and northwest Europe from the beginning of the Callovian until the Late Tithonian (Imlay 1980), but trigoniids of this age are unrecorded from the Arctic.

Siberian Province: Efimova *et al.* (1968: 93, pl. 42, figs 1-5) reported *Myophorella* (*Vaugonia*) *literata* (Young & Bird) from the lower Upper Toarcian (*Porpoceras spinatum* Zone) of the Omolon river basin of Chukotka, north-eastern USSR, and thus at about 60°N of latitude at that time.

Cordilleran Province: This province (southern Yukon, southern Alaska, British Columbia, Oregon, Alberta) was part of the Boreal Realm (Hallam 1969) and

maintained tenuous and perhaps intermittent marine connections with the Arctic between the Toarcian and Early Tithonian (Imlay 1980). Southern Yukon lay at about 60°N of latitude during the Toarcian (Fig. 2), the same latitude as the Siberian Province, with, to the south, an open marine connection to the American Province.

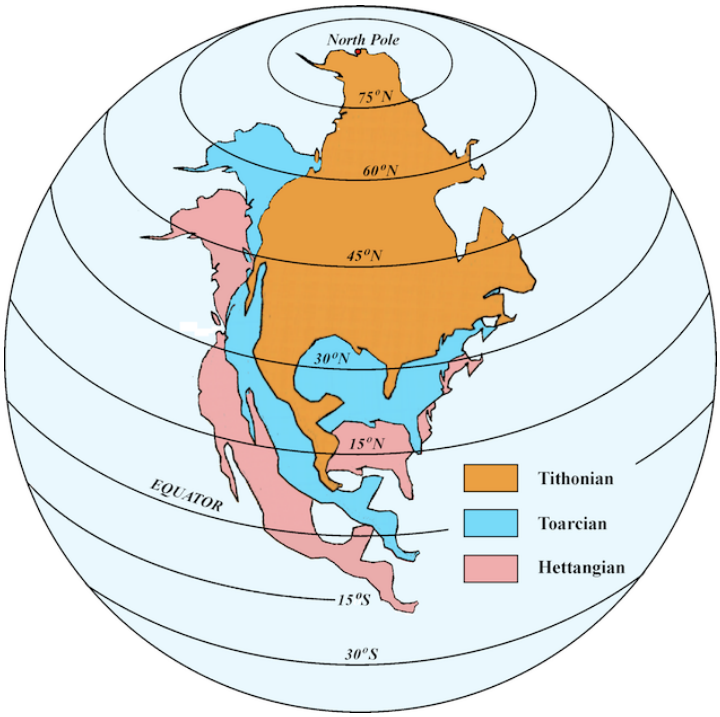

Fig. 2. The northward drift of North America during the Jurassic (adapted from Kent & Irvine (2010)).

The vaugoniines of this province have been documented by Eichwald (1871), Hyatt (1892), Packard (1921), Crickmay (1930), Sanborn (1960) and Poulton (1976, 1979, 1980, 1991). Species present, mostly if not entirely endemic, are *coatesi* Poulton, *doroschini* Eichwald, *imlayi* Poulton, *jeletzkyi* Poulton, cf. *kobayashii* Alencáster, sp. nov.? aff. *literata* (Young & Bird), *mariajosephinae* Crickmay, *oregonensis* Poulton, *vancouverensis* Poulton, *veronica* Crickmay and *yukonensis* Poulton.

Oriental Province: Vaugoniines are recorded from Primorsky Krai (= Primorye) and Japan by Yokoyama (1904), Kulzhinskaya-Voronets (1936), Shikama (1943, 1952), Kobayashi (1954), Kobayashi & Mori (1955), Kobayashi & Tamura (1959), Maeda (1962, 1963), Maeda & Kawabe (1963), Hayami (1975), Konovalov & Miroljubov (1978) and Konovalova (1979). Nominal species/subspecies/forms recorded, all endemic, are *ariminensis* Maeda & Kawabe, *awazuensis* Kobayashi & Tamura, *banevurica* Konovalova, *cuneata* Konovalova, *fukuiensis* Maeda, *geniculata* Kobayashi & Mori, *kodaijimensis* Kobayashi & Mori, *kojiwa* Kobayashi & Mori, *kuzuryuensis* Maeda, *magna* Konovalova, *namigashira* Kobayashi & Mori, *niranohamensis* Kobayashi & Mori, *subrotunda* Konovalova, *ussuriensis* Konovalova, *yokoyamai* Kobayashi & Mori and *yambarensis* Kobayashi. They range in age from Hettangian to Oxfordian.

Sinian Province: The vaugoniine *mindoroensis* Hayasaka comes from an undated locality in the Philippines (Hayasaka 1943, Kobayashi & Mori 1955, Kobayashi 1957).

Central Asian Province: Vaugoniines have been reported from this province (= Pontic Province of Vörös & Escarguel 2019) by Rouillier & Vossinsky (1849), Redlich (1894), Pčelincev (1937), Gerasimov (1955), Savel'ev (1960a, b), Sibiriakova (1961), Yungerman (1962), Dykan (1986), Dykan & Makarenko (1990) and Wen (*in* Zhang *et al.* 1979). These are *corallina* d'Orbigny, *donbassica* Dykan, *flecta* Morris & Lycett, *formosa* Lycett, *jonioi* Rouillier & Vossinsky, *koprinensis* Gerasimov, *laevicostata* Redlich, *obscura* Savel'ev, *ucrainica* Yungerman, *uralica* Savel'ev, gr. *vcostata* Lycett, *subsignata* Savel'ev, *smirnokoffensis* Dykan and *yanshipingensis* Wen. Those few species that are pandemic suggest intermittent connections with the European Province.

European Province: Palaeomagnetic data place this province, that includes parts of the Boreal and Sub-boreal provinces of ammonites (Hesselbo *et al.* 2020), between 30-45°N of latitude during the Middle and Late Jurassic. Faunal links were established with the Siberian Province in the Late Toarcian, and with the American Province in the Middle Oxfordian (Imlay 1980). Vaugoniines entered the European Province during the Toarcian rise of sea level, and have been recorded by Parkinson (1811), Goldfuss (1826, 1834), Sowerby (1826, 1829), Young & Bird (1828), Phillips (1829), Benett (1831), Fromherz (1837), Quenstedt (1837), Agassiz (1840), d'Orbigny (1844, 1850), Morris & Lycett (1850, 1853), Sharpe (1850), Lycett (1850, 1863, 1874, 1977, 1879, 1883), Forbes (1851), Quenstedt (1852, 1867 3rd ed.), Oppel (1857), Wright (1860), Dollfus (1862), Étallon (1864), Seebach (1864), Munier-Chalmas (1865), Eichwald (1865-68), de Loriol (1866), de Loriol & Pellet (1866), Waagen (1867), Quenstedt (1867), Terquem & Jourdy (1869), Greppin (1870), Branco (1879), Blake (1880), Choffat (1885), Schlippe (1888), Bigot (1893), Slosser (1901), Riche (1904), Schmidt (1905), Benecke (1905), Schmidtill (1925), Douglas & Arkell (1928), Strand (1928), Arkell (1929-37), Dechaseaux (1931), Lebküchner (1932), Anderson & Cox (1948), Cox & Arkell (1948, 1953), Freneix (1958), Fischer (1969), Pugaczewska (1975, 1976), Duff (1978), Francis (2000) and Lebrun (2021). Nominal species/varieties recorded are *angulata* Sowerby, *arata* Lycett, *bathonicola* Strand, *carrei* Munier-Chalmas, *caytonensis* Duff, *clythia* d'Orbigny, *complanata* Lycett, *conjugens* Phillips, *corallina* d'Orbigny, *cuspidata* Sowerby, *decurtata* Lycett, *depereti* Riche, *exaltata* Lycett, *eudesii* Bigot, *eugeni* Bigot, *ferryi* Munier-Chalmas, *flecta* Morris & Lycett, *flexicostata* Fischer, *gardeti* Freneix, *hudlestonei* Lycett, *irregularis* Seebach, *kerfornei* Bigot, *leckenbyi* Lycett, *literatum* Young & Bird, *moretoni* Morris & Lycett, *oxoniensis* Lycett, *producta* Lycett, *pulchella* Agassiz, *radiata* Benett, *rottwellensis* Strand (= *pulchella* var. β Quenstedt), *rugulosa* Lycett, *spinulosa* Young & Bird, *stutterdi* Lycett, *subglobosa* Lycett, *suevica* Quenstedt, *trouvillensis* Strand (= *fischeri* Bigot *non* Munier-Chalmas), *vcostata* Lycett, *williamsoni* Lycett, *windoesi* Lycett, *zieteni* Lycett and *zitteli* Branco.

Vaugoniines endemic to the *Swabian Subprovince* of eastern France, Luxembourg, Switzerland, Poland, Czechoslovakia and southwest Germany (including the Alpine Province of Enay & Mangold 1980), are *agassizi* sp. nov., *bathonica* Strand, *branconis* Strand, *brevis* Lebküchner, *clavellata* Goldfuss (*non* Parkinson 1811), *couzonensis* Riche, *engeli* Benecke, *fragilis* Lebküchner, *franconica* Lebküchner, *geographica* Agassiz, *goldfussi* Agassiz (*non* Alberti *in* von Zieten), *hauchecornei* Schmidt, *interplanata* Lebküchner, *kurri* Oppel, *metzensis* Strand, *parkinsoni* Agassiz, *reussi* Strand, *terquemi* Benecke and *trigona* Waagen.

As used here the *Mediterranean Subprovince* is restricted to Portugal, Spain, Austria, Italy and North Africa (*cf.* Page 2003, but see also Vörös & Escarguel 2019). The vaugoniines, all from the Callovian-Tithonian of Portugal, have been recorded by Goldfuss (1835, 1837), Sharpe (1850), Choffat (1885), Strand (1928) and Schneider (2009). They are the endemic species *beirensis* Choffat, *lusitanica* Sharpe, *muricata* Goldfuss, *neumayri* Choffat, *ribeiroi* Choffat and *torrevedrasi* Strand.

American Province: In the Hettangian, Costa Rica was positioned at 15°S of latitude but, by the end of the Tithonian, it was at 8°N, having drifted northwards by 23° (Kent & Irvine 2010) (Fig. 2). During this time it was directly linked to the Cordilleran Province, as far south as Baja California, with the development of the *Western Interior Embayment* (Dakota, Utah, Wyoming) (Imlay 1980), and a northerly connection with the Arctic Province from the Bathonian until the Early Tithonian (Imlay 1980).

Meek & Hayden (1860), Meek (1864), Hall & Whitfield (1877), White (1880), Hyatt (1892), Whitfield & Hovey (1906), Veatch (1907), Butler *et al.* (1920), Packard (1921), Mansfield (1927), Krömmelbein (1956, 1960), de la Torre (1960), Sanborn (1960), Imlay (1964), Poulton (1976, 1979), Pugaczewska (1978) and Echevarría *et al.* (2018) all have recorded vaugoniines from the American Province. These are *conradi* Meek, *obliqua* Hyatt, *oregonensis* Poulton, *pandicosta* Meek, *quadrangularis* Hall & Whitfield, *sturgisensis* Whitfield & Hovey, *taylori* Poulton, *tuxedniensis* Poulton and *utahensis* Imlay.

Over 2000 km to the south, in western Mexico, the *Huayococotla Embayment* was independently connected to Panthalassa (the Pacific), and from Middle Oxfordian to Tithonian times provided a direct link, via Cuba, to the European Province (Imlay 1980). Its limited fauna of Aalenian-Middle Callovian age, when it was at about 7-10°N of latitude (Fig. 2), serves to distinguish the *Mexican biochore* recorded by Alencáster (1963) from the Late Bathonian Taberna and Middle Callovian Yucuñuti formations, and Eguiluz-de Antuñano *et al.* (2021) from the Aalenian of Durango. It has yielded the endemic species *kobayashii* Alencáster and *mexicana* Alencáster, seemingly with European affiliations.

Vaugoniines recorded from the *Antillean Subprovince* of Cuba are from the Oxfordian of the Cayetano Formation (Krömmelbein 1956, 1960, de la Torre 1960, Pugac-zewska 1978), when the country lay at about 22°N of latitude (Fig. 2). It has yielded the endemic species *cayetanoensis* Pugaczewska, *cubanensis* Pugaczewska, *kroemmelbeini* de la Torre and *postutahensis* Pugaczewska.

Andean Province: Palaeomagnetic evidence places Venezuela at about 20°S at the beginning of the Jurassic, from where it drifted northwards to lie at about 5°N of the equator at the close of the Tithonian (Kent & Irving 2010). Within the province Damborenea (2002) distinguished two subprovinces. The *North Andean Subprovince* comprised Venezuela, Colombia, most of Perú and the northernmost regions of Chile up to about 26°S of present-day latitude. The *South Andean Subprovince* consisted of most of Chile and Argentina, appearing in the Aalenian but being replaced by an Austral fauna of pterotrigoniines, rutitrigoniids and steinmanellines in the Tithonian. Species are recorded by Burmeister & Giebel (1861), Gottsche (1878), Möricke

(1894), Tornquist (1898), Philippi (1899), Jaworski (1915, 1925), Behrendsen (1922), Geyer (1973), Valenzuela (1975), Pérez & Reyes (1977, 1979, 1989), Reyes & Pérez (1978, 1984), von Hildebrand (1980), Ishikawa *et al.* (1983), Leanza (1985, 1993), Pérez *et al.* (1987), Leanza & Garate (1987), Pérez *et al.* (2008) and Echevarría *et al.* (2018, 2021), represented by *bigoti* Tornquist, *chunumayensis* Jaworski, *gottschei* Möricke, *hectorleanzai* Pérez, Aberhan, Reyes & von Hillebrandt, *hugoi* Leanza, *lycetti* Gottsche, *manflarum* Philippi, *praelonga* Gottsche, *rectangularis* Gottsche and *substriata* Burmeister & Giebel.

Antarctic Province: Kelly (1995) described *Vaugonia orvillensis* from the Latardy Formation of the Orville coast, believed to be of Kimmeridgian? - Tithonian age. Earlier Fleming (1987: 34) had discussed the Antarctic specimen identified by Quilty (1978) as *V. kawhiana*, pointing out that the anterior flank costellae bifurcate and suggest better assignment to *Orthotrigonia* (*cf.* Cooper 2024).

Maorian Province: Vaugoniines are known from the Bajocian to Tithonian of New Zealand (Trechmann 1923, Fleming 1987), represented by the endemic species *kahuika* Fleming, *kawhiana* Trechmann and *spedeni* Fleming. There was a clear faunal connection with the Antarctic Province at this time (Quilty 1978).

SYSTEMATIC PALAEONTOLOGY

Repositories of material: BGS - British Geological Survey; BMNH - Natural History Museum, London; GSC - Geological Survey of Canada, Ottawa; MHNM - Natural History Museum, Paris; OUM - Oxford University Museum; SMC - Sedgwick Museum, Cambridge; USNMNH - United States National Museum of Natural History, Smithsonian Institution, Washington; UMUT - University Museum, Tokyo; UOCM - University of Oregon, Condon Museum, Eugene.

Abbreviations used in the text: LV = left valve, RV = right valve, L = valve length, W = width (inflation, tumidity, thickness) of a single valve, H = valve height, l = length of structures other than valves, h = height of structures other than valves, w = width of structures other than valves. The bar scale on all illustrations is in centimetres.

The categorization of shell features, i.e. size, position of umbones, inflation) are those of Cooper (2015a). So as to facilitate consistent comparison and description, the posterodorsal margin of the vaugoniine shell is taken to be horizontal since this corresponds internally with the orientation of the lath-like posterior tooth in both valves, as well as the ligament pit externally. In many shells with a slightly convex to almost straight anterior margin this approximates to vertical.

Order Trigoniida DALL, 1889
Suborder Myophorellina COOPER, 1991
Superfamily Myophorelloidea KOBAYASHI, 1954
Family Vaugoniidae KOBAYASHI, 1954
(*nom. transl.* Cooper, 1991 *ex* Vaugoniinae)
Subfamily Vaugoniinae KOBAYASHI, 1954

Diagnosis: Very small to very large, moderately to very inflated, with generally low, inconspicuous, anteriorly positioned umbones and opisthogyrate beaks; escutcheon

sunken, mostly unornamented with beaded rim; asymmetrically bipartite area often gabled, peaking at beaded submedian carina or longitudinal furrow, with narrower upper part depressed, lirate or smooth (with growth striae only), and broader lower part flat; marginal carina commonly with nodes increasing is size and transverse elongation posteriorly, or nontuberculate and rounded in later growth; antecarinal space present or absent; flanks with commarginal costellae in nepionic stage, later developing curved, comma-shaped, U-shaped, L-shaped or V-shaped costae; opisthocline posterior limbs to L- and V-shaped ribs mostly thick and nodate, anterior limbs finer, beaded or wiry and nontuberculate, frequently outnumbering posterior limbs due to intercalation and/or bifurcation, varying from commarginal to sinuous, downcurved, radial or irregular; where flank costae curved and oblique, posterior portion nodate and anterior portion beaded or nontuberculate; chevrons may be effaced from midflank, rarely also posteriorly, or with apices interrupted by irregularly scattered nodes. In old age last few flank costae commarginal, irregular, wiry and nontuberculate. *Hettangian – Valanginian*.

Discussion: Due to the longevity of vaugoniines, and their widespread dispersal and radiation in the Middle Jurassic, attempts to hypothesize evolutionary relationships among the large number of described species is limited, more so since this is inhibited by inadequate descriptions, frequent misidentifications, poor knowledge of intra-specific variation, and by convergences both with myophorellines and orthotrigoniines. For those vaugoniines with curved or U-shaped flank costae, lacking true chevrons and thus convergent towards Myophorellinae, the prime character used for discrimination is the nodes to the posterior portion of the ribs, and the beaded to nontuberculate and wiry anterior portions.

According to Francis (2000: 130), "Many workers have underestimated the importance of the morphological conservative nature of the area." This alleged conservatism of the area, however, stems from so little taxonomic attention having being paid to the details of this part of the shell, as has been well exposed by Echevarría *et al.* (2021). As with so many trigoniids, the nature and ornament of the area (corselet) is fundamental to interpretation of vaugoniines. Kobayashi & Mori (1955) noted that the area of *Vaugonia* is typically gabled, peaking at the submedian carina, with the narrower dorsal part more depressed than the broader flatter lower portion. This gabling results in the respiratory margin becoming geniculated, with the commarginal lirae of the area oblique dorsally and transverse ventrally (Poulton 1979). Unfortunately this detail of ornament is rarely commented upon, nor is the gabling of the area or the distinction between lirae/lamellae and growth striae.

The longitudinal furrow bounding the submedian carina of the area in vaugoniines is an external expression of the boundary between the inhalant and exhalant siphons. This suggests that the lower inhalant siphon is substantially larger than the smaller more compressed superior exhalant siphon. Where known in vaugoniines the exhalant siphon is flanked by buttresses that correspond externally to the positions of the escutcheon rim and the submedian carina, as displayed by *Morigonia yokoyamai* (Kobayashi & Mori 1955) (Fig. 3 BB), *Vaugoniella engeli* (Benecke 1905) (Fig. 11 I) and *Alcobacella lusitanica* (Sharpe) (Choffat 1885, pl. 9, fig. 21). By contrast, *Pulchelligonia* gen. nov. has its posteroventral commissures pitted internally (Benecke 1905, pl. 14, fig. 5). In true *Trigonia* (Cossman 1912, pl. 1, figs 3, 7) a third internal buttress marks the position of the marginal carina.

Pugaczewska (1976) noted a narrow, step-like depressed anterior adductor muscle scar in some representatives of *Vaugonia*, suggesting a strongly developed anterior adductor muscle and well developed leaping capabilities; the consistency of this feature within the subfamily remains to be determined. She noted also that the prisms to the prismatic layer of *Vaugonia* are smaller than in *Trigonia* and *Myophorella*.

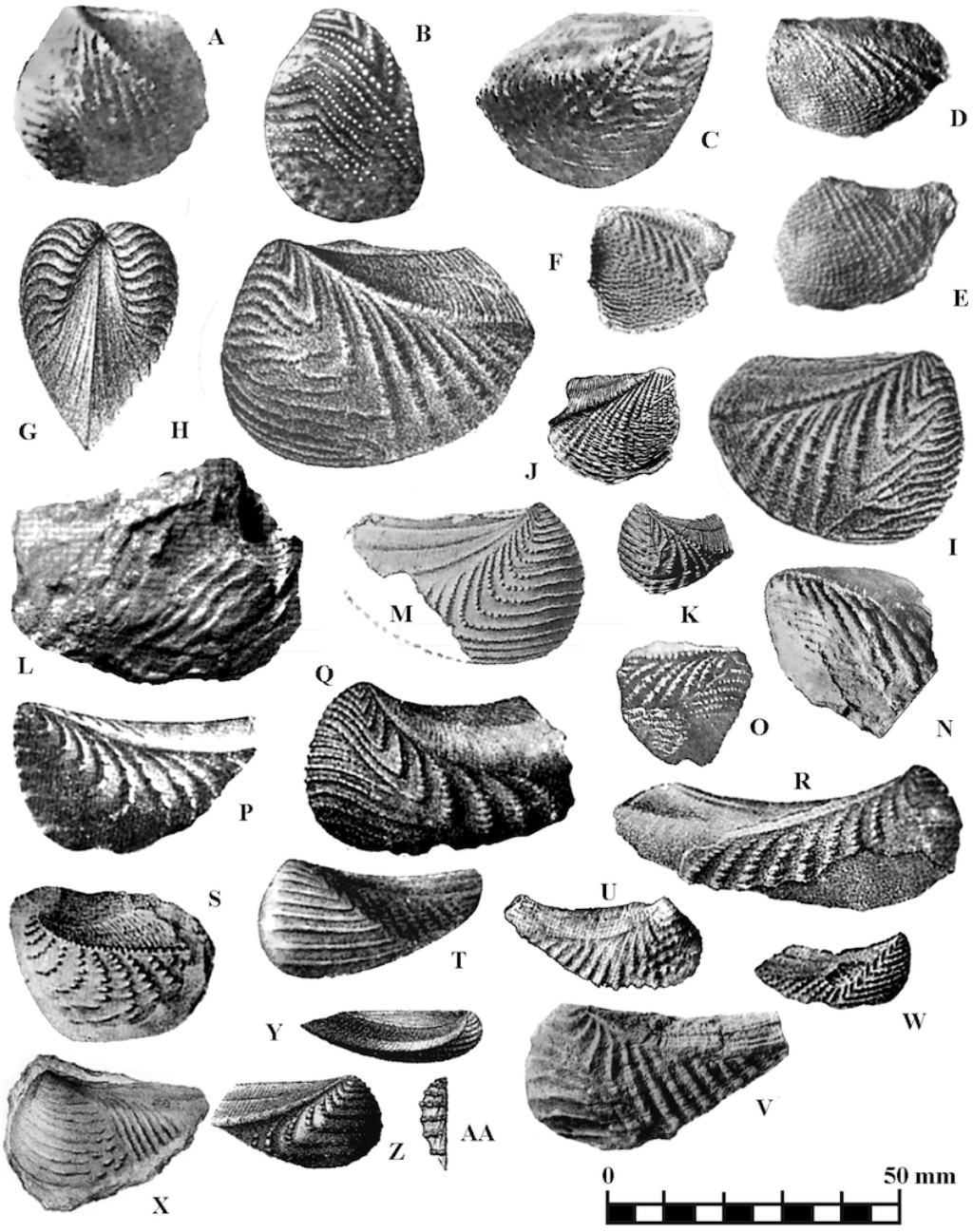

Fig. 3. A-B, N. *Hijitrigonia geniculata* (Kobayashi & Mori). A, the holotype; B, a hypopotype, both after Kobayashi & Mori (1955); N, a hypotype after Hayami (1975). **C.** *Hijitrigonia kojima* (Kobayashi & Mori), the holotype after Kobayashi & Mori (1955). **D.** *Primorskyella ussuriensis* (Konovalova), a hypotype after Konovalova (1979). **E.** *Primorskyella banevacuri* (Konovalova), a hypotype after Konovalova (1979). **F.** *Primorskyella subrotunda* (Konovalova), the holotype after Konovalova (1979). **G-I.** *Hijitrigonia literata* (Young & Bird). The provisional neotype (G-H) designated herein, and a hypotype (I) after Lycett (1874). **J.** *Flemingonia kawhiana* (Trechmann), the lectotype after Fleming (1978). **K.** *Flemingonia spedeni* (Fleming), the holotype after Fleming (1978).

L. *Hijitrigonia magna* (Konovalova), the holotype after Konovalova (1979). **M.** *Echevarria chunumayensis* (Jaworski), the holotype by monotypy after Jaworski (1925). **O.** *Hijitrigonia mindoroensis* (Hayasaka), the lectotype designated herein after Kobayashi & Mori (1957). **P.** *Echevarria substriata* (Burmeister & Giebel), the holotype by monotypy after Burmeister & Giebel (1861). **Q.** *Echevarria lycetti* (Möricke), the holotype by monotypy after Möricke (1894). **R.** *Echevarria praelonga* (Gottsche), the holotype by monotypy after Gottsche (1878). **S.** *Pseudovaugonia exotica* (Möricke), the holotype by monotypy after Möricke (1894). **T.** *Echevarria ovallei* (Philippi), the holotype by monotypy after Pérez & Reyes (1989). **U.** *Maputrigonia hugoi* Leanza, the holotype after Leanza (1985). **V.** *Maputrigonia* sp. nov. aff. *hugoi* Leanza, a hypotype after Pérez *et al.* (1987). **W.** *Echevarria gottschei* (Möricke), the holotype by monotypy after Möricke (1894). **X.** *Echevarria bigoti* (Tornquist), the holotype by monotypy after Tornquist (1898). **Y-AA.** *Echevarria rectangularis* (Möricke), the holotype by monotypy after Möricke (1894).

Middle Volgian–Ryazanian *Turbitrigonia* (Kelly, 1984) was interpreted as a myophorelline homoeomorph of *Vaugonia*, distinguished by its feeble escutcheon carina, unornamented area, lack of marginal carina, broad antecarinal space and distant curved flank costae with irregularly scattered nodes anteroventrally that sometimes fuse into ribs. A number of these characters (feeble escutcheon carina, unornamented area, broad antecarinal space, curved flank costae) are found in some vauginiines, and more work may show *Turbitrigonia* belongs in Vaugoniinae.

A number of species originally assigned to *Vaugonia* by Kobayashi & Mori (1955) belong to the Megatrigoniidae and Iotrigoniidae in which V-shaped flank costae evolved independently. These are *Trigonia foveata* Philippi (1899: 80, pl. 35, figs 3, 3a), *T. gampsorryncha* Philippi (1899: 79, pl. 34, fig. 10), *T. leucothea* Philippi (1899: 77, pl. 34, figs 6, 6a) and *T. pusilla* Philippi (1899: 78, pl. 34, fig. 7), all based on juvenile megatrigoniines, probably *Damborenella* (Cooper & Leanza, 2019). *Vaugonia fuenzalidai* Reyes & Pérez (1984: 37, pl. 1, figs 1-13) and *V. lissocostata* Reyes & Pérez (1984: 40, pl. 2, figs 1-7) were re-assigned to the pre-occupied iotrigoniid genus *Perezella* Cooper (2015b; = *Perezigonia* Ceccolini & Cianferoni 2021), and *Trigonia covuncoensis* Lambert (1944: 360, pl. 1, fig. 1) was made type of the iotrigoniid genus *Levytrigonia* (Cooper 2015b).

Trigonia albertaensis McLearn (1919: 11, pl. 4, figs 3-4) from the Middle Albian of the Peace River Formation of Alberta, overlooked by Cooper (2021), superficially resembles *Vaugonia* but its age and radiating costellae to the area suggest assignment to *Heterotrigonia* (Apiotrigoniidae). V-shaped flank costae are found also in Middle-Upper Albian *Ussuritrigonia* (Konovalov, *in* Konovalov & Mirolyubov 1978), a genus overlooked by Cooper & Leanza (2019), but the type species clearly is a subjective junior synonym of *Columbitrigonia* (Poulton 1977).

Genus *Hijitrigonia* Kobayashi & Mori, 1955

(*nom. transl.* Hayami 1975 ex *Vaugonia (Hijitrigonia)*)

Type species: *Vaugonia (Hijitrigonia) geniculata* Kobayashi & Mori 1955: 84, pl. 4, figs 4-9; by original designation.

Diagnosis: Small, trigonally ovate to oblong; broad area lirate or smooth, gabled in early growth, with beaded submedian carina; flanks with acute beaded chevrons from early growth, with thick posterior limbs and thin subcommarginal to oblique anterior limbs that are geniculated, irregularly wrinkled, intercalated or disjointed. *Hettangian - Aalenian*.

Referred species: *Hijitrigonia kojiwa* (Kobayashi & Mori 1955: 85, pl. 4, figs 2-3) (Fig. 3 C), *H. literata* (Young & Bird 1828: 225, pl. 8, fig. 23, Phillips 1929: 161, pl. 14, fig. 11, Lycett 1874: 64, pl. 14, figs 1-4, Cox 1969: N488, fig. D74, 1b, Francis 2000: 257, pl. 17, figs i-j) (Fig. 3 G-I), *H. magna* (Konovalova 1979: 46, pl. 3, figs 16-17) (Fig. 3 L), *H. mindoroensis* (Hayasaka 1943: 9, two unnumbered text figs, Kobayashi & Mori 1955: 83, unnumbered text-fig.) (Fig. 3 O).

Discussion: A pandemic genus known from the Hettangian-Aalenian of the Oriental (Primorsky Krai, Japan), Sinian (Philippines), Central Asian (NW Russia), European (England, France) and Maorian (New Zealand) provinces. It is distinguished from *Vaugonia* most obviously by its smaller size, different shape with umbones closer to the anterior, unornamented area with early loss of submedian gabling and carina, and denser flank costation with irregular crinckled, geniculated or discontinuous anterior limbs to acute chevrons.

Hijitrigonia geniculata (Kobayashi & Mori, 1955)

Fig. 3 A-B, N

1955 *Vaugonia (Hijitrigonia) geniculata* Kobayashi & Mori, p. 84, pl. 4, figs 4-9.
1969 *Vaugonia (Hijitrigonia) geniculata* Kobayashi & Mori. - Cox, p. D74, 1b.
1975 *Hijitrigonia geniculata* (Kobayashi & Mori). - Hayami, p. 167, pl. 5, fig. 8.

Type: The holotype is UMUT-MM4337 from the Aratokazi Sandstone of the Shizukawa Group, Akaiwakazi (Hosoura), Miyagi Prefecture, Japan, Aalenian according to Takahashi (1969), but Bajocian according to Hayami (1975).

Description: The holotype (Fig. 3A) is small (L = 34 mm), subquadratic, slightly longer than high (H/L = 0.94), with a low, small, inconspicuous, anteriorly positioned umbo (al/L = 0.19) and moderately incurved opisthogyrate beak. The gently convex anterior margin curves evenly into the convex ventral margin, the broad, gently convex respiratory margin is obliquely subtruncated and the moderately long posterodorsal margin (l/L = 0.55) straight. The fairly large escutcheon is shallowly concave and unornamented, with an insignificant escutcheon carina. The very large unornamented area is bipartite and gabled, with a beaded submedian carina that evanesces in middle growth; the dorsal area is narrower than the lower part and distinctly concave near the umbo. In early growth the flank is ornamented with L-shaped ribs with an obtuse apical angle that becomes very acute in middle growth, the ribs broader than the interspaces. In middle growth there are two intercalated ribs separating the anterior limbs of the chevrons, and the last 6 straight opisthocline strongly nodate posterior limbs broaden ventrally and extend to the ventral margin; they meet the marginal carina at an acute angle that increases posteriorly. The thinner commarginal anterior limbs are sharply geniculated at midlength, forming obtuse chevrons with dorsally directed apices.

Discussion: The type species appears to be highly variable both in shape and ornament. Hayami (1975, pl. 5, fig. 8) figured a paratype (Fig. 3 N) with very thick unbeaded posterior limbs to the chevrons, whereas another hypotype (Fig. 3 B) has very narrow beaded posterior limbs and, on yet another hypotype (pl. 4, fig. 6), the

anterior limbs break up into rows of beads. It is not known if they came from the same stratigraphical level in the Aratokazi Sandstone.
The holotype of *H. kojiwa* (Kobayashi & Mori) (Fig. 3 C), UMUT-MM4342, is from the Middle Hettangian Niranohama sandstone of Rikuzen Province, Japan, and thus the earliest recorded member of the genus. It is small (L = 38 mm), subrhomboidal, longer than high (H/L = 0.82), inflated (W/H = 0.36), with a low, rounded, near-terminal umbo (al/L = 0.08), acute umbonal angle, and strongly incurved opisthogyrate beak. There is a very shallow sinus to the posteroventral margin. The unornamented escutcheon is deeply sunken. The gabled area covers about a third of the valve, the lower two-thirds flat and the upper third concave, and is ornamented by commarginal lirae that strengthened on the marginal carina where a few are bundled into nodes. The bold marginal carina thickens with growth, and there is a broad shallow antecarinal depression. Following the nepionic stage the flank is ornamented with very acute beaded chevrons with narrow limbs of similar thickness and an almost straight, strongly opisthocline axial trace. The straight posterior limbs meet the marginal carina at an acute angle that increases posteriorly. In middle to later growth the subcommarginal anterior limbs become irregularly corrugated and even discont-inuous, separated by 1-2 intercalatories of various lengths.

Hijitrigonia magna (Konovalova) (Fig. 3 L) from the Pliensbachian of Primorsky Krai is poorly preserved and incomplete. The holotype is medium sized (L ~ 52 mm), trigonally elongate (H/L ~ 0.73) with a subterminal umbo and straight anterior margin. It resembles the topotype of *V. geniculata* figured by Hayami (1975, pl. 5, fig. 8) (Fig. 3 P) and differs from *H. literata* (Young & Bird) (Fig. 5 H) in its coarser flank ornament.

The whereabouts of the holotype by monotypy of *H. literata* (Young & Bird) is unknown (Francis 2000). Here the original of Lycett (1874, pl. 14, fig.1) (Fig. 3 G-H), from the Toarcian of Robin Hood's Bay, Yorkshire, is selected as provisional neotype. It is medium sized (L = 56 mm), oblong (H/L = 0.73), inflated (W/H = 0.35), with a low broadly rounded subterminal umbo (al/L = 0.17) and obtuse umbonal angle. The anterior margin is almost straight and the long posterodorsal margin (l/L = 0.62) shallowly concave. The wide escutcheon has a beaded rim, the beads becoming transversely elongated posteriorly and evanescing in maturity. The moderately wide convex area has a feebly beaded submedian carina that evanesces in middle growth when the areal ornament is reduced to growth striae. There is a nodate marginal carina in early growth but this rounds later and an antecarinal space is lacking. Following the nepionic stage, the flank is ornamented by beaded chevrons, narrower than the interspaces, which become increasingly acute with growth and have an almost straight opisthocline axial trace. The slightly curved, opisthocline posterior limbs to the chevrons are thicker than the anterior ones and meet the marginal carina at an angle that becomes increasingly acute posteriorly. The thin convex-up beaded anterior limbs persist to middle growth whereafter they disintegrate and become irregular, sub-horizontal, wavy, disjointed, bifurcating and intercalated, outnumbering the posterior limbs by up to 4:1. In maturity they are single and commarginal along the ventral margin. The smaller paralectotype (Fig. 3 I) shows acute chevrons extending almost to the ventral margin, with frequent bifurcation of anterior limbs that greatly out-number posterior limbs.

Hijitrigonia mindoroensis (Hayasaka) was based upon two undated syntypes from the neighbourhood of Mansalay, SE of Mindoro in the Philippines, of which the original of the larger specimen (Fig. 3 O) is selected here as lectotype. It resembles a paratype of *H. geniculata* (Fig. 3 N) in its acute umbonal angle but the latter has very thick unbeaded posterior limbs to its chevrons.

Genus *Primorskyella* gen. nov.

LSID:urn:lsid:zoobank.org:act:DF78DB92-C84C-46D8-83C4-2B0F3395BB24

Etymology: After Primorsky Krai (= Primorye), the Far East region of Russia where the genus is restricted.

Type species: *Vaugonia banevurica* Konovalova 1979: 43, pl. 3, 7-12; by original designation herein.

Diagnosis: Small, oval to subelliptical and posteriorly produced; fairly narrow area lirate, with persistent beaded submedian carina; antecarinal space lacking; flank chevrons with straight opisthocline axial trace; long straight nodate opisthocline posterior limbs cover 33-75% of flank; dense very finely beaded commarginal anterior limbs with numerous intercalatories, the beads sometimes arranged in a reticulate pattern. *Pliensbachian*.

Referred species: *Primorskyella cuneata* (Konovalova 1979: 44. pl. 3, fig. 13), *P. subrotunda* (Konovalova 1979: 46, pl. 3, figs 14-15) (Fig. 3 F) and *P. ussuriensis* (Konovalova 1979: 41, pl. 3, figs 1-6) (Fig. 3 D).

Primorskyella banevurica (Konovalova, 1979)

Fig. 3 E

1979 *Vaugonia banevurica* Konovalova, p. 43, pl. 3, figs 7-12.

Type: The holotype is the original of pl. 3, fig. 7, from the Pliensbachian of Primorsky Krai, Far East, USSR, but the illustration is too poor to warrant reproduction.

Description: The shell is small (L = 33 mm), oval to elongate-ovate and sub-trapezoidal, posteriorly produced (H/L = 0.77-0.80), with weakly to strongly convex anterior margin, straight posterodorsal margin and anteriorly positioned to near terminal umbones. The escutcheon is not described. The fairly narrow bipartite area has a beaded submedian carina in its upper part and is ornamented with single or looped commarginal lirae. There is a prominent straight marginal carina with transversely elongated nodes that increase in size posteriorly, without an antecarinal space below. The flank chevrons have long straight nodate opisthocline posterior limbs covering about one-third of the flank, with a straight opisthocline axial trace. Dense very finely beaded commarginal anterior limbs with numerous intercalatories cover the remainder of the flank, the beads sometimes arranged in a reticulate pattern.

Discussion: *Primorskyella banevurica* is distinguished from *Hijitrigonia kojiwa* by its posterior elongation and flank chevrons with dense fine commarginal beaded

anterior limbs, whose nodes may be arranged in a reticulate pattern, that greatly outnumber the thicker longer beaded posterior limbs.

Primorskyella cuneata (Konovalova) is small (L = 28 mm), subtrapezoidally elongate (H/L = 0.64), with a convex anterior margin and very long posterodorsal margin. Anteriorly almost straight narrow beaded horizontal costellae cover three quarters of the flank, with straight beaded opisthocline costellae posteriorly. The original illustration is too poor to warrant reproduction.

Primorskyella subrotunda (Konovalova) (Fig. 3 F) is small (L = 25 mm), subtrigonal, slightly longer than high (H/L = 0.92), with a terminal umbo, almost straight anterior margin, very obliquely truncated respiratory margin and short straight posterodorsal margin. The flank chevrons have thick, bold, gently curved, beaded, slightly opisthocline posterior limbs covering about a third of the flank, and thin finely beaded subcommarginal costellae over the remainder.

Primorskyella ussuriensis (Konovalova) (Fig. 3 D) is larger than the others (L = 46 mm), subtrapezoidally elongate (H/L = 0.70-0.78), with small obscure umbones and a weakly curved anterior margin. The thick bold posterior limbs are greatly outnumbered by the very thin, finely beaded commarginal anterior limbs that cover half or more of the flank.

Genus *Flemingonia* gen. nov.

LSID:urn:lsid:zoobank.org:act: 063B9C84-9592-47A8-89DC-17F377A74ACE

Etymology: After Sir Charles Alexander Fleming (1916-1987), expert on New Zealand trigoniids.

Type species: *Trigonia kawhiana* Trechman 1923: 277, pl. 13, figs 6-9; by original designation herein.

Diagnosis: Very small to small, with terminal umbo; broad area with persistent longitudinal furrow and looped commarginal lirae; in early growth flanks with very acute nodate chevrons with a strongly opisthocline axial trace; in middle to later growth anterior limbs replaced by commarginal rows of ellipsoidal nodes that outnumber posterior limbs 2-3:1, the nodes sometimes coalescing into commarginal riblets. *U. Toarcian - Tithonian*.

Referred species: *Flemingonia orvillensis* (Kelly 1995: 72, figs 8.5-8.7) (Fig. 4 T) and *F. spedeni* (Fleming 1987: 33, pl. 6, figs 11, 13-14) (Fig. 3 K).

Discussion: *Flemingonia* gen. nov. is pandemic to the Maorian and Antarctic provinces. The very acute beaded flank chevrons in early growth suggest derivation from *Hijitrigonia*.

Flemingonia kawhiana (Trechman, 1923)

Fig. 3 J

1923 *Trigonia kawhiana* Trechman, p. 277, pl. 13, figs 6-9.
1987 *Vaugonia (Vaugonia) kawhiana* (Trechman). - Fleming, p. 33, pl. 6, figs 6-9, 10, 12.

Type: The original of Trechman's Fig. 8, an LV, was selected as lectotype (Fleming 1987), of which his Fig. 6, an RV, is "almost certainly" the opposing valve. The species is said to be common at the type locality in the Captain King's Shellbed, Totara Peninsula, Kawhia, New Zealand, in strata of Lower Heterian age. Although originally attributed to the Early Kimmeridgian (Fleming 1987), this substage is now believed to span the Callovian-Oxfordian boundary (Raine *et al.* 2015).

Description: The lectotype (Fig. 3 J) is very small (L ~ 21 mm), subtrapezoidally elongate, longer than high (H/L = 0.67), inflated (W/H ~ 0.36), with an almost straight vertical anterior margin and low rounded terminal umbo with acute umbonal angle. Areal lirae suggest that the broken respiratory margin was fairly broad and obliquely truncate, and the long posterodorsal margin is straight. The relatively wide escutcheon is shallowly concave, with a beaded rim. The broad asymmetrically bipartite area has a persistent longitudinal furrow and is ornamented by commarginal lirae, many looped to the prominent nodes of the marginal carina that increase in size and transverse elongation posteriorly. In early growth the flank is ornamented by very acute chevrons with a strongly opisthocline axial trace. The long curved opisthocline posterior limbs to the chevrons cover almost half the flank and broaden ventrally, with nodes that increase in size and transverse elongation ventrally, and meet the marginal carina at an angle that becomes increasingly acute posteriorly. In middle to later growth the anterior limbs are replaced by a very fine ornament of commarginal rows of ellipsoidal nodes that outnumber the posterior limbs 2-3:1, the nodes sometimes coalescing.

An adult hypotype (Fleming 1987, pl. 6, fig. 12) is larger (L = 28.5 mm), ovate (H/L = 0.88), with a strongly convex anterior margin, a sinus to the posteroventral margin and a shallow antecarinal depression that emphasizes the coarsely nodate marginal carina. The area is symmetrically bipartite, and the nodate posterior limbs to the flank chevrons narrower than the interspaces. A juvenile hypotype (Fleming, 1987, pl. 6, fig. 9) has acute beaded flank chevrons in very early growth, truncated by the sub-commarginal anterior limbs that merge with the curved posterior limbs.

Discussion: Lower Temaikan (= lower Upper Toarcian, *fide* Raine *et al.* 2015) *F. spedeni* (Fleming) (Fig. 3 K) differs from *F. kawhiana* in its narrower escutcheon, stronger nodes to the marginal carina, more inclined posterior limbs to the chevrons, and anterior limbs that do not break up into commarginal rows of ellipsoidal nodes.

Flemingonia orvillensis (Kelly) (Fig. 4 W) from the Latady Formation (Kimmeridgian?-Tithonian) of Antarctica was distinguished from *K. kawhiana* (Trechmann) by its larger size (L_{max} = 38 mm) and generally coarser ornament. The marginal carina is feebly nodate and a rounded rim for much of its length. In middle growth the flank ornament is V-shaped but later the anterior limbs to the chevrons are replaced by irregularly positioned nodes, with 7 slightly curved, opisthocline, beaded posterior limbs persisting to maturity.

Genus *Echevarria* gen. nov.

LSID:urn:lsid:zoobank.org:act: 6EB5D526-7B3C-4431-9784-48F1B865139E

Etymology: For Dr Javier Echevarría (La Plata), expert on South American trigoniids.

Type species: *Trigonia chunumayensis* Jaworski 1915: 384, pl. 5, fig. 4; 1925: 83, pl. 1, fig. 4; by original designation herein.

Diagnosis: Small to medium sized, posteriorly rostrate; unornamented area with longitudinal furrow and well developed marginal carina; flank chevrons simple, with rounded to angular apices and opisthocline axial trace; posterior limbs nodate, subcommarginal anterior limbs beaded to wiry, without intercalation or bifurcation. *Pliensbachian - Callovian*.

Referred species: *Echevarria bigoti* (Tornquist 1898: 57 (189), pl. 9 (22), fig. 7) (Fig. 3 X), *E. gottschei* (Möricke 1894: 49, pl. 6, fig. 7) (Fig. 3 W), *E. lycetti* (Gottsche 1878: 25, pl. 6, fig. 3a) (Fig. 3 Q), *E. manflarum* (Philippi 1899: 77, pl. 34, fig. 4, Pérez & Reyes 1989: 23) (Fig. 4 S), *E. ovallei* (Philippi 1899: 78, pl. 34, fig. 8) (Fig. 3 T), *E. praelonga* (Gottsche 1878: 26, pl. 6, figs 2a-b) (Fig. 3 R), *E. rectangularis* (Gottsche 1878: 26, pl. 6, figs 5a-b, Pérez & Reyes 1989: 18, pl. 3, figs 8-9, Leanza & Garate 1987: 219, pl. 4, fig. 2, Leanza 1993: 37, pl. 2, fig. 13) (Fig. 3 Y-AA) and *E. substriata* (Burmeister & Giebel 1861: 134, pl. 2, fig. 4) (Fig. 3 P).

Discussion: *Echevarria* gen. nov. is an Andean (Argentina, Chile) endemic, but the difficulty of satisfactorily identifying species was emphasized by Pérez *et al.* (2008), and all are in serious need of modern revision. It differs from *Flemingonia* gen. nov. by having simple flank chevrons commonly with subrounded apices, without intercalation or bifurcation anteriorly. Its origin may lie close to *Pseudovaugonia* (Echevarría *et al.* 2021).

***Echevarria chunumayensis* (Jaworski, 1915)**

Fig. 3 M

1915 *Trigonia chunumayensis* Jaworski, p. 384, pl. 5, fig. 4.
1925 *Trigonia chunumayensis* Jaworski, p. 83, pl. 1, fig. 4.
1987 *Vaugonia (Vaugonia) chunumayensis* (Jaworski). - Pérez *et al.*, p. 41, fig. 4.
1987 *Vaugonia chunumayensis* (Jaworski). - Leanza & Garate, p. 209, pl. 4, fig. 3.
non 1993 *Vaugonia chunumayensis* (Jaworski). - Leanza, p. 36, pl. 2, fig. 15.

Type: The holotype, by monotypy, is the original of the specimen figured by Jaworski (1915, 1925) from the Aalenian of Chunumayo, Perú.

Description: The incomplete holotype (Fig. 3 M) is small (L = 43 mm), elongate-ovate and posteriorly produced (H/L ~ 0.74), moderately inflated, with a small, pointed, anteriorly positioned umbo (al/L = 0.19) and opisthogyrate beak. The convex anterior margin passes rather sharply into the long gently convex ventral margin; the obliquely convex respiratory margin is narrow and the long posterodorsal margin shallowly concave. The narrow unornamented escutcheon is bounded by a thin transversely striated rim. The fairly narrow area is asymmetrically bipartite with a deep longitudinal furrow, broader lower part and, in the nepionic stage, with commarginal costellae and a beaded submedian carina, after which it is ornamented only by growth striae. There is a prominent marginal carina with a well developed antecarinal space below that broadens posteriorly. Following the nepionic stage of commarginal costellae the flank is ornamented with beaded L-shaped chevrons with subangular to subrounded apices and a curved opisthocline axial trace. The thin

slightly wavy subcommarginal anterior limbs are unbeaded and wiry for most of their lengths, whereas the gently curved opisthocline posterior limbs are beaded and narrower than the interspaces.

Discussion: The holotype, by monotypy, of Pliensbachian to Bajocian *E. substriata* (Burmeister & Giebel) (Fig. 3 P) is from Juntas in Chile. It is small (L = 44 mm), trigonally elongate and posteriorly produced (H/L = 0.54), with a narrow unornamented area, simple well spaced flank chevrons with long curved nodate posterior limbs, subangular (juv.) to rounded (ad.) apices and beaded widely spaced commarginal anterior limbs.

The lectotype selected herein of Bajocian *E. rectangularis* (Gottsche) (Fig. 3 Y-AA) is from Espinazito, Argentina, in the same conglomerate as *E. lycetti*. It differs from *E. chunumayensis* in being smaller (L = 28 mm), trapezoidally elongate (H/L = 0.57), with a bold marginal carina that thickens posteriorly, without an antecarinal gap, and fewer more distant flank costellae whose chevrons have subrounded apices and a very opisthocline axial trace.

The holotype by monotypy of *E. ovallei* (Philippi) (Fig. 3 T), from the Bajocian of Caracoles, Chile, was “for practical reasons” (translated) included in the synonymy of *E. gottsche* (Pérez & Reyes, 1989: 23), but is larger (L = 47 mm), relatively higher (H/L = 0.61), and with more widely spaced anterior limbs to the chevrons.

Echevarria bigoti (Tornquist) from the uppermost Callovian of Espinazito-Passes, Argentina, seems to be allied to *E. ovallei*. The holotype, by monotypy (Fig. 3 X), is subtrigonal and posteriorly rostrate, with fine nontuberculate commarginal anterior limbs that are much narrower than the interspaces and are separated, in later growth, from 7 straight narrow opisthocline posterior limbs by a few scattered ellipsoidal nodes.

The holotype of Bajocian *E. praelonga* (Gottsche) (Fig. 3 R), by monotypy, from the Argentinian cordillera, differs from *E. chunumayensis* in being larger (L = 64 mm) and posteriorly very rostrate (H/L = 0.38), with a distinctly concave posterodorsal margin, narrow obliquely truncate respiratory margin, a marginal carina that evanesces in later growth, lack of an antecarinal space, and coarsely nodate posterior limbs to its flank chevrons.

Echevarria manflarum (Philippi) (Fig. 4 S) was based on a small (L = 36 mm), trigonally very elongated specimen (H/L = 0.47) from the Lautaro Formation of the Manfla valley, Copiapó, Chile, of Lias-Bajocian? age (Pérez & Reyes 1989). It differs from other *Echevarria* species in its strongly produced anterior (al/L = 0.35), pointed posterior and area with 4-6 rather thick folds “almost parallel to the ventral edge, a character that does not allow this species to be confused with some of the similar ones” (Philippi 1899: 77, translated). The latter unique character is not illustrated.

Echevarria gottschei (Möricke) (Fig. 3 W) is most abundant in the Upper Aalenian (*humphriesianum* Zone) of Chile (Pérez & Reyes 1977). It differs from *E. chunumayensis* in being smaller (L = 26 mm), much longer than high (H/L = 0.50), with a concave posterodorsal margin, acute umbonal angle, curved opisthocline

anterior margin and, most obviously, flank chevrons with acute apices and a straight opisthocline axial trace from early growth so that 7 of the posterior limbs meet the ventral border.

Echevarria lycetti (Gottsche), an Aalenian to Bajocian species, is the most divergent in the genus. The lectotype designated herein (Fig. 3 Q), from the Argentinian cordillera, is moderately large (L = 53 mm), trapezoidally elongate, longer than high (H/L = 0.45), with a very broad area and discrepant flank ornament in which the anterior limbs of the acute chevrons are replaced, in middle to latter growth, by fine oblique beaded costellae, narrower than the interspaces, that curve downwards anteriorly, and with relatively thick, curved, widely spaced posterior limbs.

Vaugonia almejensis van grassa Valenzuela (1975: 1), *V. a. van grassa* Valenzuela (1975: 2), *V. varaensis* Valenzuela (1975: 1) and *V. monteare* Valenzuela (1975: 1) are listed in collection holdings only, without illustration or description, and are all *nomina nuda.*

Genus *Maputrigonia* Leanza, 1985

Type species: *M. hugoi* Leanza 1985: 280, pl. 1, figs 1-5; by original designation.

Diagnosis: Small, pyriform and posteriorly rostrate, with small pointed umbo; narrow area with radial threads; beaded flank chevrons with triangular cross sections to posterior limbs and beaded to wiry anterior limbs that curve slightly downwards anteriorly. *U. Tithonian - L. Berriasian*.

Discussion: *Maputrigonia* is endemic to the Andean Province (Argentina, Chile). Pérez *et al.* (1987) included it in the synonymy of *Virgotrigonia* but the two are different (Cooper & Leanza 2020), and Cooper (2023) transferred *Virgotrigonia* to the Syrotrigoniinae. *Maputrigonia* is closest to *Echevarria* gen. nov., its likely antecedent.

Maputrigonia hugoi Leanza, 1985

Fig. 3 U

1985 *Maputrigonia hugoi* Leanza, p. 280, pl. 1, figs 1-5.
1987 *Maputrigonia hugoi* Leanza. - Leanza & Garate, p. 220, pl. 8, figs 8-9.
1987 *Maputrigonia hugoi* Leanza. - Pérez *et al.*, p. 39, pl. 1, figs 1-6, 10-15.
1993 *Maputrigonia hugoi* Leanza. - Leanza, p. 53, pl. 14, figs 5-9.
1997 *Virgotrigonia hugoi* (Leanza). - Pérez *et al.*, p. 39, pl. 1, figs 10-12, 14-15 (*non* pl. 1, figs 1-4, 6, 8).

Type: The holotype is from the Lower Berriasian (*Argentiniceras noduliferum* Zone) in the upper part of the Vaca Muerta Formation at Mallín Quemado, Department of Pichunches, Neuquén, Argentina.

Description: The holotype is small (L = 35 mm) (Fig. 3 U), pyriform and posteriorly rostrate, much longer than high (H/L = 0.52), moderately inflated (W/H = 0.16), with anteriorly positioned umbones (al/L = 0.21), and small moderately incurved orthogyrate beaks. The strongly convex anterior margin curves evenly into the long

gently curved ventral margin that straightens posteriorly; the narrow truncated respiratory margin is slightly oblique and the posterodorsal margin shallowly concave. The elongate escutcheon is relatively wide and smooth, rising towards the comm.-issure. The narrow asymmetrically bipartite area is ornamented with commarginal costellae in earliest growth that are replaced later by beaded radial threads faintly crenulated by the growth striae. The marginal carina is well defined and beaded along its entirety. Following the nepionic stage, the flank is ornamented by L-shaped chevrons that become more acute with growth, with an apical angle of 50°. The anterior limbs cut across growth striae anteriorly, and are about as wide as the interspaces; they are beaded in early growth but the beads increase in size with growth and later the limbs are conspicuously nodate. The 8 posterior limbs are narrower than the interspaces, triangular in section and crenulated by growth striae. They vary from subvertical to opisthocline, meeting the area at an acute angle that increases posteriorly.

A large topotype (Leanza, 1985, pl. 1, fig. 5) is 52 mm in length, higher than long (H/L = 0.60), with a concave posteroventral margin. Another fragmentary specimen (Leanza, 1985, pl. 1, fig. 2) shows the anterior flank costellae zigzagging before meeting the posterior limbs.

Discussion: Pérez *et al.* (1997) reported this species from the Calcareous Member of the Lo Valdés Formation, approximately 1 km east of the German Refugee Camp southeast of Santiago, Chile, from the Lower Berriasian *Argentiniceras bituberculatum* and "*Thurmannites" discoidalis* Zone, and also figured a rather poor specimen (pl. 1, fig. 6) from the Upper Tithonian (*Substeueroceras koeneni* Zone) of the same locality. Their largest specimen (L = 52 mm) (pl. 1, figs 1-3) (and a hypotype (Fig. 3 V)) differs from the holotype in having the umbones closer to the anterior (al/L = 0.16), being posteriorly produced but not pyriform (H/L = 0.52), with a gently curved anterior margin. In addition it is more inflated (W/H = 0.26), with a broad escutcheon (w/W = 0.55), more widely spaced, gently downcurved anterior costellae that are not obviously beaded, and less acute flank chevrons, suggesting a different species is involved.

Genus *Morigonia* gen. nov.

LSID:urn:lsid:zoobank.org:act:11EB7C77-F7AF-47F2-8CDA-6DAE4AC9F8E2

Etymology: After Prof. Kei Mori (Tokyo University), documenter of many Japanese trigoniids.

Type species: *Vaugonia namigashira* Kobayashi & Mori (1955: 83, pl. 3, figs 10-11); by original designation herein.

Diagnosis: Very small to small, subquadratic to trigonally ovate, with a small narrow unornamented depressed escutcheon; broad gabled area with submedian angulation and narrow depressed dorsal part; area smooth or with commarginal lirae kinked or thickened over submedian angulation and sometimes looped in later growth; nodate marginal carina; flanks with nodate L- to V-shaped costellae, sometimes with intercalation or geniculation anteriorly; internal commissure of respiratory margin with paired ellipsoidal buttresses. *Hettangian - Oxfordian*.

Referred species: *Morigonia ariminensis* (Maeda & Kawabe 1963: 57, pl. 1, fig. 1), *M. awazuensis* (Kobayashi *in* Kobayashi & Tamura, 1957: 39, pl. 1, fig. 4), *M. fukuiensis* (Maeda 1962: 515, pl. 1, figs 1-16, pl. 2, figs 2-16), *M. gracilis* (Kobayashi & Mori 1955: 82, pl. 3, fig. 9, Echevarría *et al.* 2020: 29, fig. 14.2) (Fig. 4 A), *M. imlayi* (Poulton 1979: 22, pl. 10, figs 7-13) (Fig. 4 I-J), *M. irregularis* (Kobayashi & Mori 1955: 80, pl. 3, 5-6) (Fig. 4 N), *M. kodaijimensis* (Kobayashi & Mori 1955: 82, pl. 3, figs 12-15), *M. kuzuryuensis* (Maeda 1963: 5, pl. 1, fig. 10), *M. niranohamensis* (Kobayashi & Mori 1955: 80, pl. 3, figs 1-4, pl. 4, fig. 1, Echevarría *et al.* 2020: 29, fig. 14.3) (Fig. 4 B), *M. yambarensis* (Kobayashi 1956: 1, pl. 1, fig. 1), *M. yokoyamai* (Shikama 1943: 180, pl. 19, fig. 13, Shikama 1952: 114, pl. 19, fig. 13, Kobayashi & Mori 1955: 81, pl. 3, figs 7-9) (Fig. 4 Q-R).

Discussion: *Morigonia* gen. nov. is pandemic to the Oriental (Japan) and Cordilleran (Alaska) provinces. According to Hayami (1975) the large number of nominal species is due to taxonomic splitting.

Morigonia namigashira (Kobayashi & Mori, 1955)

Fig. 4 C

1904 *Trigonia v-costata* Lycett. - Yokoyama, p. 8, pl. 2, figs 2-4.
1955 *Vaugonia namigashira* Kobayashi & Mori, p. 83, pl. 3, figs 10-11.
1955 *Vaugonia yokohamai* Kobayashi & Mori, p. 81, pl. 3, figs 7-8.
1955 *Vaugonia yokohamai* var. *gracilis* Kobayashi & Mori, p. 81, pl. 3, fig. 9.
1975 *Vaugonia namigashira* Kobayashi & Mori. - Hayami, p. 108.
1975 *Vaugonia namigashira* Kobayashi & Mori. - Tamura, pl. J-11, fig. 17.

Types: The holotype of *namigashira* is UMUT-MM4333 from the Niranohama Sandstone, Hoinyashiki (Hosoura), Shizukawa Group, Miyagi Prefecture, Japan, of Middle Hettangian age (Takahashi 1969), but the illustration is too poor to warrant reproduction. The syntypes of *V. yokoyamai* are UMUT-MM4324-26 from the same locality, of which the original of pl. 2, fig. 3 is selected here as lectotype. The holotype of *V. y.* var. *gracilis* is UMUT-MM4327 from Hoinyashiki. As first reviser Hayami (1975) chose *namigashira* to have name priority over *yokoyamai*.

Description: The holotype (Fig. 4 C) is very small (L ~ 23 mm), subquadratic, slightly longer than high (H/L = 0.83), moderately inflated, with a low, insignificant subterminal umbo and moderately incurved beak. The almost straight subvertical anterior margin curves rather sharply into the long gently convex ventral margin; the wide slightly oblique respiratory margin is convex (to judge by the commarginal lirae of the area), and the long posterodorsal margin shallowly concave. The small narrow escutcheon is sunken and unornamented, with a finely beaded rim. The wide area (about half the shell) is gabled with a submedian angulation and the narrower upper part recessed. Across this angulation the commarginal lirae are geniculated, and join singly or in pairs to the nodes of the slender but distinct marginal carina, the nodes outnumbering the flank costellae. Following the nepionic stage of commarginal costellae, the flank is ornamented with nodate L-shaped costellae, narrower than the interspaces, with an almost straight opisthocline axial trace. The short straight posterior limbs are opisthocline and slightly thicker than the commarginal anterior limbs, both of which are conspicuously nodate. The anterior limbs are narrower than the interspaces, and the last three curve strongly upwards at midlength to meet the

last commarginal limb perpendicularly. This latter character is not displayed by the type of *gracilis*, nor by Yokoyama's (1904) specimen of *yokoyamai*, and may be an aberration.

Discussion: *Morigonia niranohamensis* (Kobayashi & Mori) (Fig. 4 B) is very small (L = 13 mm) and difficult to define due to variability in outline, costation and strength of the marginal carina. It differs from *V. veronica* in the long curved posterior limbs to its chevrons, so that the axial trace is close to the anterior margin.

Hayami (1975: 108) included Hettangian *M. yokoyamai* (Kobayashi & Mori) in the synonymy of *M. namigashira*. Its lectotype, designated herein (Fig. 4 R), UMUT-MM 06908, is small (L = 24 mm), trigonally subovate, almost as high as long (H/L = 0.88), with a gently convex anterior margin and low anteriorly positioned umbo (al/L = 0.16). The long narrow unornamented escutcheon rises to the commissure, and there is no antecarinal space on the flank. The initially subcommarginal flank costellae become L-shaped in middle growth, with the ~16 anterior limbs separated by 1-2 intercalatories in later growth. The internal commissure of the respiratory margin of a paralectotype (Fig. 4 Q), UMUT-MM 06909, has a pair of ellipsoidal buttresses corresponding externally to the escutcheon rim and longitudinal furrow.

Morigonia irregularis (Kobayashi & Mori) was introduced as a "form" of *M. niranohamensis*. The lectotype selected herein (Fig. 4 N) is from the Aratozaki Sandstone, Gongenzaki, Shizukawa area, Rikuzen, of Aalenian age (Takahashi, 1969). It is very small (L = 17 mm), rounded quadratic, with strongly oblique, irregular, barely geniculated flank chevrons with a very obtuse apical angle and limbs of more or less equal thickness. Contemporaneous *M. kodaijimensis* (Kobayashi & Mori) was distinguished by its very broad unornamented area, with intercalated anterior limbs to its chevrons, but the original illustration is too poor for reproduce.

Morigonia awazuensis (Kobayashi) from the Awazu Formation of the Soma district of Japan, approximately Bajocian in age (Hayami 1975), was said to be allied to *M. niranohamensis* but easily distinguished by the lack of posterior branches to its flank chevrons. It has a smooth narrow area with a submedian carina, weak distinctly curved marginal carina, and anterior costellae perpendicular to the anterior margin. Again the original illustration is too poor for reproduction.

Lower Bajocian *M. imlayi* (Poulton) (Fig. 4 I-J) from the Gaikema Formation of Alaska is small (L = 24 mm), trapezoidal to subquadratic, longer than high (H/L = 0.75-0.85), very inflated (W/H~0.38), with a low, inconspicuous, rounded, sub-terminal umbo (al/L = 0.17). The transversely elongated beads of the escutcheon rim extend onto the upper area. The marginal carina is a strong narrow ridge with relatively coarse, rounded, well-spaced nodes that increase in size posteriorly and correspond with the flank costellae. A larger paratype (L = 32 mm) is more elongate (H/L = 0.78) with acute flank chevrons, the anterior limbs of which break up into elongated commarginal nodes.

Morigonia kodaijimensis (Kobayashui & Mori) from the Bathonian Kodaijima Formation on the Ojika Peninsula, northeast Honshu, Japan, is small (L = 25.5 mm), quadratic, as long as high (H/L = 1.00), with an unornamented area half as wide as the flank, a beaded submedian carina and nodate L-shaped flank costellae with 1-2 intercalated anterior limbs.

Oxfordian *M. kuzuryuensis* (Maeda) has a thick test and is small (L = 28 mm), longer than high (H/L ~ 0.68), inflated (W/H ~ 0.42), with a rounded respiratory margin. The escutcheon rim is faintly crenulated. The bipartite area has a finely beaded submedian carina and, following its nepionic stage of commarginal costellae, is ornamented only by growth striae. The gently curved marginal carina is crenulated, with a wide shallow antecarinal space below. The flank has three commarginal costellae followed by 5 chevrons.

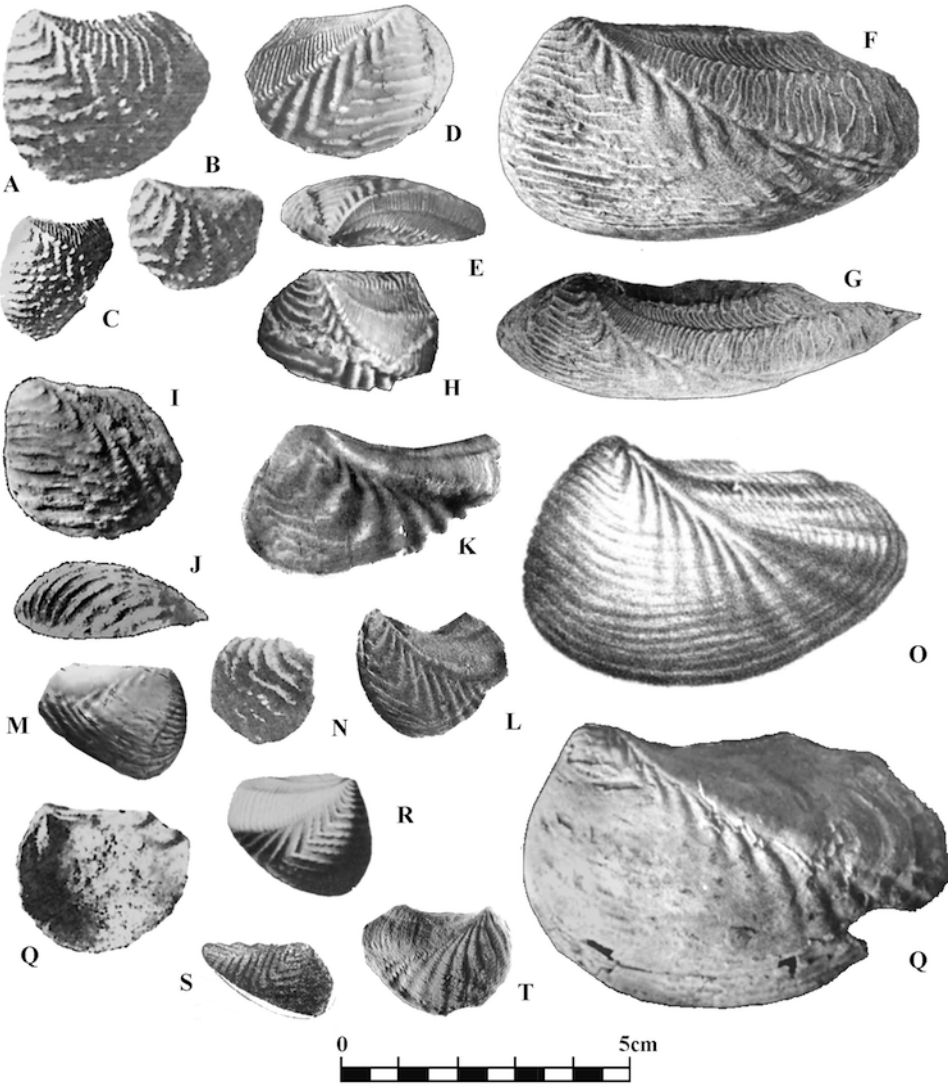

Fig. 4. A. *Morigonia gracilis* (Kobayashi & Mori), the holotype after Kobayashi & Mori (1955). **B.** *Morigonia niranohamensis* (Kobayashi & Mori), the holotype after Kobayashi & Mori (1955). **C.** *Morigonia namigashira* (Kobayashi & Mori), a hypotype after Kobayashi & Mori (1955). **D-G.** *Vaugonia veronica* Crickmay. The holotype (D-E) and a topotype (F-G) after Poulton (1979). **H.** *Vaugonia mariajosephiniae* Crickmay, the holotype after Poulton (1979). **I-J.** *Morigonia imlayi* (Poulton), the holotype after Poulton (1979). **K-L.** *Vaugonia jeletzkyi* Poulton, the holotype (K) and a paratype (L) after Poulton (1979). **M.** *Vaugoniella utahensis* (Imlay), the holotype after Imlay (1980). **N.** *Morigonia irregularis* (Kobayashi & Mori), the lectotype selected herein after Kobayashi & Mori (1955). **O-P.** *Lissotrigonia doroschini* (Eichwald). The lectotype designated herein (O) after Eichwald (1871), and a hypotype (P) after Poulton (1979). **Q-R.** *Morigonia yokoyamai* (Kobayashi & Mori). Q, the paralectotype, and (R) lectotype designated herein after Yokoyama (1904). **S.** *Echevarria manflarum* (Philippi), the holotype by monotypy after Pérez & Reyes (1989). **T.** *Flemingonia orvillensis* (Kelly), the holotype after Kelly (1995).

Genus *Vaugonia* Crickmay, 1930

Type species: *V. veronica* Crickmay 1930: 53, pl. 7, fig. 1; by original designation.

Diagnosis: Small to moderately large, subovate to oblong, posteriorly produced in maturity; beaded escutcheon, submedian and marginal carinae connected by looped and intercalated commarginal lirae; area gabled with submedian angulation and recessed dorsal part; flank chevrons with opisthocline axial trace; thin nontuberculate subcommarginal anterior limbs outnumber short straight thick opisthocline posterior limbs that are sometimes discontinuous and subnodate. *Pliensbachian - U. Toarcian*.

Referred species: *Vaugonia jeletzkyi* Poulton (1976: 46, pl. 8, figs 7-12) (Fig. 4 K-L), *V. mariajosephinae* Crickmay (1930: 54, pl. 7, fig. g, Poulton 1979: 22, pl. 10, fig. 4) (Fig. 4 H).

Discussion: An endemic genus to the Cordilleran Province (British Columbia). It differs from *Morigonia* gen. nov. most obviously in its larger size, greater elongation and nontuberculate chevrons.

Vaugonia veronica Crickmay, 1930

Fig. 4 D-G

1930 *Vaugonia veronica* Crickmay, p. 53, pl. 7, fig. 1.
1979 *Vaugonia veronica* Crickmay. - Poulton, p. 21, pl. 10, figs 1-6.
2021 *Vaugonia veronica* Crickmay. – Echevarría *et al,* p. 29, fig. 14.1.

Type: The holotype is GSC-27715 from the head of the Portland Canal, British Columbia, for which a Late Toarcian - Aalenian age is suggested (Poulton 1979; but see discussion below of *L. doroschini*).

Description: The immature holotype (Fig. 4 D-E) is small (L = 35 mm), ovate, longer than high (H/L = 0.63), very inflated (W/H = 0.52), with a small, insignificant, anteriorly positioned umbo (al/L = 0.17) and moderately incurved opisthogyrate beak. The convex anterior margin passes evenly into the long gently curved ventral margin and the posterodorsal margin (l/L = 0.55) is straight; the broad respiratory margin is broken, but areal lirae show that it was obliquely subtruncate and angulated. The distinct rim to the narrow shallowly sunken escutcheon (l/L = 0.49) is beaded by the elongate terminations of the areal lirae, some of which extend onto the outer escutcheon. The broad bipartite area is gabled, with the dorsal part sunken and concave peaking at the beaded submedian carina that is flanked by a distinct longitudinal furrow. The area is ornamented with regularly spaced commarginal lirae that are single or looped between the escutcheon and marginal carinae, with those on the dorsal area deflected anteriorly and becoming coarser and more irregular with growth, while those of on the ventral area remain transverse. There is a well developed, narrow, finely beaded marginal carina without an antecarinal space, the beads becoming increasingly elongated transversely with growth. Following the nepionic stage (H<8 mm) the flank is ornamented by obtuse chevrons with a straight opisthocline axial trace, the thick bold opisthocline subnodate posterior limbs as wide as the interspaces. The thin wiry nontuberculate anterior limbs are commarginal,

frequently broken into offset segments, and separated by an intercalatory in later growth.

An adult topotype (Fig. 4 F-G), GSC-43007, is moderately large (L = 75 mm), oblong and posteriorly produced (H/L = 0.49), with a weakly convex anterior margin. The lower part of the respiratory margin is convex, the upper part concave, and the long posterodorsal margin shallowly concave. The upper area has arcuate lirae arising in pairs from nodes of the escutcheon carina. The lower area has similar commarginal lirae but in early to middle growth mostly single. The persistent marginal carina is prominent, with transverse nodes that become larger and more distant posteriorly. In middle to later growth the anterior limbs to the flank chevrons greatly outnumber the swollen posterior ones due to the regular occurrence of intercalatories.

Discussion: Even though Poulton (1979: 22) noted that *V. veronica* "does not closely resemble any other species known to the writer", the generic name has continued to be applied indiscriminately to Jurassic trigoniids with V-shaped flank costae.

Vaugonia mariajosephinae Crickmay (Fig. 4 H), from the same locality as *V. veronica*, has an unusually broad area with prominent submedian and marginal carinae but, otherwise, is similar to *V. veronica* of which it is considered a subjective junior synonym (Packard 1921, Poulton 1979).

Vaugonia jeletzkyi Poulton from "probable Pliensbachian beds" on Vancouver Island, British Columbia, was re-assigned to the genus *Pseudovaugonia* by Echevarría *et al.* (2021). However the holotype (Fig. 4 K) is small (L_{max} = 25.5 mm), posteriorly rostrate, with a concave posterodorsal margin, long narrow escutcheon (l/L = 0.75) and a relatively narrow area with lirae uninterrupted by the longitudinal furrow. The flank chevrons have strong bold curved opisthocline posterior limbs that broaden ventrally and cover almost half the flank, the curved opisthocline axial trace close to midflank. They connect singly to very thin, wiry, wavy, nontuberculate subcommarginal anterior limbs, as in the early growth stages of *Vaugonia* (compare Figs 4 F and 4 K). A paratype (pl. 8, fig. 10) (Fig. 4 L) 20 mm long is very different from the type, with an acute umbonal angle, strongly concave posterodorsal margin, curved opisthocline anterior margin, very broad area, and flank chevrons with narrow posterior limbs and apices that become increasingly acute with growth. In the writer's opinion this species cannot be assigned to *Pseudovaugonia*.

Genus *Lissotrigonia* gen. nov.

LSID:urn:lsid:zoobank.org:act:FDF8F0DF-3624-4596-A3A6-4A868F27094B

Etymology: *Lissus* (L.) - smooth.

Type species: *Vaugonia postutahensis* Pugaczewska 1978: 173, pl. 10, fig. 4 a-d; by original designation herein.

Diagnosis: Small to moderately large, elongate ovate to oblong; escutcheon rim nodate; asymmetrically bipartite area with growth striae and feeble submedian carina that evanesces in later growth; marginal carina evanesces in middle growth leaving a rounded rim, with antecarinal space below; flanks with chevrons in nepionic stage,

later with short subcommarginal to oblique anterior limbs widely separated by feebly to unornamented midflank from strongly opisthocline posterior limbs. *Pliensbachian – Hauterivian, ?Valanginian*.

Referred species: *Lissotrigonia athena* (Poulton & Callomon 1977: 156, figs 1-6) (Fig. 5 A-B), *L. cayetanoensis* (Pugaczewska 1978: 175, pl. 9, figs 1a-c), *L. cubanensis* (Pugaczewska 1978: 174, pl. 10, figs 3a-b), *L. doroschini* (Eichwald 1871: 180, pl. 14, figs 12-14, pl. 15, figs 1-4, Packard 1921: 15, pl. 3, figs 1-2, Poulton 1979: 24, pl. 10, figs 25-28, pl. 11, figs 1-3 (*non* figs 4-5) (Fig. 4 O-P), *L. eudesii* (Bigot 1893: 40, pl. 12, figs 1-2) (Fig. 5 D), *L. fragilis* (Lebküchner 1932: 74, pl. 8, figs 2-5; = *Trigonia subglobosa* Schmidtill (*non* Morris & Lycett) 1925, pl. 6, fig. 11) (Fig. 5 F), *L. obliqua* (Hyatt 1892: 407, Packard 1921: 16, pl. 3, figs 5-6, Poulton 1979: 25) (Fig. 5 E and *L. scapha* (Agassiz 1840: 15, pl. 7, fig. 20 (Fig. 5 C).

Discussion: *Lissotrigonia* gen. nov. is pandemic to the Cordilleran (southern Alaska), American (Cuba, California, Wyoming), European (Greenland, England, France, Germany, Switzerland) and Arctic (Ryazan Oblast) provinces.

***Lissotrigonia postutahensis* (Pugaczewska, 1978)**

Fig. 5 H-K

1978 *Vaugonia postutahensis* Pugaczewska, p. 173, pl. 10, fig. 4 a-d.

Type: The holotype is from the upper part of the San Cayetano Formation at El Abra, San Cayetano, Sierra de los Organos, Pinar del Rio province, Cuba, of Oxfordian age.

Description: The holotype (Fig. 5 H-K) is damaged along the anterior and ventral margins. It is small (L~32 mm), thick shelled, elongate ovate, longer than high and moderately inflated, with a low, rounded, inconspicuous subterminal umbo, obtuse umbonal angle (115°), and moderately incurved opisthogyrate beak. The straight, vertical anterior margin passes rather abruptly into the convex ventral margin; although the respiratory margin is not preserved, growth striae indicate it was obliquely subtruncate, and the fairly long posterodorsal margin is slightly convex. The escutcheon and its rim were not described. The narrow bipartite area, about one fifth the width of the flank, is ornamented by growth striae only. The almost straight marginal carina strengthens with growth and is irregularly crenulated by growth striae. Following the commarginal costellae of the nepionic stage, the flank ornament becomes discrepant with the anterior flank ornamented by strong, beaded, subcommarginal costellae that, in middle to later growth, become wavy and curve downwards anteriorly, cutting across growth striae. The central part of the flank is virtually unornamented, with only growth striae and a hint of commarginal ribbing. The posterior flank has strong, straight, opisthocline ribs that broaden ventrally, are as wide as (early growth) or wider than (later growth) than the interspaces, and are crenulated by the growth striae; they meet the marginal carina at an acute angle that increases posteriorly. In maturity, finely beaded radial costellae, some bifurcating, form a narrow skirt to the central part of the ventral margin.

Discussion: The holotype of *L. fragilis* (Fig. 5 F) is from the Dogger Sandstone (*murchisonae* Zone) of Appenberg, southern Germany of Aalenian age, and is the

earliest recorded member of the genus. It is moderately large (L = 95 mm), thin shelled and trigonally elongate (H/L = 0.60), with a straight marginal carina that strengthens with growth. Narrow subcommarginal costellae cover a quarter of the flank anteriorly, and there are up to 10 thick bold straight strongly opisthocline ribs posteriorly, leaving most of the central flank unornamented save for growth striae.

Lissotrigonia doroschini (Eichwald) is widespread and locally common in southern Alaska and British Columbia where it ranges in age from Lower Bajocian to Oxfordian and possibly Kimmeridgian (Poulton 1979). Eichwald (1871) had a number of syntypes, of which the original of pl. 13, figs 12-14 (Fig. 4 O) is selected here as lectotype; the remainder becoming paralectotypes. They were collected from a black "Neocomian" limestone near Egge in the Tukisnitsu Bay of Kiua Gulf, southern Alaska. According to Poulton (1979: 24) the species is common "in the Jurassic strata in the same vicinity in which Eichwald collected his specimens." Although the species is said to be most abundant in the lower part of the Bowser Lake Group of northern British Columbia, of Early Oxfordian age, the specimens figured by Poulton (1979, pl. 10, figs 25-28) (Fig. 4 Q) that most closely resemble the type are from the "probable Callovian" of the Chinitina Valley of southern Alaska. The lectotype (Fig. 4 O) is medium sized (L = 62 mm; L_{max} = 82.5 mm), elongate-ovate (H/L = 0.61), inflated (W/H = 0.33), with a small, pointed anteriorly positioned umbo (al/L~0.25) and strongly incurved orthogyrate beak. The gently curved anterior margin passes rather abruptly into the long evenly convex ventral margin, the respiratory margin is obliquely subtruncate, and the posterodorsal margin shallowly concave. The ligament pit is short (l/L = 0.14) and narrow. The escutcheon is rather short (l/L = 0.28), fairly narrow (w/l = 0.21), sunken and unornamented except where encroached by lirae from the area, with a prominent rim with oblique nodes that become thinner and transversely more elongated posteriorly. The asymmetrically bipartite area is gabled with a low weak longitudinal ridge finely crenulated by growth striae, and a narrower more deeply concave dorsal portion that, at the commissure, leaves a gape. For most of its length the area is ornamented by growth striae only.

There is a thin marginal carina that evanesces in middle growth to leave a rounded rim below which is an antecarinal space that broadens posteriorly. Following the commarginal costellae of the nepionic stage, the flank is ornamented by acute chevrons, the strongly opisthocline axial trace of which results in short posterior limbs to the chevrons that are straight, bold, and much wider than the interspaces, broad-ening ventrally. The anterior limbs to the chevrons are fine, straight, subcommarginal, about as wide as the interspaces, and may reduce to thin horizontal ribs on the anterior face where they meet the commissure perpendicularly.

Poulton (1979: 24) emphasized the variability of *L. doroschini*, some showing almost complete effacement of the anterior and central flank costellae (Fig. 4 Q). In shape and size it is very similar to *V. veronica*. A hypotype (Poulton 1979, pl. 10, fig. 26) shows the RV substantially more inflated than the LV. In addition Poulton (1979) figured an Oxfordian-Kimmeridgian specimen (Fig. 6A-B) from the Naknek Formation of Alaska that differs markedly from the typical "probably Callovian" specimens in being smaller (L = 63 mm), oblong (H/L = 0.65), with strong wrinkles to the escutcheon and area, escutcheon and marginal carinae restricted to earliest growth, a few opisthocline posterior ribs, and most of the unornamented flank with

broad commarginal growth bands. Poulton (1979: 25) suggested that, with better material and tighter stratigraphical control, a different species may be involved.

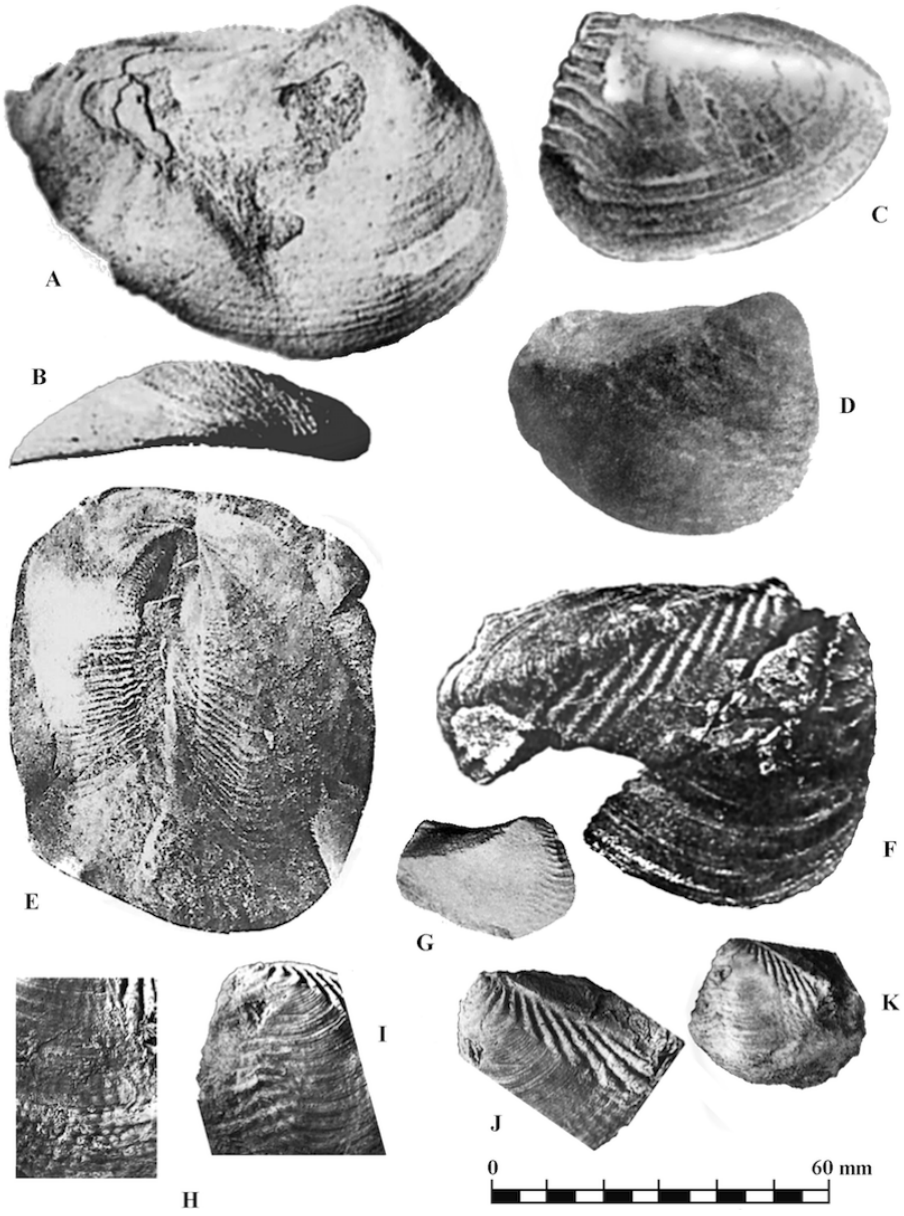

Fig. 5 A-B. *Lissotrigonia athena* (Poulton & Callomon), the holotype after Poulton & Callomon (1977). **C.** *Lissotrigonia scapha* (Agassiz), the lectotype designated herein, after Agassiz (1840). **D.** *Lissotrigonia eudesii* (Bigot), the holotype by monotypy, after Bigot (1893). **E.** *Lissotrigonia oblonga* (Hyatt), the lectotype designated by Packard (1921), after Packard (1921)). **F.** *Lissotrigonia fragilis* (Lebküchner), the holotype after Lebküchner (1932). **G.** *Wyomingella poststriata* (Whitfield & Hovey), the lectotype designated herein after Whitfield & Hovey (1906). **H-K.** *Lissotrigonia postutahensis* (Pugaczewska), the holotype after Pugaczewska (1978).

Lissotrigonia athena (Poulton & Callomon) (Fig. 5 A-B) from the Bathonian of East Greenland is moderately large (L_{max} = 90 mm), thick shelled, subtrigonal and posteriorly produced, subequilateral (al/L = 0.25-0.33), moderately inflated (W/H = 0.25), with a strongly convex anterior margin and short posterodorsal margin (l/L~50%). The long narrow escutcheon is shallowly concave and smooth, with a rounded rim. The narrow asymmetrically bipartite area is ornamented only by growth striae, and the marginal carina is a sharpened rim in early growth, rounding later. The

subdued flank ornament is dominated by growth striae and growth rugae of irregular strength and spacing, but with short broad straight opisthocline ribs posteriorly and thin commarginal ribs close to the anterior and ventral margins.

The lectotype of *L. eudesii* (Bigot) designated herein (Fig. 5 D) is from the Upper Bathonian (Couches à *Z. cardium*) at Luc et Langrune (Calvados), Normandy. It is medium sized (L = 53 mm), longer than high (H/L = 0.77), moderately inflated (W/H = 0.33), with low broadly rounded subterminal umbones. The almost straight anterior margin passes evenly into the well-rounded ventral margin, the rather narrow oblique respiratory margin is slightly convex, and the long posterodorsal margin shallowly concave. There is an elongate sunken escutcheon. Following the nepionic stage of commarginal costellae, the narrow area is unornamented save for growth striae, with a bluntly nodate marginal carina. The flanks are ornamented with 6-7 subcommarginal costellae on the umbones, where after they are smooth except for about 20 short weak oblique ribs close to the anterior margin.

Lissotrigonia obliqua (Hyatt) (Fig. 5 E) from the Callovian "Trigonia Bed" of the Bicknell Formation of California was characterized by its incomplete costae and "extraordinary size" but is not well described and the illustration is poor. The lectotype is less produced posteriorly than *L. doroschini*, with a broadly rounded respiratory margin, large unornamented escutcheon, conspicuously lirate area, beaded marginal carina in early growth and short oblique ribs to the anterior face.

Lissotrigonia cubanensis (Pugaczewska) was collected from the same locality as *L. postutahensis* and distinguished by its trigonally ovate shape, and scattered nodes and longitudinal striae to the central part of the flank. *Lissotrigonia cayetanoensis* (Pugaczewska), also from the same locality, is based upon a damaged holotype that is small (L = 31 mm), subtrigonally elongate (H/L = 0.78) and moderately inflated (W/H = 0.26), with a sinus to the ventral margin, sinuous respiratory margin with a "posteroventral lobe" and radial fan-shaped folds to the flank.

Lissotrigonia scapha (Agassiz) is from the Berriasian blue marls in the vicinity of Neuchâtel, Switzerland, with other specimens from the Neocomian at Voray, near Besançon in France. The lectotype selected herein (Fig. 5 C) is preserved as a composite internal mould. It is medium sized (L = 70 mm), though some specimens are said to be significantly larger, elongate-subovate (H/L = 0.74) with a near terminal umbo, straight inclined anterior margin, very broad strongly oblique respiratory margin and short shallowly concave posterodorsal margin (l/L = 0.48). The escutcheon is not described but the unornamented wide area has a rounded marginal rim for most of growth. The flank ornament comprises strong short wavy downcurved ribs near the anterior margin, much narrower than the interspaces, separated from the straight opisthocline posterior ribs that appear to have been subnodate, with very distinct growth halts near the ventral margin.

Gerasimov (1955) identified material from the Leshchinsky ravine, near the town of Mikhailov, in the Ryazan Oblast of Russia as *Trigonia scapha* Agassiz that was said to be fairly common in the Upper Volgian (*Craspedites nodiger* Zone) to Valanginian of the area. The described specimen (Fig. 8 K) is medium size (L = 50 mm), oblong, longer than high (H/L = 0.70), with slightly convex anterior and ventral margins. There is a narrow shallow escutcheon with finely beaded rim, and the bipartite area

has a weak longitudinal furrow. The blunt marginal carina has infrequent small nodes. The flank has chevrons whose apices become increasingly acute ventrally, with 12-17 narrow subhorizontal anterior limbs that substantially outnumber the curved thick subvertical posterior limbs. It is said to be slightly inequivalve, the LV with a wider umbonal angle (100-105°) than the RV (90°). The description has all the features of *Vaugoniella* gen. nov., but the undescribed LV (Fig. 8 L) has the ornament effaced from the central part of the flank and has the features of *Lissotrigonia* gen. nov. This contradiction requires closer investigation.

Both *Trigonia? inflata* Roemer (1839: 35, pl. 19, fig. 22) and *T. roemeri* Agassiz (1840: 10; = *Unio suprajurensis* Roemer 1839: 35, pl. 19, fig. 1) from the Portlandian of northern Germany, and *T. paradoxa* Agassiz (1840: pl. 10, figs 12-13) from the Neocomian of Switzerland were assigned to "Glabrae" (Agassiz 1840: 10) but both are based upon specifically indeterminate internal moulds and hence *nomina dubia*.

Genus *Wyomingella* gen. nov.

LSID:urn:lsid:zoobank.org:act:144C5C16-472F-4166-B43E-074A20F38D01

Etymology: After the American state of Wyoming.

Type species: *Trigonia poststriata* Whitfield & Hovey 1906: 396, pl. 48, figs 4-6; by original designation herein.

Diagnosis: Small, cuneiform, posteriorly rostrate, with obliquely truncated respiratory margin and concave posterodorsal margin; area slightly concave with growth striae only and sharp concave marginal rim, lacking submedian carina and longitudinal furrow; anterior quarter of flank with fine costellae, initially horizontal but later concave up, with remainder of flank with growth striae and growth halts only; opisthocline posterior ribs lacking. *Jurassic*.

Discussion: A monotypic genus distinguished from *Lissotrigonia* gen. nov. by its small size, elongate cuneiform shape and lack of straight opisthocline ribs to the posterior flank.

Wyomingella poststriata (Whitfield & Hovey, 1906)

Fig. 5 G

1906 *Trigonia poststriata* Whitfield & Hovey, p. 396, pl. 48, figs 4-6.

Types: The lectotype designated herein is the original of Whitfield & Hovey (1906, pl. 48, fig. 6) from sandy shales of Jurassic age in the Belle Fourche valley, 4 miles southwest of Hulet, Wyoming. The remaining syntypes (pl. 48, figs. 4-5) become paralectotypes.

Description: The lectotype (Fig. 5 G) is small (L = 33 mm), moderately inflated, cuneiform, posteriorly rostrate, much longer than high (H/L = 0.64), with a convex anterior margin passing rather abruptly into the long gently convex ventral margin. The respiratory margin is obliquely truncated and the long posterodorsal margin (l/L = 0.50) concave, with a low broadly rounded umbo situated anteriorly (al/L = 0.27).

The area is slightly concave, only with growth striae. No mention is made of a submedian carina or longitudinal furrow and there is a sharp concave marginal rim. The anterior quarter of the flank is ornamented by fine costellae as wide as the interspaces, initially horizontal by later concave up and oblique, with the remainder of the flank only with growth striae and deeper growth halts. Opisthocline posterior ribs are lacking.

Discussion: No other species warrants close comparison.

Genus *Fribourgella* gen. nov.

LSID:urn:lsid:zoobank.org:act:A7866191-5C55-4CD4-8D32-43F04111D7DF

Etymology: After Fribourg, the city in Switzerland near where the type species was collected.

Type species: *Trigonia undulata* Fromherz 1838: 22, Agassiz 1840: 34, pl. 6, fig. 1 only; by original designation herein.

Diagnosis: Small, ovate to ovately oblong; broad asymmetrically bipartite area with longitudinal furrow and commarginal costellae and beaded submedian carina in nepionic stage; prominent marginal carina strengthens with growth; flanks with simple L-shaped then V-shaped chevrons with subangular often thickened apices; anterior limbs horizontal to commarginal, without intercalation or bifurcation; thicker posterior limbs opisthocline, sometimes subnodate. *Aalenian - Bathonian*.

Referred species: *Fribourgella agassizi* sp. nov. (see below) (Fig. 7 A-C), *F. arata* (Lycett 1863: 52, pl. 40, fig. 2) (Fig. 6 K), *F. franconica* (Lebküchner 1932: 71, pl. 7, figs 10-14) (Fig. 6 J), *F. painei* (Lycett 1874: 59, pl. 12, figs 2-5) (Fig. 6 L).

Discussion. *Fribourgella* gen. nov. is a pandemic genus reported from the American (California) and European (England, France, Italy, Switzerland) provinces.

Fribourgella undulata (Fromherz, 1838)

Fig. 6 E-F

1838 *Trigonia undulata* Fromherz, p. 22.
1840 *Trigonia undulata* Fromherz. - Agassiz, p. 34, pl. 6, fig. 1 (*non* pl. 10, figs 14-16).
1888 *Trigonia flecta* Lycett. - Schlippe, p. 155, pl. 5, fig. 6.
1932 *Trigonia undulata* Fromherz. - Lebküchner, p. 71, pl. 7, figs 10-14.

Type: Fromerz (1838) provided only a short description of the species and it was left to Agassiz (1840, pl. 6, fig. 1) to illustrate the holotype, by monotypy, from the Inferior Oolite (Aalenian-Bajocian) of Fribourg in the Swiss Jura.

Description: The holotype (Fig. 6 F) is small (L = 42 mm), subtrapezoidal, longer than high (H/L = 0.74), with a small terminal umbo and moderately incurved beak. The anterior margin is straight, vertical, and passes abruptly into the long convex ventral margin. The broad respiratory margin is obliquely truncate and the relatively

short posterodorsal margin shallowly concave (l/L = 0.49). The escutcheon is not described, but there is a beaded escutcheon rim. The broad asymmetrically bipartite area appears to be gabled, with a narrower concave upper part and persistent longitudinal furrow and, for most of its length, is ornamented only by growth striae. The shallowly concave marginal carina is nodate, the nodes becoming larger and transversely more elongate posteriorly, with a narrow antecarinal space in later growth. Following the nepionic stage of commarginal costellae, the flank is ornamented with L- to V-shaped nontuberculate chevrons with a strongly opisthocline axial trace and rounded to subangular crests that become more acute with growth. They have short, thick, strongly opisthocline posterior limbs that broaden ventrally and narrower commarginal anterior limbs.

Discussion: Schlippe (1888) regarded *Trigonia undulata* Fromherz and *T. flecta* Morris & Lycett synonymous, but erred in subsuming the former into the latter; the specimen he figured (Fig. 5 P) is regarded as conspecific with *F. undulata* (Lebküchner 1932). A specimen from the Middle Bajocian of California (Poulton 1979: 25, fig. 23), identified as *Vaugonia* sp. cf. *kobayashi* Aléncaster (Fig. 6 G), closely resembles *F. undulata*.

The holotype of *F. franconica* (Lebküchner) (Fig. 6 J) is from Aalenian Haupt-muschelbank of the Dogger Sandstone at Appenberg, northern France. It is very small (L = 18 mm), trigonally ovate to subquadratic, almost as high as long (H/L = 0.94), inflated (W/H = 0.35), with well rounded anterior and ventral margins, and a fairly large escutcheon that rises to the commissure and is bounded by a smooth rim.

Fribourgella arata (Lycett) (Fig. 6 K) from the Bathonian Forest Marble at Farleigh Hungerford, Somerset, England, is based upon a small crushed specimen (L = 28 mm), the holotype by monotypy. It differs from *F. undulata* in being oblong-ovate (H/L = 0.73), with a convex anterior margin, inconspicuous marginal carina that becomes obsolete in later growth, and in having far more obtuse flank chevrons with narrower posterior limbs that, in middle growth, are perpendicular to the marginal carina, and finer commarginal anterior limbs.

The lectotype designated herein of *F. painei* (Lycett) (Fig. 6 L is from the Great Oolite (Bathonian) of Minchinhampton, England, in the beds called “planking”. It is medium sized (L = 63 mm), elongate-ovate, longer than high (H/L = 0.71), with a long shallowly concave posterodorsal margin (l/L = 0.59). The long narrow escutcheon rises towards the commissure, with an inconspicuous beaded rim that becomes obsolete posteriorly. The wide striated area is asymmetrically bipartite with a feeble longitudinal furrow and narrow antecarinal space. The flank has strong ribs, initially commarginal, then U-shaped, L-shaped, and finally with acute thickened crests. Thick nodate opisthocline posterior limbs cover a third of the flank, with thinner subnodate horizontal costellae the remainder.

***Fribourgella agassizi* sp. nov.**

Figs 7A-C

LSID: urn:lsid:zoobank.org:act:6556E459-8964-4F57-8D8E-6A925981A86B

1840 *Trigonia undulata* Fromherz. - Agassiz, p. 34, pl. 10, figs 14-16 only.

Etymology: After Louis Rudolphe Agassiz (1807-1873), recorder of the holotype.

Type: The holotype is the original of the specimen figured by Agassiz (1840, pl. 10, figs 14-16) in the Agassiz Collection of the Natural History Museum, Neuchâtel, Switzerland, from Piémont, northwest Italy.

Diagnosis: Like *F. undulata* but larger, subtrigonal, with straight posterodorsal margin, prominently nodate marginal carina and more numerous flank chevrons with subnodate posterior limbs and approximated anterior limbs in later growth.

Description: The holotype (Figs 7 A-C) is moderately large (L = 76 mm), subtrigonal, higher than long (H/L = 0.85), with a strongly convex ventral margin and moderately long straight posterodorsal margin (l/L = 0.54). In early to middle growth it has a moderately long lanceolate escutcheon (l/L = 0.55) whose rim is beaded in early to middle growth. The broad asymmetrically bipartite area has a longitudinal furrow in the upper part that persists to maturity, its straight marginal carina ornamented by nodes that become larger and transversely more elongate posteriorly, with an antecarinal space below. Following the nepionic stage of commarginal costellae, the flanks are ornamented with L- to V-shaped chevrons with thickened subrounded to subangular apices that become more acute with growth. The short straight posterior limbs to the chevrons are subnodate, and the commarginal anterior limbs thin and crowded as they approach the anterior margin, becoming concave up on the anterior face where there is a large shallow lunule.

Discussion: The holotype was excluded from *F. undulata* by Lycett (1874), Schlippe (1888) and Lebküchner (1932).

Genus *Pseudovaugonia* Echevarría, Damborenea & Manceñido, 2021

Type species: *Vaugonia hectorleanzai* Pérez & Reyes (*in* Pérez *et al.*) 2008: 91, pl. 13, fig. 9, pl. 15, figs 3, 5-11, pl. 16, figs 1, 3, 8-9, 11-12, 14-15); by original designation.

Diagnosis: Small to medium sized, subrectangular to subtrapezoidal, ovate and trigonally elongate; escutcheon rim beaded; lirate bipartite area with submedian longitudinal furrow, submedian carina lacking; marginal carina beaded, often rounding in later growth; antecarinal space narrow to absent; flank chevrons with very obtuse well rounded to subangular apices with axial trace generally close to midflank; beaded posterior limbs slightly thicker than thin, wavy, finely beaded to wiry anterior limbs. *Upper Sinemurian - Bathonian*.

Referred species: *Pseudovaugonia coatesi* (Poulton 1976: 49, pl. 8, figs 21-26) (Fig. 6 S-T), *P. exotica* (Möricke 1894: 49, pl. 6, fig. 9) (Fig. 3 S), *P. gardeti* (Freneix 1958: 37, pl. 2, figs 3-5) (Fig. 6W), *P. lycetti* sp. nov. (see below) (Fig. 6 H-I), *P. sharpiana* (Lycett 1874: 79, pl. 15, fig. 11, pl. 16, figs 3-6) (Fig. 6 R), *P. spinulosa* (Young & Bird 1828: 225, Lycett 1872: 44, pl. 3, figs 4-6, Benecke 1905: 195, pl. 14, figs 9-10, Lebkűchner 1932: 68, pl. 7, figs 4-9) (Fig. 6 Q), *P. vancouverensis* (Poulton 1976: 48, pl. 8, figs 13-20) (Fig. 6 N).

Discussion: *Pseudovaugonia* is pandemic to the Andean (Chile, Argentina), Cordilleran (British Columbia, Oregon), American (Nevada) and European (England, France, Germany) provinces, distinguished mainly by chevrons with narrow beaded posterior limbs, rounded apices and an axial trace close to midflank.

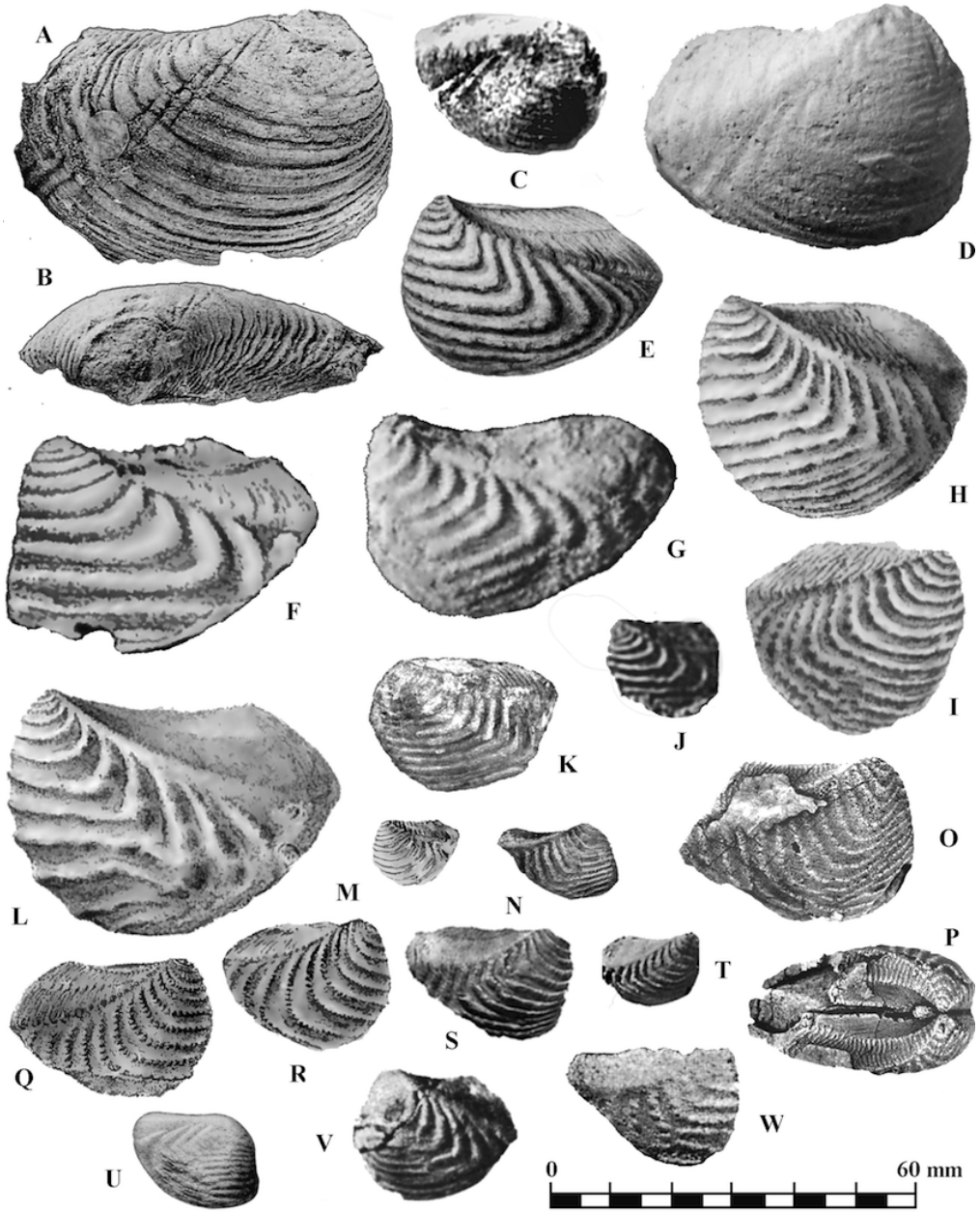

Fig. 6. A-B. *Lissotrigonia* sp. nov. aff. *doroschini* (Eichwald), a hypotype after Poulton (1979). **C-D.** *Pseudapiotrigonia sturgisensis* (Whitfield & Hovey). C, a paralectotype after Whitfield & Hovey (1905); D, the lectotype after Cooper (2021). **E-F.** *Fribourgella undulata* (Fromurze). E, a hypotype after Schlippe (1888); F, the holotype by monotypy after Agassiz (1840). **G.** *Fribourgella* cf. *undulata* (Fromurze), a hypotype after Poulton (1979). **H-I.** *Pseudovaugonia lycetti* sp. nov. The holotype (H) and paratype (I) after Lycett (1874). **J.** *Fribourgella franconina* (Lebküchner), the holotype after Lebküchner (1932). **K.** *Fribourgella arata* (Lycett), the holotype by monotypy; SMC-J5797, https://www.3d-fossils.ac.uk/fossilType. **L.** *Fribourgella painei* (Lycett), the lectotype designated herein after Lycett (1874). **M.** *Vaugoniella windoesi* (Lycett), the lectotype designated herein after Lycett (1883). **N.** *Pseudovaugonia vancouverensis* (Poulton), the holotype after Poulton (1976). **O-P.** *Pseudovaugonia hectorleanzai* (Pérez, Aberhan, Reyes & von Hildebrandt), the holotype after Pérez *et al.* (2008). **Q.** *Pseudovaugonia spinulosa* (Young & Bird), the lectotype designated herein after Lycett (1872). **R.** *Pseudovaugonia sharpiana* (Lycett), the lectotype designated herein after Lycett (1874). **S-T.** *Pseudovaugonia coatesi* (Poulton), a paratype (S) and the holotype (T) after Poulton (1976). **U.** *Vaugoniella quadrangularis* (Meek & Hayden), a hypotype after Butler *et al.* (1920). **V.** *Vaugoniella* cf. *moretoni* (Lycett), a Caucasian hypotype, after Pčelincev (1937). **W.** *Pseudovaugonia gardeti* (Freneix), the holotype after Freneix (1958).

Echevarría *et al.* (2021) looked to *Moerickella* for the origin of the genus and placed it in the Myophorellidae. However its gabled area, V-shaped flank costellae in early growth, and strongly recurved flank costellae with beaded posterior limbs and wavy nontuberculate anterior limbs are features of Vaugoniinae. The writer regards partitioning of flank costae into a beaded or nodate posterior portion, and a finely beaded to nontuberculate and wiry anterior portion, of prime importance in distinguishing Vaugoniinae from similar Myophorellinae.

Pseudovaugonia resembles *Echevarria chunumayensis* (Jaworski) but the latter is posteriorly rostrate with well-developed escutcheon and marginal carinae, an area with simple widely spaced lirae with a distinct longitudinal furrow and an antecarinal space that broadens with growth. Initially *Pseudovaugonia* has L-shaped flank chevrons that develop broadly rounded crests later, with beaded posterior limbs and fine straight to undulating and dichotomizing nontuberculate anterior limbs (Pérez *et al.* 2008, pl. 16, fig. 7).

Pseudovaugonia differs from *Vaugoniella* gen. nov. in having longer curved beaded posterior limbs to its chevrons and in lacking intercalated anterior limbs to the chevrons. *Munierchalmasia* gen. nov. is larger, with a beaded submedian carina, prominently nodate marginal carina and nodate posterior limbs to the chevrons that cover up to half the flank and are greatly outnumbered by the fine anterior limbs.

***Pseudovaugonia hectorleanzai* (Pérez, Aberhan, Reyes & von Hillebrandt, 2008)**
Fig. 6 O-P

1980 *Vaugonia* n.sp. - Hillebrandt, pl. 2, fig. 1.
2008 *Vaugonia hectorleanzai* Pérez & Reyes (*in* Pérez *et al.*), p. 91, pl. 13, fig. 9, pl. 15, figs 3, 5-11, pl. 16, figs 1, 3, 8, 9, 11, 12, 14, 15.
2021 *Pseudovaugonia hectorleanzai* (Pérez & Reyes). - Echevarría *et al.*, p. 31, fig. 15.

Type: The holotype is from the Lower Toarcian (*Dactylioceras hoelderi* Zone) at Quebrada Chanchoquín-Paitepén, southeast of Vallenar, Atacama, Chile. The species is found also in the Upper Sinemurian and Lower Toarcian of Antofagasta and Atacama (Pérez *et al.* 2008) and, in Argentina, the Lower Toarcian of Las Overas, Mendoza Province, Arroyo Lapa of the central Neuquén Province and, probably, the Pliensbachian or Toarcian at Arroyo La Laguna (Los Patos region), San Juan Province.

Description: The holotype (Fig. 6 O-P) has its posterior end broken off. It is small (L = ~38 mm), subrectangular, longer than high (H/L = 0.74) and inflated (W/H = 0.39); paratypes show a weakly incurved opisthogyrate beak. The long wide escutcheon (w/W = 0.49) is deeply sunken and unornamented, with its rim beaded by the terminal swellings of the areal lirae. The rather narrow area, a quarter of the valve surface, is asymmetrically bipartite, the upper part narrower than the lower, with an indistinct longitudinal furrow. The positions of the escucheon and submedian carinae are marked, on the internal commissure of a paratype, by short longitudinal buttresses. The area is ornamented with simple fine commarginal lirae that become increasingly wavy and irregular posteriorly, with occasional bifurcation and intercalation. The thin marginal carina is crenulated by the terminations of areal lirae.

Following a nepionic stage of commarginal costellae, the flanks are ornamented by oblique widely spaced L-shaped chevrons of uniform width with rounded apices that become increasingly obtuse posteriorly, and meet the marginal carina at a slightly acute angle, with the curved opisthocline axial trace close to midflank. The long curved opisthocline posterior limbs to the chevrons are ornamented with small crowded ellipsoidal nodes, whereas the closely spaced commarginal anterior limbs are nontuberculate, wavy and often segmented, with occasional bifurcation and intercalation.

Discussion: Echevarría *et al.* (2021) assigned Late Pliensbachian *V. oregonensis* Poulton to *Pseudovaugonia* but its holotype (Fig. 10 M) is very different, with long thick curved posterior limbs to its chevrons and, here, is transferred to *Munier-chalmasia* gen. nov.

Pseudovaugonia vancouverensis (Poulton) (Fig. 6 N), from the probable Pliens-bachian of Vancouver Island, differs from *P. hectorleanzai* in being much smaller (L_{max} = 20 mm), with a strongly convex anterior margin, umbones well away from the anterior (al/L = 0.28), concave posterodorsal margin, narrower area with thin antecarinal gap, thick marginal carina and bowl-shaped flank costellae in early to middle growth that become geniculate later to form very obtuse round-crested chevrons with slightly curved subnodate posterior limbs that are thicker than the thin straight nontuberculate commarginal anterior limbs. The specimens identified by Poulton (1979: 23, pl. 10, figs 23-24) as *Vaugonia* sp. cf. *V. vancouverensis* Poulton from the Upper Sinemurian Sunrise Formation of Nevada are additional examples of *Pseudovaugonia*.

Probable Toarcian *P. coatesi* Poulton (Fig. 6 S-T) is based on a very small reniform holotype (L = 18 mm), longer than high (H/L = 0.72), with a prominent, rounded anteriorly positioned umbo (al/L = 0.17). Initially the flank costellae are sub-commarginal but later become obtuse chevrons with rounded crests (see pl. 8, figs 23-26) with short curved posterior limbs and fine subcommarginal anterior limbs of similar width. Near the umbo (in early growth) its ribs are finely beaded.

The lectotype designated herein of *P. sharpiana* (Lycett) is the original of Lycett (1874, pl. 16, fig. 3) (Fig. 6 R) from the Dogger (Toarcian) of Blea Wyke, northern Yorkshire, England. It is small (L = 27 mm), ovate, longer than high (H/L = 0.78), with convex anterior and ventral margins and an almost straight posterodorsal margin. Its short wide escutcheon has a finely crenulated rim, and the very wide flattened bipartite area, one-third of the valve, has commarginal lirae that evanesce in later growth. Its narrow concave marginal carina is finely beaded by the terminations of the areal lirae, without an antecarinal space below. Following a nepionic stage of 4-5 commarginal costellae, the flank is ornamented by curved costellae of uniform width, narrower than the interspaces, that bend obliquely forward at midflank so that most terminate along the anterior margin and are uniformly beaded.

Aalenian *P. gardeti* (Freneix) (Fig. 6 W) is small (L= 23 mm), trigonally elongate (H/L = 0.60), with a convex anterior margin, straight ventral margin, moderately wide escutcheon with finely beaded rim, broad asymmetrically bipartite finely lirate area without submedian carina, and a fine slightly curved rounded marginal carina without an antecarinal gap. Following the nepionic stage of four feebly beaded

commarginal costellae, the flank is ornamented with very obtuse beaded flank chevrons with rounded apices, the posterior limbs with three nodes and the finer straight closely spaced beaded anterior limbs with an occasional intercalatory.

Chilean *P. exotica* (Möricke) (Fig. 3 S) from the *humphresianus*-Schichten near Manflas, is small (L = 28 mm), subquadratic (H/L = 0.79), with a broad lirate area with feebly beaded submedian carina and curved nodate marginal carina that persist to maturity without an antecarinal space below. In early to middle growth the flank is ornamented by well-spaced chevrons, much narrower than the interspaces, with very obtuse subrounded apices, the posterior limbs with ellipsoidal nodes and the anterior ones with thin disjointed commarginal riblets.

The lectotype designated herein of *P. spinulosa* (Young & Bird) (Fig. 6 Q) is the original of the specimen figured by Lycett (1872, pl. 3, fig. 5a) from the same locality as *P. sharpiana*, i.e. the Inferior Oolite (Toarcian) of Blea Wyke, northern Yorkshire. It is small (L = 33 mm), ovate (H/L = 0.65) with a very large escutcheon (l/L = 0.50), wide stepped area, the upper half recessed, with a delicately beaded submedian carina bordering a longitudinal furrow, and irregular commarginal lirae. The marginal carina is a curved row of small rounded nodes with a narrow antecarinal space below. Following the nepionic stage of 7 fine commarginal costellae, the remainder of the flank is covered by well spaced curved rows of beads, each surmounted by a minute spine, the axial trace of the curvature close to midflank. The rows are subhorizontal anteriorly, or directed slightly downwards, and are irregularly beaded. Posteriorly they have larger nodes that curve upwards to meet the marginal carina at an angle that becomes increasingly acute posteriorly.

Echevarría *et al.* (2021) assigned *Vaugonia oregonensis* (Poulton 1979, pl. 10, figs 14-19) (Fig. 10 M-N) to *Pseudovaugonia*, but the American species has thick bold curved posterior limbs to its chevrons and intercalated anterior limbs. Here it is assigned to *Munierchalmasia* gen. nov.

***Pseudovaugonia lycetti* sp. nov.**

Figs 6 H-I

LSID: urn:lsid:zoobank.org:act:5CB371E2-8EFD-4F88-A0D7-7CEEC578A0BE

Etymology: After John Lycett, monographer of the British Trigoniida.

Types: The holotype is the original of the *Trigonia undulata* Fromherz figured by Lycett (1874, pl. 17, fig. 5) (Fig. 6 H) from the Blisworth Limestone of the Great Oolite near Bourne, Lincolnshire, of Bathonian age. The originals of pl. 16, figs. 9-11 and pl. 17, fig. 6, from the same locality, serve as paratypes, all presumably in the BMNH.

Diagnosis: Like *P. hectorleanzai* but younger, larger, subovate, with more convex anterior margin, axial trace to chevrons closer to the anterior, and anterior limbs evenly spaced, not approximate.

Description: The holotype (Fig. 6 H) is **s**mall (L = 47 mm), subovate, longer than high (H/L = 0.87), moderately inflated, with a subvertical anterior margin passing imperceptibly into the strongly convex ventral margin. The broad obliquely subtruncate respiratory margin is gently convex, and the moderately long posterodorsal margin (l/L = 0.55) almost straight, with a small pointed subterminal umbo (al/L = 0.17) and moderately incurved opisthogyrate beak. The deeply excavated narrow escutcheon is smooth, its rim beaded by the terminations of areal lirae, and rises towards the commissure. The moderately wide area, a third of the flank, has a well defined submedian furrow and wrinkled commarginal costellae. The narrow gently curved marginal carina is beaded for its entirety, with the beads becoming increasingly transversely elongated posteriorly; there is no antecarinal gap. Following a nepionic stage of uniform subcommarginal costellae, the flank is ornamented by numerous fine costellae, as narrow as the interspaces, forming very obtuse chevrons with rounded apices and a curved opisthocline axial trace about a third of the width of the flank from the marginal carina. The slightly curved posterior portion to the chevrons is nodate, whereas the straight commarginal anterior portion is beaded to subtuberculate and cord-like.

Discussion: Lycett (1874: 78) noted that, among topotypes, "the costae have great variability, both in their figure and in the presence or absence of tubercles". In a juvenile paratype (L = 30 mm) (pl. 16, fig. 11) the costellae are nontuberculate or only "slighted knotted" and on another (Fig. 6 I) the chevrons have angulated apices, relatively thick subnodate posterior limbs and thin straight nontuberculate anterior limbs.

Genus *Glevenella* gen. nov.

LSID:urn:lsid:zoobank.org:act:B97A3F5A-3B55-4970-AF2F-04497E4399EC

Etymology: From *Glevum*, the Roman name for Gloucestershire; the county was granted the official title of *Colonia Nervia Glevensis* by Emperor Nerva in 97 AD.

Type species: *Trigonia producta* Lycett (*in* Wright) 1860: 45; 1874: 60, pl. 13, figs 1-4; by original designation herein.

Diagnosis: Moderately large, trigonally ovate and posteriorly produced with straight to slightly concave posterodorsal margin; large flattened escutcheon; narrow bipartite area with irregular commarginal rugae, longitudinal furrow and minutely beaded submedian carina; nodate marginal carina rounding in middle growth, with well developed antecarinal space; in early to middle growth flanks with curved to subrounded beaded costellae with rounded crests and axial trace close to midflank; in middle growth chevron apices feeble to evanescent; curved opisthocline posterior limbs coarsely nodate, covering quarter of flank; subcommarginal anterior limbs with adpressed beads fusing anteriorly. *Lower Bajocian*.

Discussion: A monotypic genus from the European Province (England, France).

Glevenella producta (Lycett, 1860)

Fig. 12 H

1860 *Trigonia producta* Lycett (*in* Wright), p. 45.
1874 *Trigonia producta* Lycett. - Lycett, p. 60, pl. 13, figs 1-4.

Types: The lectotype designated herein is the original of the specimen figured by Lycett (1874, pl. 13, fig. 2) from the Trigonia Grit of the Inferior Oolite (= Salperton Limestone) at Rodborough Hill near Stroud, Gloucestershire, England.

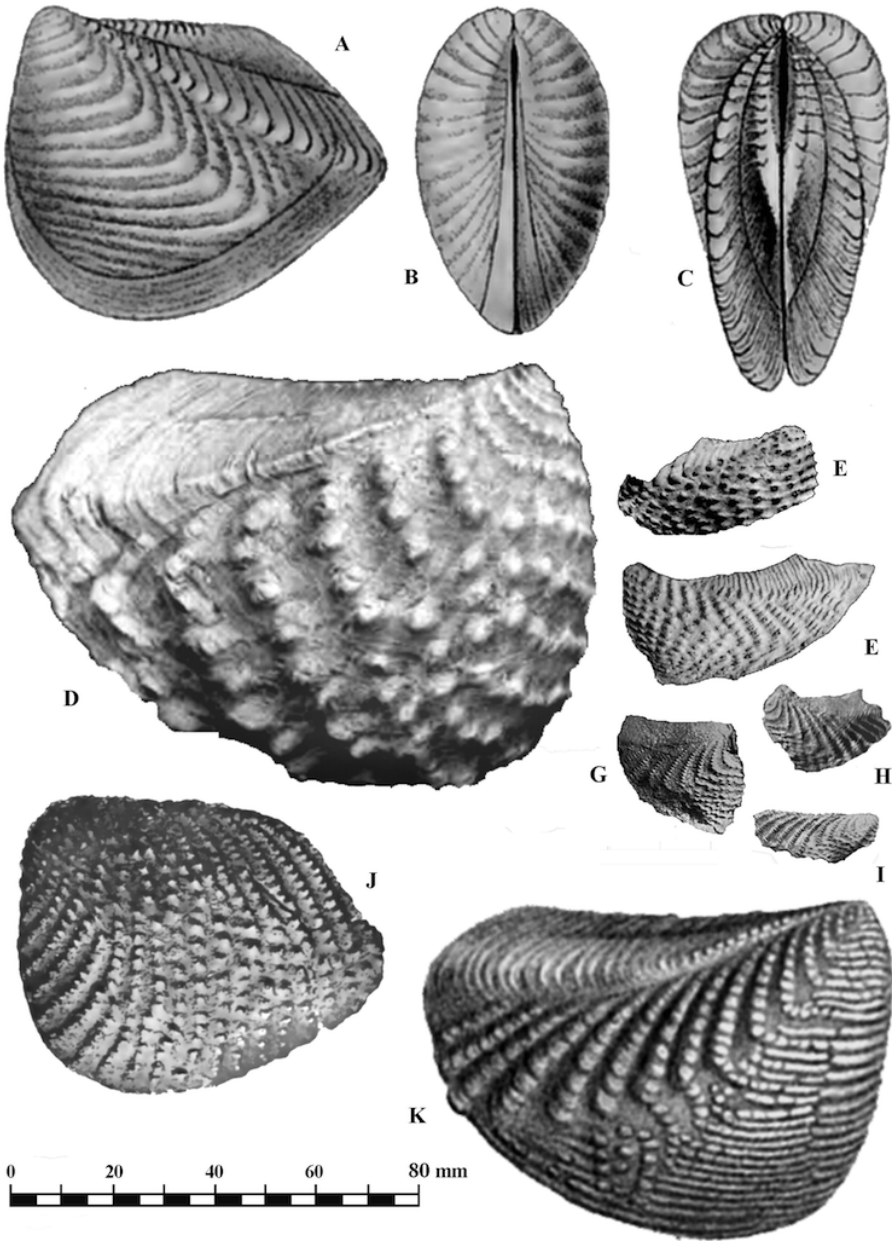

Fig. 7. A-C. *Fribourgella agassizi* sp. nov., the holotype after Agassiz (1840). **D.** *Lebkuechnerella caytonensis* (Duff), the holotype, SMC-J11377, after Duff (1974). **E-F.** *Inuitella yukonensis* (Poulton). E, the holotype and F a paratype, after Poulton (1979). **G-I.** *Inuitella krommelbeini* (de la Torre). G-H, hypotypes after Krömmelbein (1956); I, the holotype after de la Torre (1960). **J.** *Alcobacella torrevedrasi* (Strand), the holotype after Choffat (1885). **K.** *Lebkuechnerella zitteli* (Branco), the holotype by monotypy after Branco (1879).

Description: The lectotype (Fig. 12 H) is moderately large (L = 89 mm), longer than high (H/L = 0.71), with a thick test. The curved anterior margin passes evenly into the weakly convex ventral margin; the respiratory margin is obliquely subtruncate and the long posterodorsal margin (l/L = 0.59) shallowly concave with a rounded anteriorly positioned umbo and weakly incurved opisthogyrate beak. The large flattened escutcheon (l/W~0.50) has a beaded rim formed by the tiny swollen

terminations of the areal lirae. The flat narrow area is asymmetrically bipartite with irregular commarginal plicae and rugae, a persistent longitudinal furrow and minutely beaded submedian carina. The gently curved marginal carina is nodate to middle growth, after which it becomes a rounded rim with a well developed antecarinal space below. Following its nepionic stage, the flank is ornamented by curved to L-shaped chevrons of more or less uniform width, narrower than the interspaces, with broadly rounded apices. The curved nodate opisthocline posterior limbs cover a quarter of the flank, with the subcommarginal anterior limbs of adpressed beads the remainder. In middle growth the chevron apices are feeble to evanescent, leaving the middle of the flank barely ornamented.

Discussion: This is a monotypic genus known only from the Bajocian of England (Gloucestershire) and France (Normandy). An origin in *Pseudovaugonia* seems likely.

Genus *Pseudapiotrigonia* Cooper, 2021

Type species: *Trigonia sturgisensis* Whitfield & Hovey 1906: 394, pl. 47, pl. 48, figs 1-3, 7; by original designation.

Diagnosis: Medium sized, ovate (juv.) to reniform (ad.); broad area without submedian carina and longitudinal furrow, with growth striae only; bold marginal carina evanescing in maturity, with antecarinal space below; in early to middle growth flanks with very acute chevrons with straight, opisthocline axial trace; straight, bold, opisthocline posterior limbs persist to maturity, greatly outnumbered by very fine straight anterior limbs that are feeble to evanescent in middle to later growth. *Bajocian - Bathonian*.

Discussion: *Pseudapiotrigonia* is a monotypic endemic to the American Province (South Dakota, Wyoming, Utah, Mexico) that differs from *Vaugoniella* gen. nov. in its reniform shape, more prominent broadly rounded umbo, lack of longitudinal furrow to the area, early rounding of the marginal carina, broad antecarinal depression in some, and finer, more numerous anterior limbs that, in middle to later growth, are feeble to evanescent at midflank.

Pseudapiotrigonia sturgisensis (Whitfield & Hovey, 1906)

Fig. 6 C-D

1906 *Trigonia sturgisensis* Whitfield & Hovey, p. 396, pl. 47, pl. 48, figs 1-3, 7.
2021 *Pseudapiotrigonia sturgisensis* (Whitfield & Hovey). - Cooper, p. 146, fig. 3L.

Types: The species was based upon material from “three different localities, and each in a different matrix, which gives them a somewhat different appearance one from the other. Still I am inclined to consider them as belonging to the one species” (Whitfield & Hovey 1906: 394-395). Cooper (2021) selected the original of pl. 48, fig. 7, one of the first “forms”, as lectotype. It was from 2.5 miles northwest of Sturgis, South Dakota, from the Redwater Shale Member of the Sundance Formation (Imlay 1964: C31); the other syntypes were “probably from the Hulett Sandstone Member of the Sundance Formation.”

Description: The lectotype (Fig. 6 D), a composite internal mould, is medium sized (L = 60 mm), reniform, longer than high (H/L = 0.76), very inflated (W/H = 0.43), with a prominent, rounded anteriorly positioned umbo (al/L = 0.21) and strongly incurved opisthogyrate beak. The anterior margin is convex, passing evenly into the gently convex ventral margin; the respiratory margin is weakly convex, obliquely subtruncate and the long posterodorsal margin (l/L = 0.60) shallowly concave. The escutcheon is not described but, following the nepionic stage, the broad area is ornamented only by growth striae, with no evidence of a submedian carina or longitudinal furrow. There is a bold beaded marginal carina in early growth but this becomes blunt and rounded in middle growth and evanesces in maturity, with a fairly broad, very shallow antecarinal depression below. In early to middle growth the flank is ornamented by acute chevrons with a straight, strongly opisthocline axial trace. The short straight opisthocline posterior limbs to the chevrons broaden with growth, and are greatly outnumbered by the fine commarginal anterior limbs that weaken considerably and evanesce at midflank, before revitalising along the ventral margin.

An immature ovate syntype (L = 33 mm) (Fig. 6 C) from the Hulett Sandstone has a slightly comvex posterodorsal margin and shows numerous fine commarginal anterior costellae covering three-quarters of the flank, outnumbering the straight, thicker, bolder posterior limbs 2-3:1.

Discussion: A monotypic genus that resembles *Vaugoniella quadrangularis* (Meek & Hayden) (*cf.* Fig. 6 U) in earliest growth, but later is much larger and reniform, with feeble to effaced flank ornament.

Genus *Vaugoniella* gen. nov.

LSID:urn:lsid:zoobank.org:act:C687F8D4-2A9F-450C-A1AD-92F6083094A9

Etymology: *Vaugonia*, *-ella* (neuter suffix to form a diminutive).

Type species: *Trigonia v-costata* Morris & Lycett, 1850: 422; 1874: 66, pl. 13, fig. 5, pl, 15, figs 1-4; by original designation herein.

Diagnosis: Small to medium sized, elongate ovate and posteriorly produced; broad area with beaded submedian carina in early growth and persistent longitudinal furrow; flank chevrons with short thick opisthocline posterior limbs outnumbered by thin commarginal anterior limbs due to bifurcation and intercalation, with apices often thickened. *Upper Toarcian - Upper Kimmeridgian*.

Referred species: *Vaugoniella conradi* (Meek & Hayden 1860: 183, 418, 1865: 83, pl. 3, fig. 11, Imlay 1964: C30, pl. 3, figs 14-21) (Fig. 8 S-T), *V. detrita* (Terquem & Jourdy 1869: 111, pl. 12, figs 1-2, Lycett 1874: 75, pl. 10, figs 3-4) (Fig. 8 C-D), *V. engeli* (Benecke 1905: 189, pl. 15, figs 2-3) (Fig. 8 U-W), *V. eugeni* (Bigot 1893: 304, pl. 12, fig. 5) (Fig. 8 J), *V. guisei* (Lycett 1882: 14, pl. 3, figs 1-6) (Fig. 8 H), *V. interplanata* (Lebküchner 1932: 74, pl. 8, fig. 6) (Fig. 8 F), *V. kahuika* (Fleming 1987: 35, pl. 6, fig. 15), *V. lycettensis* (Strand, 1928: 70, = *T. angulata* Sowerby, *in* Lycett, 1874: 54, pl. 14, figs 5-6) (Fig. 8 G), *V. mexicana* (Alencáster 1963: 29, pl. 8, figs 7-8) (Fig. 8 B), *V. moretoni* (Morris & Lycett, 1853: 57, pl. 5, figs 19, 19a) (Fig. 8 R), *V. pandicosta* (Meek 1864: 48, pl. 8, fig. 7) (Fig. 8 BB), *V. quadrangularis*

(Hall & Whitfield 1877: 293, pl. 7, fig. 22, Imlay 1964: C30, pl. 4, fig. 22) (Figs 6 U, 8 AA), *V. staffinensis* (Anderson & Cox 1948: 108, pl. 1, fig. 9) (Fig. 8 Q), *V. subglobosa* (Lycett 1850: 421, Morris & Lycett 1853: 55, pl. 5, fig. 21, Lycett 1874: 68, pl. 12, figs 8-10, Cox & Arkell 1948: 54, pl. 5, fig. 21) (Fig. 8 O), *V. tripartita* (Forbes, 1851: 111, pl. 5, fig. 11, Lycett 1874: 74, pl. 12, fig. 7) (Fig. 8 I), *V. utahensis* (Imlay 1980: C31, pl. 3, figs 23-26) (Fig. 4 M), *V. walfordi* (Lycett, 1883: 16, pl. 2, fig. 8) (Fig. 8 P), *V. windoesi* (Lycett 1883: 17, pl. 1, figs 7-10) (Fig. 6 M), *V. yanshipingensis* (Wen *in* Zhang *et al.* 1979): 279, pl. 80, fig. 9) (Fig. 8 E).

Discussion: *Vaugoniella* gen. nov. is a widespread pandemic genus known from the Cordilleran (Yukon, Oregon), American (Mexico, California, Wyoming, Montana, Utah), European (England, France, Germany, Poland), Central Asian (Caucasus, Moscow), Sinian (Qinghai Province, China) and Maorian (New Zealand) provinces. It differs from *Vaugonia* in its early loss of submedian carina, curved marginal carina with finer tuberculation, flank chevrons often with thickened crests and, in middle to later growth, thick posterior limbs outnumbered by thin subcommarginal to oblique anterior limbs. It differs from *Fribourgella* gen. nov. most obviously in having intercalated anterior limbs to the chevrons.

Vaugoniella vcostata (Lycett, 1850)

Fig. 8 A

1850 *Trigonia v-costata* Lycett, p. 422.
1857 *Trigonia v-costata* Lycett. - Lycett, p. 232, pl. 11, fig. 7.
1874 *Trigonia v-costata* Lycett. - Lycett, p. 66, pl. 6, fig. 5.
1905 *Trigonia v-costata* Lycett. - Benecke, p. 199, pl. 15, figs 4-5.
1952 *Vaugonia vcostata* (Lycett). - Cox, p. 56.

Type: The lectotype designated herein is the original of Lycett (1874, pl. 15, fig. 1) from the Inferior Oolite (Aalenian) at Rodborough, Stroud, in the collections of the Royal School of Mines (= BGS).

Description: The lectotype (Fig. 8 A) is medium sized (L = 62 mm), elongate ovate and posteriorly produced, longer than high (H/L = 0.76), with a small, low, anteriorly positioned umbo (al/L = 0.23). The anterior margin is strongly convex passing evenly into the equally convex ventral margin; the wide respiratory margin is obliquely truncate and the posterodorsal margin (l/L = 0.37) concave. The long moderately wide escutcheon is flat bottomed and smooth, in early growth with a finely beaded rim. The broad asymmetrically bipartite area is initially concave, flattening posteriorly, with a beaded submedian carina in early growth and longitudinal furrow in the upper part, and commarginal lirae to the upper part and growth striae to the lower. The curved narrow marginal carina is well developed for much of growth, with a narrow antecarinal space below. Following the nepionic stage of subcommarginal costellae, the flank is ornamented by chevrons with thickened crests that become increasingly acute with growth. The short bold strongly opisthocline smooth to subnodate posterior limbs cover about a quarter of the flank, with the last 5 reaching the posteroventral margin. The thin straight subhorizontal slightly wavy anterior limbs are, in middle to later growth, commonly separated by an intercalatory, with an occasional bifurcation, so that they outnumber the posterior limbs 2:1. In maturity the disconnected fine anterior limbs become commarginal.

Discussion: *Vaugoniella kahuika* (Fleming) from the Lower Temaikan (= lower Upper Toarcian, *cf.* Raine *et al.* 2015) of New Zealand is a small trapezoidal species (L = 30 mm), almost as high as long (H/L = 0.93), with a virtually straight posterodorsal margin that differs from *V. tripartita* in its almost straight anterior margin, more conspicuous umbo, stronger marginal carina whose nodes form curved bars in maturity, and whose posterior limbs cover more than half the flank and are not noticeably nodate. The illustration is too poor for reproduction.

Vaugoniella interplanata (Lebküchner) is from the Hauptmuschelbank of the Dogger Sandstone of northern France, of Aalenian age. The holotype (Fig. 8 F) is small (L = 36 mm), subtrigonal, longer than high (H/L = 0.72) with a strongly convex anterior margin and low inconspicuous umbo (al/L = 0.25). There are 10 strong commarginal anterior ribs, as wide as the interspaces, and 6 well separated arcuate posterior ribs that appear to be weakly connected.

Pčelincev (1937: 40, pl. 3, figs 15-18) reported a *Trigonia* sp. indet. ex gr. *v-costata* Lycett from the Aalenian of the Caucasus (Kuban) (Fig. 6 V) that differs from *V. vcostata* in being smaller and ovate, with a rounder anterior margin and fewer posterior costae that cover a third of the flank; it is closer to *V. moretoni*.

Vaugoniella detrita (Terquem & Jourdy) (Fig. 8 C-D) from the Bathonian of the Great Oolite at Meurthe-et-Moselle, France, is moderately large (L = 78 mm), trapezoidal, slightly longer than high (H/L = 0.91) and very inflated (W/H = 0.48). The escutcheon is fairly large (l/L = 0.48), narrow (l/w = 0.16), smooth and with a beaded carina. The narrow bipartite area has a beaded submedian carina and persistent longitudinal furrow, and the tubercles to the curved marginal carina become larger and increasingly elongate posteriorly. The flank costae are initially commarginal, forming simple chevrons in middle growth with straight opisthocline posterior limbs and commarginal anterior limbs, the latter frequently separated by an intercalatory in later growth.

The lectotype of *Vaugoniella subglobosa* (Lycett) designated herein (Fig. 8 O) is from the Great Oolite (Bathonian, *morrisi-subcontractus* Zones) of Minchinhampton Common, Gloucestershire, England. It is small (L = 30 mm), ovate, longer than high (H/L = 0.72) and subglobose, with a short concave posterodorsal margin (l/L = 0.63). The submedian carina to the fairly broad area evanesces in later growth, and the nodes to the marginal carina increase in size and spacing posteriorly. Following the nepionic stage, the flank is ornamented with simple acute chevrons with short thickened posterior limbs, a strongly opisthocline axial trace and long thin anterior limbs that curve downwards anteriorly cutting across growth striae. In middle growth two wavy subnodate costellae are intercalated anteriorly, after which the anterior limbs to the chevrons evanesce to be replaced by broad, low, commarginal growth bands leaving only the opisthocline posterior ribs. On a large hypotype (L = 46 mm) from the Lower Oolite (Bajocian) near Stroud (Lycett, 1874, pl. 12, fig. 9) there is a distinct antecarinal space and the anterior limbs are effaced from the lower third of the flank.

Vaugoniella yanshipingensis (Wen) (Fig. 8 E) from the Bathonian Yanshiping Group of southwest Qinghai Province, China, was compared only with *V. clythia*. It seems

however closer to *V. tripartita* from which it differs in being larger (L = 27 mm), almost as high as long (H/L = 0.91), with a straight posterodorsal margin and at least 10 nodate posterior costellae that truncate most of the fine commarginal costellae to the anterior.

Vaugoniella moretoni (Morris & Lycett) (Fig. 8 R) is based upon a specimen, the holotype by monotypy, from the Stonefield Slate of the Minchinhampton district of Gloucestershire, of Bathonian age. It is small (L = 32 mm), trigonally ovate, longer than high (H/L = 0.76) with a gently convex anterior margin and strongly convex ventral margin. The respiratory margin is obliquely truncate, the long posterodorsal margin shallowly concave (l/L = 0.58) and there is a small pointed subterminal umbo. Following the nepionic stage of commarginal costellae, the wide bipartite area is irregularly lirate, with a persistent longitudinal furrow. There is a prominent curved marginal carina, the nodes of which increase in size posteriorly, without an antecarinal space below. The first 6 flank costellae are subcommarginal and smooth, following which they form chevrons initially with obtuse apical angles, later acute, with a gently curved strongly opisthocline axial trace. The posterior limbs to the chevrons are thick and subnodate whereas the anterior limbs are thin and nontuberculate. In later growth the anterior limbs are separated by a thin intercalatory and break up posteriorly into a few isolated nodes.

Vaugoniella walfordi (Lycett) (Fig. 8 P) is based upon a specimen, the holotype by monotypy, from the Stonefield Slate of the Minchinhampton district of Bathonian age. It is small (L = 21 mm), thick shelled, posteriorly produced, longer than high (H/L = 0.69) with a barely convex subvertical anterior margin and long shallowly concave posterodorsal margin (l/L = 0.59), with a small pointed subterminal umbo. The rim of the rather wide flattened escutcheon is beaded by the terminations of the areal lirae, the rather narrow area is inconspicuously striated and there is a persistent longitudinal furrow. The smooth curved marginal carina lacks an antecarinal space below. The first 6 flank costellae are nodate and commarginal, following which 7 straight opisthocline nodate ribs, narrower than the interspaces, appear posteriorly and meet the marginal carina at an acute angle that increases posteriorly. The anterior half of the flank is ornamented with beaded commarginal ribs that outnumber the posterior ones.

Vaugoniella mexicana (Alencáster) (Fig. 8 B) was introduced as a subspecies of *V. vcostata* (Lycett) from the Lower Bajocian of the Taberna Formation of Mexico. The holotype is small (L = 38 mm), rounded subovate, longer than high (H/L = 0.84) and moderately inflated (W/H = 0.24), with an anteriorly positioned umbo (al/L = 0.17). The truncated respiratory margin is strongly oblique and the straight posterodorsal margin moderately long (l/L = 0.49). The escutcheon is long and narrow. The bipartite area occupies a quarter of the flank and is smooth and flat, with a longitudinal groove that weakens in later growth, and a fairly prominent, rounded, unbeaded marginal carina. The flank is ornamented with 14-15 ribs, initially arcuate and narrower than the interspaces, but becoming increasingly V-shaped with growth, with a slightly curved, strongly opisthocline axial trace close to the marginal carina. The posterior limbs to the chevrons are bold, straight, opisthocline and narrower than the interspaces. The anterior limbs are subcommarginal, about as wide as the interspaces, becoming narrow in middle to later growth when they become separated by intercalatories.

Vaugoniella utahensis (Imlay) (Fig. 4 M) from the Bajocian of Utah is very small (L = 25 mm), subtrigonal, longer than high (H/L = 0.80), with a straight posterodorsal margin and escutcheon about half as wide as the narrow striated bipartite area with a submedian longitudinal furrow and blunt marginal carina. The flank chevrons have a straight strongly opisthocline axial trace. The nontuberculate commarginal anterior limbs outnumber the thick posterior limbs 2-3:1 and are irregularly fine, closely to moderately spaced and wavy to geniculate, tending to fade at midflank and become very crowded and irregular near the ventral margin (an indication of maturity). The very short posterior limbs are thick and strongly opisthocline.

The holotype of *V. conradi* (Meek & Hayden, 1857) (Fig. 8 T) is from the southwest base of the Black Hills, Wyoming, and is a small corroded subovate composite internal mould (L = 30 mm), as high as long (H/L = 1.00), moderately compressed (W/H = 0.30), with an oblique respiratory margin and long straight posterodorsal margin. The flanks are "not in a condition to have retained fine surface markings if there were any" (Meek & Hayden 1865: 84) and, according to Imlay (1964: C30), "The shape is more elongate posteriorly than is suggested by the holotype because the posterior end of the holotype is not preserved." The thick bold strongly opisthocline posterior limbs are outnumbered by thinner commarginal anterior limbs. A better preserved plesiotype (Fig. 8S) with the same shape shows sharper ribbing, with thinner posterior limbs and regularly intercalated anterior limbs.

Vaugoniella guisei (Lycett) was based upon a number of specimens, from various localities. The lectotype designated herein (Fig. 8 H) from the Inferior Oolite (Bajocian) near Minchinhampton, is moderately large (L = 82 mm), elongate-ovate, longer than high (H/L = 0.61), with gently convex anterior and long ventral margins, a narrow obliquely rounded respiratory margin and long shallowly concave postero-dorsal margin (l/L = 0.59), with low rounded subterminal umbo (al/L = 0.20) and moderately incurved beak. The long narrow lanceolate escutcheon (l/L = 0.58) is unornamented and concave, with a minutely beaded carina. The long narrow flattened area has a submedian furrow with a thin carina on its outer side, and a smooth marginal carina. Following the nepionic stage of 3-4 commarginal costellae, the flank is ornamented with nodate chevrons with a curved opisthocline axial trace. Thick curved opisthocline posterior limbs cover about a third of the flank. The finer more numerous subhorizontal anterior limbs are made of small irregular nodes, sometimes fused and sometimes discontinuous, the last few becoming thin and crowded along the ventral margin, with minute fringing papillae.

The lectotype of *V. lycettensis* (Strand) designated herein (Fig. 8 G), from the Upper Trigonia Grit at Rodborough Hill, Stroud (Upper Bajocian, *garantiana* Zone), was introduced as a replacement name for a specimen that "in its posteal portion is so defective and incomplete that I always entertained doubts of the correctness of that identification: the more recently obtained specimens … enable me to separate this hitherto doubtful form from *T. angulata*, and to unite it to the present species" (Lycett 1882: 15), i.e. *V. guisei*.

The lectotype of *V. tripartita* (Forbes) (Fig. 8 I), from the Callovian-Lower Kimmeridgian Estuarine Beds of the Oxford Clay at Loch Staffin, Skye, is very small (L = 17 mm), with a straight posterodorsal margin, gabled area with the upper part more depressed that the lower, prominently nodate marginal carina and thick nodate

posterior limbs to chevrons that in middle to later growth are outnumbered by fine more numerous nontuberculate commarginal anterior limbs.

Vaugoniella quadrangularis (Hall & Whitfield) (Fig. 8 AA) is based upon a small umbonal fragment with acute chevrons showing bold opisthocline posterior limbs that broaden distally and are connected to fine nontuberculate commarginal anterior limbs separated by an intercalatory. It resembles the earliest growth stages of many *Vaugoniella* spp. The hypotype figured by Butler *et al.* (1920: 79, pl. 10, fig. 18) (Fig. 6 U), but not described, is ovate with a broadly rounded umbo, no obvious marginal carina, narrow area, and subhorizontal anterior costellae outnumbering the short broad strongly opisthocline posterior limbs. It is from the Stump Formation near Bear River City, Wyoming.

Vaugoniella pandicosta (Meek) (Fig. 8 BB) is from the Jurassic of Genesee valley, Plumas County, California, but the holotype by monotypy is lost (Crickmay 1933: 58). It is very small (L = 14 mm), subrhomboidal, longer than high (H/L = 0.67) and moderately inflated (W/H = 0.24), with a prominent near-terminal umbo, broad subvertical respiratory margin, and long gently curved posterodorsal margin. The wide unornamented area occupies nearly half the surface of the valve and there is a thin, curved marginal carina without an antcarinal space below. The flank is ornamented by 10 chevrons with thickened apices, narrower than the interspaces, apparently without nodes. It resembles the early growth stages of *V. vcostata* and is based either on a juvenile or progenetic dwarf.

The lectotype designated herein of *V. engeli* (Benecke) (Fig. 8 U-W) is from the grey deposit of the Orne mine near Moyeuvre, northeast France. It is medium sized (L = 50 mm), ovate, longer than high (H/L = 0.78), with a long straight posterodorsal margin (l/L = 0.52), asymmetrically bipartite area with a longitudinal furrow and, following the nepionic stage, growth lamellae, a beaded marginal carina that rounds and becomes obsolete at midlength, and a distinct antecarinal space. The opisthocline posterior limbs to the flank chevrons cover a third of the flank and have well separated rounded nodes whereas the thinner commarginal anterior limbs have smaller nodes and, in later growth, become nontuberculate, disjointed and irregular separated by 1-2 intercalatories. Internally the right valve (Fig. 8 V) has ellipsiodal buttresses on the commissure, corresponding to the positions of the escutcheon and submarginal carinae.

Vaugoniella windoesi (Lycett) is from the lower beds of the Inferior Oolite at Hook Norton, Oxfordshire, England, presumably the Upper Trigonia Grit Member of Aalenian age. The lectotype selected herein (Fig. 6 M) is very small (L = 15 mm), subovate, longer than high (H/L = 0.83, moderately inflated (W/H = 0.33), with a narrow flattened escutcheon whose rim is crenulated by the terminations of areal lirae. The large flat area has a persistent longitudinal furrow and variable lination that evanesces in maturity, with a plain curved marginal carina and narrow antecarinal space. Following the nepionic stage of 5-6 commarginal costellae, there are 6 flank chevrons with thick very short opisthocline posterior limbs that are partially detached from their more numerous commarginal anterior limbs. A paralectotype (pl. 1, fig. 7) has broadly rounded apices to the flank chevrons but with an opisthocline axial trace. The suggestion is that this species is a progenetic dwarf.

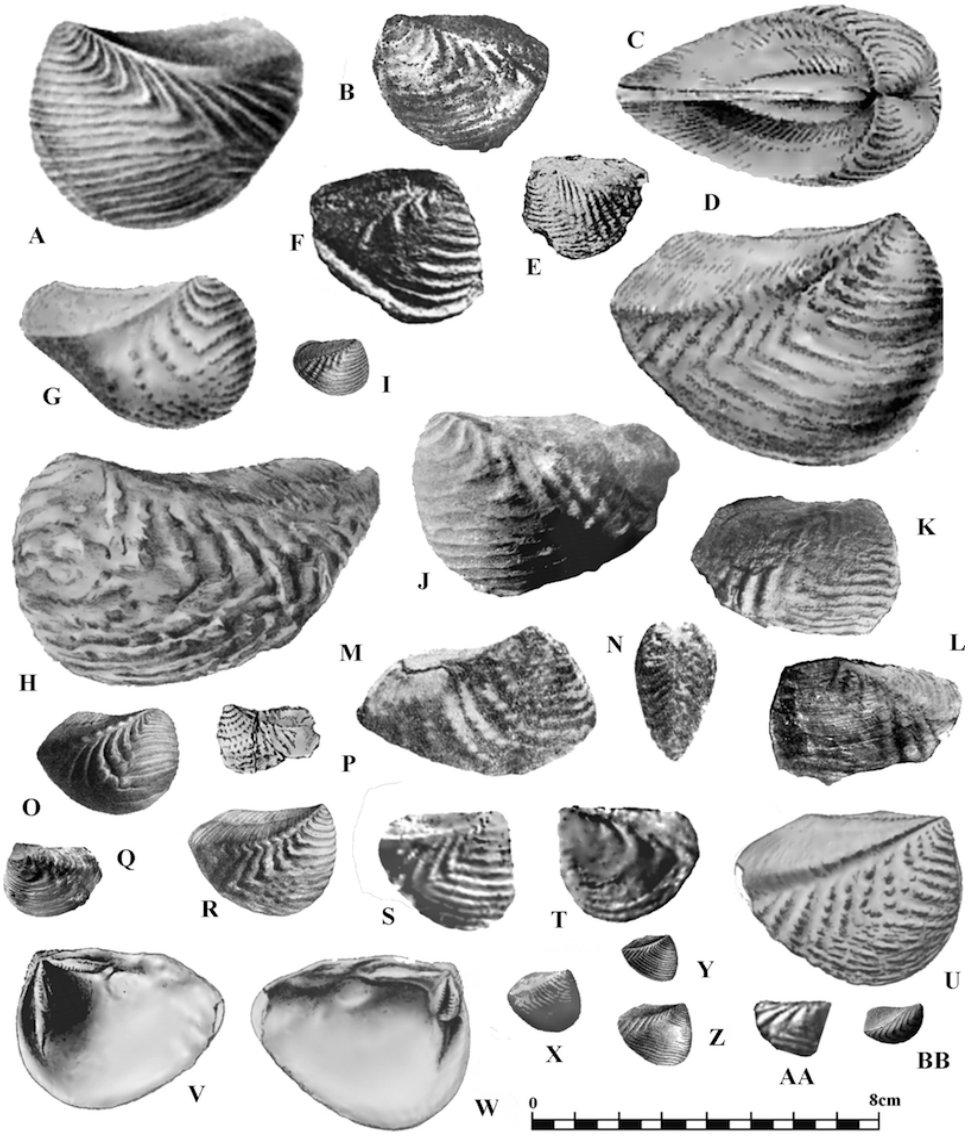

Fig. 8. A. *Vaugoniella vcostata* (Lycett), the lectotype designated herein, after Lycett (1874). **B.** *Vaugoniella mexicana* (Alencáster), the paratype after Alencáster (1963). **C-D.** *Vaugoniella detrita* (Terquem & Jourdy), the holotype by monotypy, after Terquem & Jourdy (1869). **E.** *Vaugoniella yanshipingensis* (Wen), the holotype after Wen (*in* Zhang *et al.* 1979). **F.** *Vaugoniella interplanata* (Lebküchner), the holotype after Lebküchner (1932). **G.** *Vaugoniella lycettensis* (Strand), the lectotype designated herein, after Lycett (1874). **H.** *Vaugoniella guisei* (Lycett) the lectotype designated herein, after Lycett (1883). **I.** *Vaugoniella tripartita* (Forbes) the lectotype designated herein, after Forbes (1851). **J.** *Vaugoniella eugenii* (Bigot), the holotype by monotypy, after Bigot (1893). **K-L.** Hypotypes of *L. scapha* (Gerasimov *non* Agassiz) from the Ryazan region of Russia; (K) the LV showing the features of *Lissotrigonia* gen. nov. and (L) the RV showing the features of *Vaugoniella* gen. nov., after Gerasimov (1955). **M-N.** *Myophorelloides ucrainica* (Yungerman), the holotype after Yungerman (1962). **O.** *Vaugoniella subglobosa* (Morris & Lycett), the lectotype designated herein, after Morris & Lycett (1853). **P.** *Vaugoniella walfordi* (Lycett), the lectotype designated herein, after Lycett (1883). **Q.** *Vaugoniella staffinensis* (Anderson & Cox), the holotype, BGS photograph. **R.** *Vaugoniella moretoni* (Morris & Lycett), the holotype by monotypy, after Morris & Lycett (1853). **S-T.** *Vaugoniella conradi* (Meek & Hayden). S, an hypotype and (T) the holotype, after Imlay (1964). **U-W.** *Vaugoniella engeli* (Benecke), the lectotype designated herein after Benecke (1905). **X.** *Vaugonina flexicosta* (Fischer) the holotype after Fischer (1969). **Y-Z.** *Vaugonina clythia* (d'Orbigny). A paralectotype (Y) and the lectotype (Z), after Lycett (1863). **AA.** *Vaugoniella quadrangularis* (Hall & Whitfield), the holotype by monotypy, afer Hall & Whitfield (1877). **BB.** *Vaugoniella pandicosta* (Meek), the holotype by monotypy, after Meek (1864).

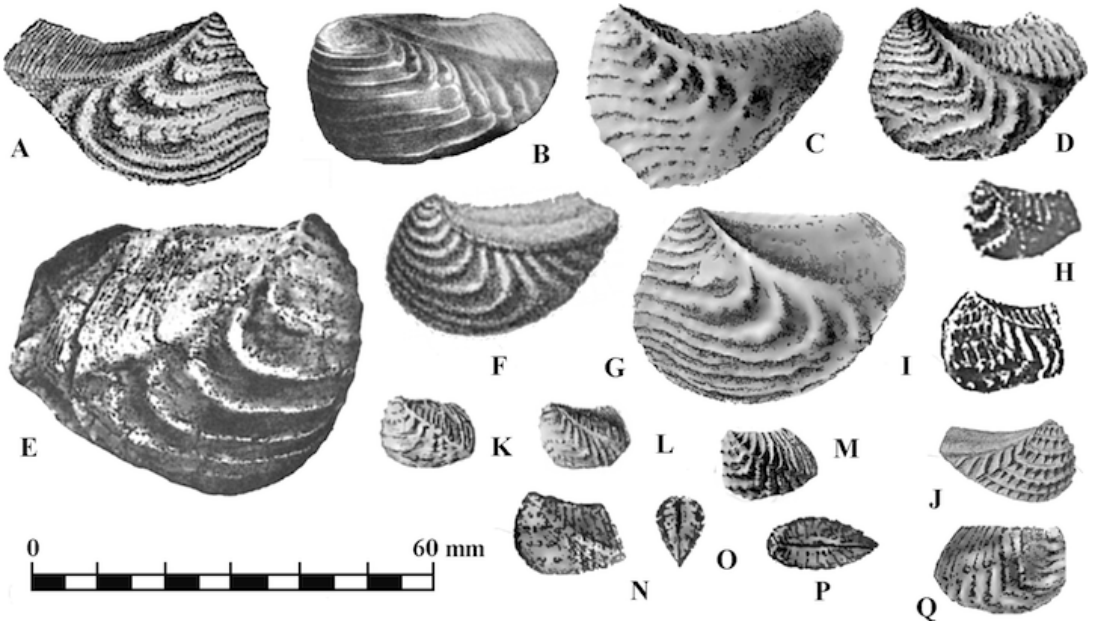

Fig. 9. A. *Galliciella angulata* (J. de C. Sowerby), the lectotype designated herein, after J. de C. Sowerby (1829). **B, G.** *Galliciella flecta* (Morris & Lycett). B, the holotype by monotypy after Morris & Lycett (1853), G a hypotype after Lycett (1874). **C.** *Galliciella paucicostata* (Lycett), the lectotype designated herein, after Lycett (1874). **D.** *Galliciella conjugens* (Lycett), the lectotype designated herein, after Lycett (1874). **E.** *Galliciella kobayashii* (Alencáster), the paratype after Alencáster (1963). **F.** *Galliciella branconis* (Strand), the holotype after Branco (1879). **H.** *Pulchelligonia aculeatula* (Lebküchner), the holotype after Lebküchner (1932). **I.** *Pulchelligonia kurri* (Oppel), the lectotype designated herein, after Lebküchner (1932). **J.** *Pulchelligonia* cf. *kurri* (Oppel), a hypotype after Schlippe (1888). **K-P.** *Pulchelligonia pulchella* (Agassiz). K-L, hypotypes after Lycett (1883), M, a hypotype after Schneider (1927); N-P, the lectotype designated herein after Agassiz (1840). **Q.** *Pulchelligonia rottwellensis* (Strand 1928: 71, = *pulchella* Agassiz var. β, Quenstedt 1837: 522, pl. 43, fig. 14).

Genus *Vaugonina* gen. nov.

LSID:urn:lsid:zoobank.org:act:D6231EF3-C964-457E-864C-54A007CF7B7A

Etymology: -*ina*, diminutive; a very small vaugoniine.

Type species: *Trigonia clythia* d'Orbigny 1850: 309; Lycett 1863: 48, pl. 40, fig. 5; by original designation herein.

Diagnosis: Very small, trigonally ovate to subelliptical; escutcheon smooth with beaded rim; broad area with submedian carina and nodate marginal carina, after nepionic stage only with growth striae; flanks with 6-7 commarginal costellae in early growth (H < 5mm), later forming chevrons with dense fine commarginal anterior limbs outnumbering sparse, coarse, short opisthocline posterior limbs; nontuberculate anterior limbs with asymmetrical profiles, convex below, concave above; posterior limbs broad, flat topped, smooth, separated by very narrow interspaces. *Upper Bathonian.*

Referred species: *Vaugonina flexicostata* (Fischer 1969: 98, pl. 11, 8-9) (Fig. 8 X).

Discussion: Endemic to the European Province (England, France). A paedomorphic descendent of *Vaugoniella* gen. nov.

Vaugonina clythia (d'Orbigny, 1850)

Fig. 8 Y-Z

1850 *Trigoni clythia* d'Orbigny, p. 309.
1863 *Trigoni clythia* d'Orbigny. - Lycett, p. 48, pl. 37, fig. 2, pl. 40, fig. 5.
1874 *Trigoni clytia* (sic) d'Orbigny. - Lycett, p. 76, pl. 11, figs 4-5 only, pl. 17, fig. 7.
1893 *Trigoni clytia* (sic) d'Orbigny. - Bigot, p. 302, pl. 12, figs 3-4.
1913 *Trigoni clytia* (sic) d'Orbigny. - Thevenin, p. 145, pl. 27, figs 17-18.
2021 *Trigoni clytia* (sic) d'Orbigny. - Lebrun, p. 22.

Types: The lectotype selected by Cox & Arkell (1948: 92), SMC-J5838 (Fig. 8 Z), is from the Great Oolite (Upper Bathonian) at Box Tunnel near Bath; a paralectotype is SMC-J5839 (Fig. 8 Y), and there are two other paralectotypes in the d'Orbigny Collection, MNHN-F-RO8229.

Description: The shell is very small (L = 18 mm), trigonal to oval, longer than high (H/L = 0.80), moderately inflated, with a low rounded subterminal to terminal umbo and incurved orthogyrate beaks. The subvertical to vertical weakly convex anterior margin curves evenly into the gently convex ventral margin, the respiratory margin is obliquely truncate, and the long posterodorsal margin straight. The small shallowly concave escutcheon is unornamented, with a finely beaded rim. The rather broad asymmetrically bipartite area has a finely beaded submedian carina and is ornamented with fine commarginal lirae. There is a prominently beaded shallowly concave marginal carina. On the flank the first 5-6 ribs are commarginal, about as wide as the interspaces, whereafter they form chevrons, initially obtuse but becoming increasingly acute posteriorly, meeting the marginal carina at an acute angle. The short straight posterior limbs become flat topped and very broad posteriorly, connecting to every second or third of the 17-25 fine commarginal nontuberculate anterior limbs that are broader than the interspaces. In maturity the last few ventral ribs become undulose, breaking up and becoming nodose posteriorly, before finally evanescing

Discussion: Upper Bathonian *V. flexicostata* (Fischer) (Fig. 8 X) is very small (L = 18 mm), ovate, slightly longer than high (H/L = 0.89), moderately inflated (W/H = 0.31), with a feeble escutcheon rim. The wide area has an indistinct longitudinal furrow and in the nepionic stage is crossed by ribs from the flank. The marginal carina is thin and undulated by endings of the flank costellae. There are 19-20 smooth, regularly spaced flank costellae, only the last 4-5 of which form chevrons. Lebrun (2021: 22) suggested *V. clythia* might be a junior subjective synonym of *V. subglobosa* (Lycett), but the early growth stages of the two are different.

Genus *Pulchelligonia* gen. nov.

LSID:urn:lsid:zoobank.org:act:8AB529B6-33FC-494A-AFE2-A5C105210BFB

Etymology: *Pulchellus* (L) - pretty.

Type species: *Trigonia pulchella* Agassiz 1840: 14, pl. 2, figs 1-7; by original designation herein.

Diagnosis: Very small to small, trapezoidally elongate to rectangular with subvertical anterior margin; area with strong simple well spaced commarginal lirae; submedian carina lacking and longitudinal furrow feeble to obsolete; flanks with L-shaped chevrons with simple well-spaced nodate to spinose commarginal anterior limbs, often with ventral projections, and thicker subvertical posterior limbs; internally posteroventral commissure pitted. *Upper Bajocian - Middle Callovian*.

Referred species: *Pulchelligonia aculeatula* (Lebküchner 1932: 64, pl. 6, figs 8-10) (Fig. 9 H), *P. bathonicola* (Strand 1928: 71; = Deeke 1925: 227, = Greppin 1870: 49), *P. kurri* (Oppel 1857: 486; Schlippe 1888: 154, pl. 2, fig. 21; Lebküchner 1932: 82, pl. 9, figs 8-11) (Fig. 9 I), *P. rottwellensis* (Strand 1928: 71, = *pulchella* Agassiz var. β, Quenstedt 1837: 522, pl. 43, fig. 14) (Fig. 9 Q).

Discussion: Endemic to the European Province (England, France, Luxembourg, Switzerland, Germany).

***Pulchelligonia pulchella* (Agassiz, 1840)**

Fig. 9 K-P

1840 *Trigonia pulchella* Agassiz, p. 14, pl. 2, figs 1-7.
1832 *Trigonia pulchella* Agassiz. - Quenstedt, p. 522, pl. 43, fig. 14.
1852 *Trigonia pulchella* Agassiz. - Quenstedt, p. 311, pl. 43, fig. 1.
1867 *Trigonia pulchella* Agassiz. - Quenstedt, p. 311, pl. 43, fig. 1.
1877 *Trigonia pulchella* Agassiz. - Lycett, p. 185, pl. 38, figs 10-12.
1882 *Trigonia pulchella* Agassiz. - Lycett, p. 11, pl. 3, figs 7-12.
1905 *Trigonia pulchella* Agassiz. - Benecke, p. 184, pl. 14, figs 5-6.
1927 *Trigonia pulchella* Agassiz. - Schneider, p. 70, pl. 5, figs 4-5.

Type: The lectotype designated herein is the original of pl. 2, figs 1-3 of Agassiz (1840) from the Upper Lias (?Aalenian) of Urweiler and Mulhausen, Department of Bas-Rhin, northeast France, presumably in the Agassiz Collection, Natural History Museum, Neuchâtel, Switzerland. The remaining figured syntypes become para-lectotypes.

Description: The lectotype (Fig. 9 N-P) is very small (L = 18 mm), trapezoidal, almost as high as long (H/L = 0.94), inflated (W/H = 0.36), with a weakly convex subvertical anterior margin that passes evenly into the almost straight ventral margin. The broad respiratory margin is slightly oblique and the long posterodorsal margin (l/L = 0.81) shallowly concave, with small near terminal umbones and moderately incurved beaks. There is a distinct peaked anterior face ornamented by oblique widely spaced prolongations of the flank costellae, with a small lunule. There is a long narrow unornamented escutcheon, presumably with a beaded rim. The bipartite area occupies about half the flank and is ornamented with simple widely spaced commarginal lirae interrupted by an indistinct longitudinal furrow, bounded by a well developed curved marginal carina with tiny rounded nodes that persist to maturity. Following the nepionic stage, the flanks are ornamented with nodate L-shaped chevrons, the widely spaced anterior limbs subhorizontal and almost perpendicular to the approximated vertical posterior limbs, four of which reach the posteroventral margin

Discussion: The English specimens of *P. pulchella* (Fig. 9 K-L) are from the middle Lower Toarcian of the Bracefield brick-pits near Lincoln, Lincolnshire, England, associated with the ammonites *Hildoceras bifrons* (Bruguière) and *Dactylioceras commune* (Sowerby), and it "has not been obtained at any other British locality" (Lycett 1877: 187). The hypotype figured by Benecke (1905, pl. 15, fig. 5) has a internally pitted posteroventral commissure.

The holotype of *P. aculeatula* (Lebküchner) (Fig. 9 H) is from the Upper Bajocian (*parkinsoni* Zone) at Eningen, Germany. It is very small (L = 18 mm; L_{max} = 22.5 mm), trapezoidal, longer than high (H/L = 0.76), with an obliquely truncated respiratory margin. The long narrow sunken escutcheon is smooth, fastigiate on conjoined valves, its rim beaded by swollen terminations of the areal lirae, as is the curved marginal carina. The area has strong straight commarginal lirae, without an antecarinal gap. Following the nepionic stage of commarginal costellae with ventral spurs, the flank is ornamented with oblique nodate costellae, narrower than the interspaces, the first 5 of which curve to meet the anterior margin.

Pulchelligonia kurri (Oppel) (Fig. 9 I) from the uppermost Lower Bathonian (*Varians* Marl, = *Morrisiceras morrisi* Zone) of Vögisheim, Baden, Germany, differs from *P. aculeatula* in being relatively shorter (H/L = 0.90), with a straight subvertical respiratory margin, more concave posterodorsal margin, more pointed umbo, longer posterior ribs the last 2-3 of which reach the posteroventral margin, and most spinose anterior ribs with long ventral projections. The specimen figured by Schlippe (1888) (Fig. 9 J) is posteriorly rostrate, much longer than high and with growth striae to the area; it may be a different species.

Pulchelligonia rottwellensis (Strand) (Fig. 9 Q) is small (L= 21 mm), rectangular (H/L = 0.63) with a straight subvertical anterior margin, straight posterodorsal margin, convex ventral margin, insignificant near terminal umbo and straight marginal carina.

Pulchelligonia bathonicola (Strand) is from the Upper Bathonian of Switzerland, but I have been unable to find a figure or description and it may be a *nomen nudum*.

Genus *Inuitella* gen. nov.

LSID:urn:lsid:zoobank.org:act:113B3EA2-354F-4E1C-9EF1-1265F5F881A0

Etymology. After the Inuits, the indigenous people who traditionally lived in the Yukon, where the type species was collected.

Type species. *Vaugonia(?) yukonensis* Poulton 1979: 25, pl. 8, figs 6-9 only; by original designation herein.

Diagnosis. Small to medium sized, posteriorly elongate and rostrate, with subterminal umbones; small unornamented escutcheon with finely beaded rim; narrow area with feeble longitudinal furrow and single and looped commarginal lirae; marginal carina nodate, nodes becoming increasingly transversely elongate posteriorly; flanks with nodate chevrons with straight to gently curved opisthocline posterior limbs covering half or more of flank, with rounded well separated nodes;

midflank with discrete nodes arranged in irregular or reticulate pattern; anterior flank with short, straight, fine, fused rows of beads perpendicular to anterior margin. *Aalenian - Oxfordian.*

Referred species. *Inuitella kroemmelbeini* (Krömmelbein 1956: 332, pl. 1, figs 1-4, de la Torre 1960: 66, pl. 1, figs 1-2) (Fig. 7 G-I).

Discussion. *Inuitella* gen. nov. is pandemic to the Cordilleran (southern Yukon) and American (Oregon, northern California, Cuba) provinces. It differs from *Echevarria* gen. nov. in having flank chevrons restricted to early to middle growth, later with short straight subcommarginal costellae of fused beads along the anterior margin, and the irregular to reticular arrangement of nodes at midflank.

***Inuitella yukonensis* (Poulton, 1979)**

Fig. 7 E-F

1979 *Vaugonia(?) yukonensis* Poulton, p.25, pl.8, figs 6-9 only (*non* figs 10-11, = *Agassigonia taylori* (Poulton), text-fig. 7.

Types. The holotype GSC 43284 and paratypes GSC 43283, 43285 and 43286, all from the Laberge Group of southern Yukon, of Early Bajocian age.

Description. The holotype (Fig. 7 E) is medium size (L~50 mm), posteriorly rostrate and much longer than high, moderately convex with small subterminal umbo and orthogyrate beak. The subvertical anterior margin is almost straight and the absent ventral margin likely to have been long and gently convex. The respiratory margin also is not preserved but areal ornament suggests it was obliquely subtruncate, and the long posterodorsal margin (l/L ~0.75) is shallowly concave. The small sunken escutcheon is unornamented, with a rim of fine sharp beads that do not conform to the areal lirae. The relatively narrow area is ornamented with generally straight and regular commarginal lirae that become slightly irregular in maturity and are interrupted by a faint longitudinal groove in early growth, without a submedian carina. The marginal carina is a fine sharply raised ridge near the umbo and finely beaded in early growth (L<13 mm), whereafter it becomes a broad ridge with prominent adpressed transversely elongated nodes. Following the nepionic stage (L<3mm) of three commarginal costellae, the next three are very finely beaded chevrons with an opisthocline axial trace. Thereafter the posterior flank is ornamented by straight, narrow, nodate opisthocline costellae that increase in length posteriorly, with rounded well separated nodes, and meet the marginal carina at an increasingly acute angle. These are separated from an anterior set of very short, fine, subcommarginal costellae of fused nodes that are perpendicular to the anterior margin, by a reticulate arrangement of discrete nodes at midflank, with the nodes becoming elongated parallel to growth lines anteroventrally.

Discussion. The quadratic paratype figured by Poulton (1979, pl. 8, figs. 10-11) (Fig. 13 R) is now identified as *Agassigonia* cf. *taylori* (Poulton 1980: 194, pl. 30.1, fig. 11).

Inuitella kroemmelbeini (de la Torre) (Fig. 7 G-I) is from the San Cayetano Formation of Cuba (Pugaczewska 1978: 175) of Oxfordian age. It is small (L~26

mm), very elongate and posteriorly rostrate (H/L~0.77), with an almost straight subvertical anterior margin, near terminal umbo, and long straight posterodorsal margin. The relatively wide area is unornamented with a finely beaded marginal carina and no antecarinal space. L-shaped flank chevrons with an opisthocline axial trace comprise 6 long, well spaced, gently curved nodate posterior limbs covering two-thirds of the flank, the anterior one third with short thin beaded subcommarginal anterior limbs that include intercalatories and become irregular at midflank.

Genus *Galliciella* gen. nov.

LSID:urn:lsid:zoobank.org:act:474A5340-8CD0-4F27-8413-9585B960B712

Etymology: After the Gallic Empire, 260-274 AD, that covered much of the area in which this trigonia flourished.

Type species: *Trigonia angulata* J. de C. Sowerby 1829: 9, pl. 508, fig. 1; by original designation herein.

Diagnosis: Very small to medium sized, trigonally ovate and posteriorly produced, commonly with small pointed umbones; area with growth striae or lamellae that become irregular and crinkled posteriorly, with antecarinal space below; flanks with comma-shaped chevrons with rounded apices, thick short subnodate to nodate posterior limbs and fine sinuous beaded to nontuberculate anterior limbs. *Toarcian - Lower Callovian*.

Referred species: *Galliciella branconis* (Strand, 1928: 70, Deecke 1925:73, = *Trigonia angulata* Branco (*non* Sowerby), 1879: 119, pl. 8, fig. 3) (Fig. 9 F), *G. conjugens* (Phillips, 1829: 156, Lycett 1874: 62, pl. 10, figs 5, 7-8, pl. 13, fig. 6) (Fig. 9 D), *G. flecta* (Morris & Lycett, 1853: 60, pl. 5, fig. 20, Lycett 1874: 55, pl. 14, figs 7-10, Douglas & Arkell 1928: 172, pl. 12, figs 1-2) (Fig. 9 B, G), *G. kobayashii* (Alencáster, 1963: 27, pl. 2, fig. 9, pl. 3, figs 1-6) (Fig. 9 E), *G. paucicosta* (Lycett, 1874: 57, pl. 11, figs 8-9, pl. 16, fig. 7) (Fig. 9 C).

Discussion: *Galliciella* gen. nov. is pandemic to the European (England, France, Germany), Central Asian (Caucasus) and American (Mexico) provinces. It differs from *Vaugonia* most obviously in its generally smaller size, ovate to trigonally ovate shape, growth striae to the area, more coarsely beaded marginal carina, and fewer coarser comma-shaped flank chevrons with rounded apices and sinuous to subcommarginal anterior limbs.

Galliciella angulata (J. de C. Sowerby, 1829)

Fig. 9 A

1829 *Trigonia angulata* J. de C. Sowerby, p. 9, pl. 508, fig. 1.
1874 *Trigonia angulata* J. de C. Sowerby. - Lycett, p. 54, pl. 14, figs 5-6.
1905 *Trigonia angulata* J. de C. Sowerby. - Benecke, p. 204.
1948 *Trigonia angulata* J. de C. Sowerby. - Cox & Arkell, p. 24.
2000 *Trigonia angulata* J. de C. Sowerby. - Francis, p. 257, pl. 18, figs a-c, e.

Types: Sowerby had several specimens from Brewham, near Nunney, close to Frome, Dorset. England, although he figured only one which is selected as lectotype. According to Lycett (1874) they were from the Upper Ragstones of the Inferior Oolite, but Cox & Arkell (1948) suggested they came from the Lower Cornbrash, probably the Lower Bathonian Astarte Bed (*garantiana* Zone) according to Francis (2000: 258).

Description: The lectotype (Fig. 9 A) is small (L = 35 mm; according to Sowerby the species seldom exceeds 38 mm in length), elongate ovate and posteriorly produced, longer than high (H/L = 0.67), with a tiny anteriorly positioned umbo (al/L = 0.22) and incurved beak. The almost straight anterior margin passed rather sharply into the convex ventral margin with a broad shallow posteroventral sinus; the moderately wide respiratory margin is obliquely truncate and the long posterodorsal margin (l/L = 0.63) deeply concave. The escutcheon is not described but has a concave rim. The fairly broad area is bipartite in early to middle growth, with a longitudinal furrow that evanescing later, and is ornamented by commarginal lirae. Although the illustration does not show a submedian carina, according to Sowerby's description of the area "there is generally a crenulated ridge in the middle of it; the crenulations upon this and also upon the bounding lines are often elevated into small spines". The narrow marginal carina is curved and beaded. Following its nepionic stage of commarginal costellae, the flank has comma-shaped costellae that are thick and coarsely nodate for their posterior half and thin and nontuberculate for their anterior half when they curve downwards across the growth striae. The final two anterior limbs are thin and commarginal, indicating maturity.

Discussion: The lectotype of Aalenian *G. conjugens* (Lycett) (Fig. 9 D), designated herein, from the Millepore Bed of the Cloughton Formation at Cloughton, north Yorkshire, England, is small (L = 36 mm) and posteriorly produced (H/L = 0.72), with the thickened posterior limbs occupying a quarter of the flank. The large area accounts for a third of the valve and is ornamented by lamellae that become prominent, irregular and wrinkled posteriorly. Cox & Arkell (1950: 57) questionably included it in the synonymy of *T. moretoni* but the types are different.

The holotype by monotypy of *G. flecta* (Morris & Lycett) (Fig. 9 B) came from the Bathonian Forest Marble in the Trewsbury Quarry, near Tetbury Road station of the Great Western Railway, close to Cirencester, Gloucestershire, England. It is small (L_{max} = 36 mm), oblong, longer than high (H/L = 0.85), moderately inflated (H/W = 0.26) with scarcely distinguishable carinae, a longitudinal furrow to the upper area that evanesces later leaving only growth striae, with an antecarinal space below. The narrow L-shaped flank chevrons have horizontal anterior limbs and short perpendicular nodate posterior limbs. Material subsequently assigned here (Lycett 1874: 55, pl. 14, figs. 7-10) (Fig. 9 G) is larger (L = 45 mm), elongate-ovate (H/L = 0.71), with a beaded escutcheon rim and submedian carina, an area with a well defined longitudinal furrow and commarginal lirae, and a strongly curved nodate marginal carina that increases in strength posteriorly. Following its nepionic stage of 7 subcommarginal costellae, there are 3-4 chevrons with broadly rounded crests with 2-3 enlarged fused nodes at their apices, and nontuberculate sinuous subhorizontal anterior limbs that curve downwards anteriorly. In maturity the last 2-3 anterior limbs become thin and wiry, indicating maturity.

As recognized by Lycett, *G. paucicosta* (Lycett) from the Lower Callovian Kellaways Sand Member (= Kelloway Rock) of Yorkshire is closely allied to *G. angulata*. The lectotype designated herein, the original of pl. 11, fig. 8 (Fig. 9 C), differs in being longer and posteriorly subrostrate (H/L = 0.78), with larger nodes to the marginal carina, a distinct antecarinal space, and fewer larger nodes to the posterior limbs of the more numerous flank chevrons.

Galliciella kobayashii (Alencáster) (Fig. 9 E) is from the Callovian Yucuñuti Formation of Mexico, in the Huayacocotla Embayment (Imlay, 1980) and differs somewhat from the European representatives. The holotype is small (L = 48.5 mm), subtrigonally elongate (H/L = 0.89) and moderately inflated (W/H = 0.28) with a wide flat unornamented feebly bipartite area. The almost straight marginal carina is rounded and lacks beading, its prominence due to a shallow antecarinal depression. Following the nepionic stage of 3-4 commarginal costellae, there are 13-14, strong, widely spaced comma-shaped non-tuberculate ribs, much narrower than the inter-spaces, thickest posteriorly and subnodate, with thin nontuberculate to wiry commarginal anterior limbs. One paratype (pl. 3, fig. 1) shows transverse nodes to the marginal carina in later growth, to which lirae occasionally loop.

Poulton (1980: 190, pl. 30.2, figs. 1-2) recorded *V.* cf. *kobayashii* Alencáster from the upper Lower Bajocian (upper Murchisonae Zone) of central Oregon but, here, this specimen is identified as a *Fribourgella* gen. nov.

Galliciella branconis (Strand) (Fig. 9 F) from the Murchisonae Zone of the La Sauvage iron ore mine near Longwy, France, is small (L = 34 mm), posteriorly rostrate, with more sharply curved barely nodate ribs than *G. angulata*. The poorly preserved area is perpendicular to the flank and unornamented save for the suggestion of a longitudinal furrow.

Genus *Munierchalmasia* gen. nov.

LSID:urn:lsid:zoobank.org:act:B031EDAE-02C1-4DCB-B1CF-84AEC819A586

Etymology: After Ernest Charles Philippe Auguste Munier-Chalmas (1843-1903), French geologist and palaeontologist, describer of the type species.

Diagnosis: Medium sized to moderately large, subovate to elongate-ovate; area finely lirate with beaded submedian carina, nodate marginal carina with or without antecarinal space; flank chevrons with long, bold, strongly curved, well spaced nodate to entire posterior limbs covering up to half of flank, mostly disconnected from finer more numerous commarginal to oblique anterior limbs that evanesce in some. *Upper Pliensbachian - Berriasian*.

Type species: *Trigonia ferryi* Munier-Chalmas 1865: 415, pl. 1, fig. 1; by original designation herein.

Referred species: *Munierchalmasia carrei* (Munier-Chalmas, 1865: 417, de Loriol & Pellat, 1866: 86, pl. 8, fig. 5, Lycett 1874: 72, pl. 12, fig. 1) (Fig. 10 D), *M. hauchecornei* (Schmidt, 1905: 166: pl. 7, figs 7-9, pl. 8, fig. 1) (Fig.10 F-H), *M. jonioi* (Rouillier & Vosinsky, 1849: 349, fig. 80) (Fig. 10 B), *M. laevicostata*

(Redlich, 1894: 72, pl. 2 (11), fig. 5) (Fig. 10 C), *M. oregonensis* (Poulton, 1979: 23, pl. 10, figs 14-19) (Fig. 10 M-N), *M. radiata* (Benett, 1831, pl.18, fig. 3, de Loriol & Pellat 1866: 83, pl. 8, fig. 1, Lycett 1874: 73) (Fig. 10 E), *M. williamsoni* (Lycett, 1874: 58, pl. 16, fig. 8) (Fig. 10 L).

Discussion: A pandemic genus known from the Cordilleran (Alaska, Oregon), European (England, France, Germany) and Central Asian (Russia) provinces. While the genus is characteristically Tithonian-Berriasian, two much earlier species (*oregonensis*, *williamsoni*) are provisionally assigned here but future work may show them to be distinct.

Munierchalmasia ferryi (Munier-Chalmas, 1865)

Fig. 10 A

1865 *Trigonia ferryi* Munier-Chalmas, p. 415, pl. 1, fig. 1.

Type: The holotype by monotypy is the original of the specimen figured by Munier-Chalmas (1865) from the Upper Portlandian (Upper Tithonian) of Alprecht, Boulogne -sur-Mer, Pas-de-Calais, France.

Description: The holotype (Fig. 10 A) is medium sized (L = 57 mm), ovate, longer than high (H/L = 0.81), moderately inflated, with a low rounded subterminal umbo (al/L = 0.14) and incurved beak. The gently convex anterior margin passes evenly into the broadly rounded ventral margin; the convex respiratory margin is oblique, and the long posterodorsal margin (l/L = 0.55) almost straight, with a low rounded anteriorly positioned umbo (al/L = 0.13). The lanceolate escutcheon is smooth, with a beaded rim. The moderately wide bipartite area has a beaded submedian carina and is ornamented by commarginal lirae. The prominent marginal carina is regularly nodate, with a very narrow antecarinal space below. The flank has 8 strong, well spaced, arcuate, coarsely nodate, opisthocline posterior ribs that cover about half the flank and are outnumbered up to 5:1 by the fine nontuberculate commarginal anterior costellae.

Discussion. The earliest species to be assigned here is *M. oregonensis* (Poulton) from the Upper Pliensbachian Suplee Formation of Oregon, but also with well preserved specimens from the Aalenian Gaikema Formation of Alaska. The holotype (Fig. 10 M) is small (L = 34 mm), elongate ovate, posteriorly produced and much longer than high (H/L = 0.67), inflated (W/H = 0.29), with a strongly convex anterior margin that curves evenly into the ventral margin that straightens posteriorly; the oblique respiratory margin is subrounded and the posterodorsal margin concave. The small pointed umbo is well behind the anterior margin (al/L = 0.24), with a moderately incurved orthogyrate beak. The shallowly sunken escutcheon is long (l/L = 0.67), relatively wide and unornamented, with a sharp rim. Following its nepionic stage of commarginal costellae, the moderately wide area is ornamented by fine commarginal lirae that become slightly wavy and irregular posteriorly, with a weak longitudinal furrow in later growth. The marginal carina is not preserved, but is a fine sharp rim with a narrow antecarinal space in a referred specimen. Following the nepionic stage of commarginal costellae, the flank is ornamented by obtuse chevrons with long thick curved posterior limbs perpendicular to the marginal carina that cover a third of the flank. The anterior flank is covered by fine comarginal lirae that outnumber the

posterior limbs 2:1. A paratype (Fig. 10 N) differs in having the posterior limbs to the chevrons covering almost half the flank, recurving to meet the antecarinal space at an acute angle, and with fewer wavy more widely spaced anterior limbs.

Lower Callovian *M. williamsoni* (Lycett) (Fig. 10 L) from Kellaway Rock, Cayton Bay, near Scarborough, England, is moderately large (L = 82 mm) and ovately oblong (H/L = 0.65), its long narrow escutcheon with a minutely beaded rim. The relatively narrow flattened area has an indistinct finely beaded submedian carina, and commarginal lirae that increase in prominence posteriorly. The thin weak minutely beaded marginal carina has a prominent antecarinal space below that broadens with growth. On the flank there are 10 long curved ribs with fused ellipsoidal nodes that cover the posterior half of the flank and are perpendicular to the antecarinal space. Anteriorly these are weakly connected to irregular almost straight wavy oblique finely nodate limbs, narrower than the interspaces, a few of which are intercalated.

Portlandian *M. carrei* (Munier-Chalmas) (Fig. 10 D), lectotype designated herein MNHN.F.J. 08552 from the same locality as *M. ferryi*, is medium sized (L = 62 mm), elongate-ovate (H/L = 0.80), with a gabled striated bipartite area with beaded escutcheon, submedian and marginal carinae. The nodes to its marginal carina increase in size and spacing posteriorly, with a distinct antecarinal space below. Following L-shaped chevrons in early growth, the flank has fine, slightly wavy, subcommarginal beaded anterior costellae, about as wide as the interspaces, and distinctly nodate, curved, swollen posterior ribs that cover more than half the flank.

Munierchalmasia hauchecornei (Schmidt) (Fig. 10 F-H) is from the Lower Portlandian of Pomerania (= East Germany). The lectotype designated herein (Fig. 10 H) is a medium sized (L = 56 mm) butterflied pair of valves that are posteriorly rostrate with anteriorly positioned umbones (al/L = 0.15) (Fig. 10 H). The ornament is best shown however by a paralectotype (Fig. 10 F) that is 62 mm long, elongate-ovate and subrostrate (H/L = 0.73), with the curved subnodate posterior limbs covering almost half the flank. The escutcheon is deeply excavated with a sharp rim that is finely beaded in early growth. The broad bipartite area is striated with a distinct longitudinal furrow and rounded marginal rim with an antecarinal space below. Following the nepionic stage of dense, commarginal costellae, the flank is ornamented by chevrons whose thin beaded anterior limbs flex downwards anteriorly and outnumber the bold curved nodate opisthocline posterior limbs 2-3:1.

Munierchalmasia radiata (Benett) (Fig. 10 E) from the Portlandian of Tisbury village, Wiltshire, Emgland, is moderately large (L = 82 mm), longer than high (H/L = 0.86) with a relatively broad area that lacks a submedian carina or longitudinal furrow in middle to later growth, and is ornamented with commarginal lirae. It has a sharp marginal carina in early growth, with a few large nodes in middle growth, after which it evanesces. There is a prominent antecarinal space that broadens with growth. More than half the flank is covered by 7 well spaced, bold, curved, subnodate posterior limbs to chevrons that are outnumbered by fine, weak, commarginal anterior limbs that are nontuberculate.

The lectotype designated herein of *M. jonioi* (Rouillier & Vosinsky) (Fig. 10 B), from the Neocomian greensands of the Wealdian Formation at Katelniki, Moscow, is large (L = 75 mm), suborbicular, longer than high (H/L = 0.81), moderately inflated (W/H

= 0.32), with a low rounded subterminal umbo (al/L = 0.22), evenly convex anterior and ventral margins, obliquely subtruncate respiratory margin and a fairly long damaged (but probably straight) posterodorsal margin (l/L = 0.58). The escutcheon is not described, but the wide asymmetrically bipartite area is ornamented by commarginal lirae with a longitudinal furrow that evanesces in later growth. The straight marginal carina is beaded, becoming nodate in middle growth and rounded in maturity, with a prominent antecarinal space below. Almost half the flank is covered by the strong, distant, curved posterior limbs of chevrons with small nodes. The anterior half of the flank is feebly ornamented by fine commarginal limbs, with up to 3 for each posterior rib.

Munierchalmasia laevicostata (Redlich) (Fig. 10 C) is much like *M. jonioi*. It is small (L~40 mm), strongly compressed (W/H = 0.20), longer than high (H/L = 0.78), with strongly convex anterior and ventral margins. The broad respiratory margin is obliquely truncate, and the long posterodorsal margin concave with a small pointed terminal umbo.The escutcheon rim is beaded, and there is a finely beaded submedian carina to the broad lirate area. The curved marginal carina is entire, with a narrow antecarinal space below. The flank is ornamented with 10-11 bold strongly curved nontuberculate posterior limbs that meet the narrow antecarinal gap at a very acute angle that increases posteriorly; the anterior flank costellae are obsolete. The reason that compelled Redlich (1894: 72) to create this species was due to "the smooth ribs, which certainly correspond to their original state of preservation, since the extremely fine and delicate streaking of the area has been preserved down to the last detail" (translated).

Genus *Gerasimovella* gen. nov.

LSID:urn:lsid:zoobank.org:act:B1D79925-5E07-4C86-8E06-253E36EDE13C

Etymology: After P.A. Gerasimov (Moscow), renowned Russian palaeontologist and describer of the type species.
Type species: *Trigonia (Clavotrigonia) koprinensis* Gerasimov 1955: 55, pl. 3, figs 9-10; by original designation herein.

Diagnosis: Small, very inflated, with insignificant umbo; escutcheon lacks bounding carina; area with (primitive) or without (derived) beaded submedian carina, with growth striae (primitive) or wrinkled commarginal lirae (derived); fine marginal carina beaded, with prominent antecarinal space below; most of flank with thin widely spaced subcommarginal costellae posteriorly disconnected singly or in pairs to prominent rounded to triangular tubercles that increase in size with age; in maturity these tubercles may merge with smaller additional tubercles to form short thick tuberculate ribs perpendicular to the ventral margin. *Bajocian - L. Tithonian*.

Referred species: *Gerasimovella compta* (Lycett 1863: 50, pl. 40, fig. 1, Pugaczewska 1976: 90, pl. 17, figs 4-5, pl. 20, fig. 5) (Fig. 10 J), *G. uniclavata* (Cossman 1922: 19, pl. 6, figs 27-29, Lebrun 2021: 23, fig. 25E) (Fig. 10 K).

Discussion: A pandemic genus known only from the European (England, Poland) and Central Asian (Russia) provinces. As suggested by Gerasimov (1955), it may be an extreme development of the *Munierchalmasia* gen. nov. lineage.

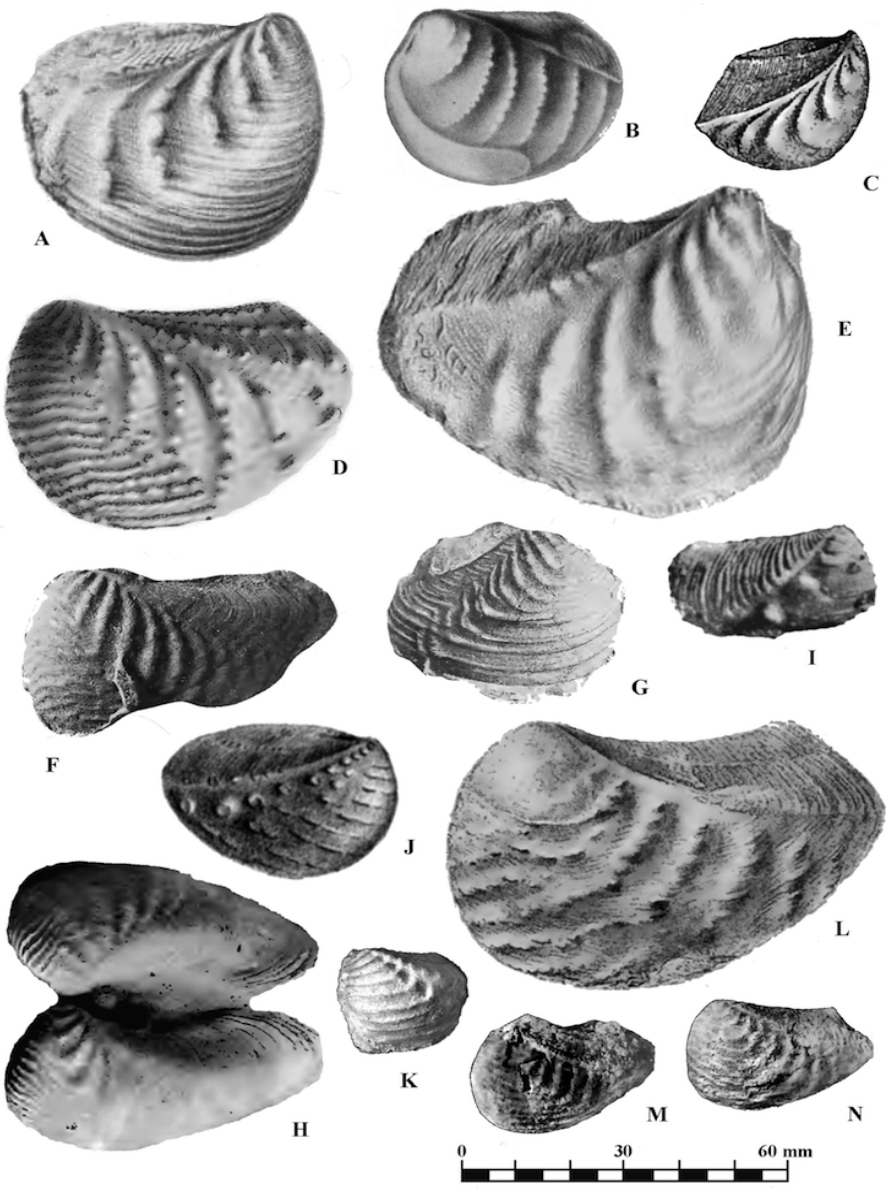

Fig. 10. A. *Munierchalmasia ferryi* (Munier-Chalmas), the lectotype designated herein after Munier-Chalmas (1865). **B.** *Munierchalmasia jonioi* (Rouillier & Vossinsky), the lectotype designated herein after Rouillier & Vossinsky (1849). **C.** *Munierchalmasia laevicostata* (Redlich), the holotype by monotypy after Redlich (1894). **D**. *Munierchalmasia carrei* (Munier-Chalmas), the lectotype designated herein after Munier-Chalmas (1865). **E.** *Munierchalmasia radiata* (Benett), the holotype by monotypy, after Benett (1831). **F-H.** *Munierchalmasia hauchecornei* (Schmidt), the paralectotypes (F-G) and lectotype (H) designated herein, after Schmidt (1905). **I.** *Gerasimovella koprinensis* (Gerasimov), the holotype after Gerasimov (1955). **J.** *Gerasimovella compta* (Lycett) the holotype by monotypy after Lycett (1854). **K.** *Gerasimovella uniclavata* (Cossman), the lectotype designated herein, MNHN.F.JO9565, after Lebrun (2021). **L.** *Munierchalmasia williamsoni* (Lycett) the lectotype designated herein after Lycett (1874). **M-N.** *Munierchalmasia oregonensis* (Poulton). The holotype (M), and a paratype (N), after Poulton (1979).

Gerasimovella koprinensis **(Gerasimov, 1955)**

Fig. 10 I

1955 *Trigonia (Clavotrigonia) koprinensis* Gerasimov, p. 55, pl. 3, figs 9-10.
1984 *Laevitrigonia koprinensis* (Gerasimov). - Kelly, p. 94.

Types: The holotype is from the bank of the Volga R. in the Rybinsk district, Yaroslavl Oblast of central Russia, from strata of Lower Volgian (*Virgatites virgatus* Zone) age.

Description: The holotype (Fig. 10 I) is small (L = 32 mm, L_{max} = 39 mm), longer than high (H/L = 0.75), very inflated (H/W = 0.54) with a very low insignificant umbo and obtuse umbonal angle (100°). The anterior margin is gently convex and the long posterodorsal margin straight. The escutcheon lacks a bounding carina and the gently convex to flat area is feebly bipartite with an indistinct longitudinal furrow, and is covered with strong wrinkled commarginal costellae that become thinner in later growth. The nodate marginal carina is formed by the thickened terminations of the areal costellae. After the nepionic stage of commarginal costellae most of the flank is covered by very thin, widely spaced subcommarginal costellae that posteriorly terminate, usually in pairs, in pointed triangular tubercles that increase in size and spacing with growth. In maturity the tubercles of some specimens merge with 1-2 small additional tubercles to form short thick tuberculate ribs perpendicular to the ventral margin.

Discussion: The holotype, by monotypy, of Bajocian *G. compta* (Lycett) (Fig. 10 J) from the Collyweston Slate of Northamptonshire, England, is small (L = 29 mm), ovate, longer than high (H/L = 0.70) with an obtuse umbonal angle, a curved strongly oblique respiratory margin, broad lirate area with beaded escutcheon and submedian carinae, slightly curved nodate marginal carina with antecarinal space below. The flank ornament comprises a posterior radial row of rounded nodes that increase in size posteriorly, paralleled by a shorter row of nodes in middle growth. These are disconnected from very thin widely spaced disjointed commarginal lirae that cover the anterior two-thirds of the flank. The Polish specimens assigned here from the Upper Bajocian *Parkinsonia ferruginea-compressa* Zones (Pugaczewska 1976) have a wide antecarinal depression.

Gerasimovella uniclavata (Cossman) (Fig. 10 K) from the Bathonian of Perrogney-les- Fontaines, Haute-Marne, Champagne-Ardenne, France, is small (L = 28 mm), subovate, longer than high (H/L = 0.79), with a straight conspicuously nodate marginal carina, narrow antecarinal space, very short swollen posterior limbs connected to long thin straight anterior limbs without intercalations.

Genus *Arkelligonia* gen. nov.

LSID:urn:lsid:zoobank.org:act:48921064-51F4-4D89-9D93-4A4ADE47FD6E

Etymology: After William Joscelyn Arkell (1904-1958), authority on the Jurassic and its faunas.

Type species: *Trigonia scarburgensis* Lycett 1863: 48, pl. 37, fig. 1, 1872: 31, pl. 4, figs 1-4, 1874: 31, pl. 4, fig. 1; by original designation herein.

Diagnosis: Small to moderately large, subtrigonal to elongate ovate; long narrow sunken escutcheon unornamented; narrow lirate area with beaded submedian carina; strong curved marginal carina with prominent transversely elongated nodes in early

to middle growth, weakening later and evanescing in maturity; well developed antecarinal space; well spaced nodate commarginal flank costae in early growth; posterior one-third to half of flank with prominent strongly curved oblique nodate ribs connected anteriorly to downturned and oblique beaded anterior portions. *Pliensbachian - Valanginian, ?Aptian*.

Referred species: *Arkelligonia donbassica* (Dykan 1986: 7, fig. 2, Dykan & Makarenko 1990: 108, pl. 28, figs 5-6, 9-12) (Fig. 12 N), *A. exaltata* (Lycett 1877: 184, pl. 38, fig. 2 (Fig. 11 I-K), *A. ingens* (Lycett 1872: 24, pl. 8, figs 1-3), *A. irregularis* (Seebach 1864: 118; nom. nov. pro *T. clavellata* Damon (*non* J. Sowerby), 1860, pl. 2, fig. 3), Lycett 1872: 39, pl. 5, figs 1-2, pl. 7, fig. 6, Duff 1978: 85, pl. 9, figs 13-17, pl. 10, figs 1, 3-4, 6, text-fig. 26, Dykan & Makarenko 1990: 103, pl. 25, fig. 1, pl. 26, fig. 1, Francis, 2000: 185, pl. 13, figs a-g) (Fig. 11 E), *A. supra-bathonica* (Greppin 1870: 344, pl. 3, figs 1a-c) (Fig. 15 F).

Discussion: *Arkelligonia* gen. nov. is a pandemic genus recorded from the European (England, France, Germany, Poland) and Central Asian (Ukraine, Mangyshlack) provinces.

Arkelligonia scarburgensis (Lycett, 1863)

Fig. 11 C-D

1863 *Trigonia scarburgensis* Lycett, p. 48, pl. 37, fig. 1.
1872 *Trigonia scarburgensis* Lycett. - Lycett, p. 31, pl. 4, figs 1-4.
1874: *Trigonia scarburgensis* Lycett. - Lycett, p. 48, pl. 37, fig. 1.
1893: *Trigonia scarburgensis* Lycett. - Bigot, p. 317, pl. 13, fig. 6.
1929 *Myophorella scarburgensis* Lycett. - Arkell, p. 31, pl. 1, figs 4-6.
1990 *Myophorella scarburgensis* (Lycett). - Dykan & Makarenko, p. 102, pl. 26, figs 2-13.
2000 *Myophorella scarburgensis* Lycett. - Francis, p. 31, pl. 9, fig. g, pl. 12, figs a-g.
2021 *Myophorella scarburgensis* Lycett. - Lebrun, p. 32.

Type: The holotype by monotypy, the original of the specimen figured by Lycett (1863), GSM10610 (= BGS/825092), from the Upper Cornbrash (Lower Callovian) of Scarborough, Yorkshire, England.

Description: The holotype (Fig. 11 C) is moderately large (L = 87 mm), elongate subovate, much longer than high (H/L = 0.65), with a gently convex anterior margin curving evenly into the long convex ventral margin; the curved respiratory margin is obliquely subtruncate, and the long posterodorsal margin (l/L = 0.74) concave with a small rounded anteriorly positioned umbo (al/L = 0.26), and incurved opisthogyrate beak. The long narrow escutcheon is sunken and unornamented, with a beaded rim. The long, narrow, slightly convex to flat area is lirate, with a beaded submedian carina. The strongly curved marginal carina has prominent transversely elongated nodes in early to middle growth, but these weaken later and evanesce in maturity, with a well developed antecarinal space below. Following the nepionic stage of well spaced nodate commarginal ribs, the posterior half of the flank has prominent curved oblique ribs, much narrow than the interspaces, with large rounded nodes. These

are disconnected from more numerous, short, downturned, strongly oblique, beaded anterior limbs.

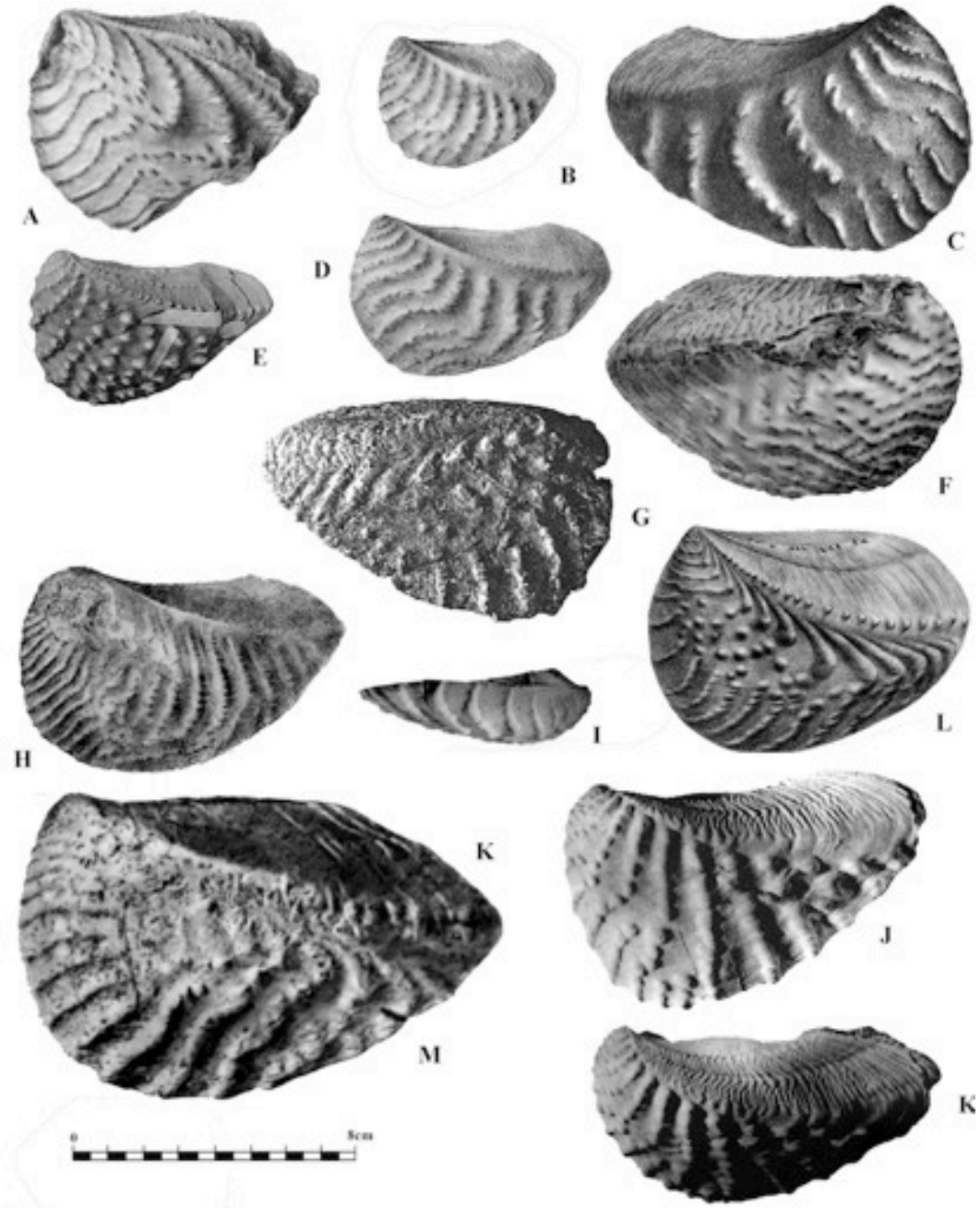

Fig. 11. A. *Lebkuechnerella difficilis* (Tornquist), the holotype by monotypy, after Tornquist (1898). **B.** *Myophorelloides corallinus* (d'Orbigny), the lectotype designated, herein after Lycett (1874). **C-D.** *Arkelligonia scarburgensis* (Lycett). C, the holotype by monotypy, after Lycett (1853); D, a juvenile hypotype after Lycett (1874). **E.** *Arkelligonia irregularis* (Seebach), the holotype by monotypy, BMNH-L6773, after Francis (2000). **F.** *Lebkuechnerella joassi* (Lycett), the lectotype designated herein, after Lycett (1877) **G.** *Lebkuechnerella trigona* (Waagen), the lectotype designated herein, after Lebküchner (1932). **H.** *Arkelligonia leckerbyi* (Lycett), the lectotype designated herein after Lycett (1874), in the SMC. **I-K.** *Arkelligonia exaltata* (Lycett), the holotype by monotypy, after Francis (2000). **L.** *Lebkuechnerella goldfussiana* nom. nov., the holotype after Goldfuss (1832). **M.** *Lebkuechnerella couzonensis* (Riche), the holotype after Lebküchner (1932).

A well preserved topotype (Fig. 11 D), BMNH-L17517, from the Upper Bajocian near Chipping Norton, shows a gabled area with lirae single and looped between the nodes as in *Vaugonia*, with those of the lower area transverse and those on the narrower upper part oblique. A hypotype figured by Dykan & Makarenko (1990, pl. 26, fig. 3) confirms this ornamental arrangement.

Discussion: *Arkelligonia leckenbyi* (Lycett) (Fig. 11 H) is from the Supra-Liassic Sandstone (= Stathness Sandstone Formation) at Robin Hood's Bay, Yorkshire, England, of Middle Pliensbachian age. It is moderately large (L = 88 mm), elongate-ovate and posteriorly produced (H/L = 0.59), much more densely ribbed than *A. scarburgensis*, with the posterior limbs covering three quarters of the flank and finer more numerous anterior limbs.

The holotype by monotypy of *A. irregularis* (Seebach) is BMNH-L6773 from the Upper Callovian Oxford Clay of Weymouth (Fig. 11 E). It is medium sized (L_{max} = 68 mm), elongate and posteriorly produced, with a very large depressed escutcheon (l/L>0.50) bounded by a rim with transverse elongated nodes that evanesce in maturity. The bipartite area is initially gabled, with the upper part more depressed than the lower, but flattens later and, following the nepionic stage, ornamented only by growth striae. The fine submedian carina is similar to the escutcheon carina, and the curved marginal carina has nodes that increase in size and transverse elongation posteriorly. Large specimens have a distinct antecarinal space. The flanks have well spaced strongly curve nodate flank costae that in middle growth become disjointed, with a dorsal portion of 4 large rounded nodes separated from a ventral part of smaller adpressed nodes that are deflected to become almost perpendicular to the growth striae.

Arkelligonia exaltata (Lycett) (Fig. 11 I-K) from the Sandringham Sands Formation (?Valanginian) of Norfolk is very large (L = 133 mm), posteriorly much produced (H/L = 0.67), compressed (H/W = 0.18) with a small near-terminal umbo, opistho-gyrate beak, weakly convex subvertical anterior margin, long convex ventral margin, obliquely convex respiratory margin, long concave posterodorsal margin and a narrow flattened anterior face. The narrow sunken unornamented escutcheon has a raised upper margin, the rim with the thickened terminations of areal lirae. The narrow asymmetrically bipartite area has the dorsal part sunken, and is transversed by numerous, irregular, wrinkled, and rugose commarginal lirae that strengthen at the position of the submedian furrow. There is a beaded marginal carina in early growth but this evanesces later, with a wide antecarinal space below. The flank is ornamented by about 14 well spaced nearly straight ribs with up to 6 large round nodes that meet the marginal rim at an angle that becomes increasingly opisthocline posteriorly. These are weakly connected or disconnected from shorter slightly offset curved contin-uations of smaller irregular nodes with very short intercalations of 1-2 rows.

Arkelligonia ingens (Lycett), lectotype designated herein the original of Lycett (1872, pl. 8, 1) (Fig. 15 B) from the Carstone Formation at Downham, Norfolk, which dates to the Early Albian but includes Lower Aptian remanié. It is moderately large (L ~ 80 mm), subtrigonally elongate (H/L = 0.80), compressed (W/L = 0.25), with a very low near-terminal umbo, opisthogyrate beak, straight vertical anterior margin, long convex ventral margin, narrow obliquely convex respiratory margin and long

shallowly concave posterodorsal margin. The large sunken unornamented escutcheon has a raised upper margin, with a minutely beaded rim. The moderately large asymmetrically bipartite area is slightly convex, with a beaded submedian carina, its striated surface becoming rugose posteriorly. There is a beaded marginal carina in early growth but this evanesces later, with a wide antecarinal space below. The flank is ornamented by well spaced nearly straight oblique ribs with up to 6 round nodes that meet the marginal rim almost at right angles. These are weakly connected to, or disconnected from, 12 subvertical rows of small nodes that are about as wide as the interspaces.

Arkelligonia donbassica (Dykan) (Fig. 12 N), from the Lower Oxfordian of the Kharkov region of Ukraine, is small (L = 38.5 mm), subquadratic (W/H = 1.02), with a narrow area, prominently nodate marginal carina, wide antecarinal space, very obtuse flank chevrons with the curved posterior limbs covering two-thirds of the flank, and the straight anterior limbs of fused beads deflected obliquely downwards.

Arkelligonia suprabathonica (Greppin) (Fig. 15 F) is from Sceut, west of Glovelier, Haute-Sorne, Switzerland, from the upper part of the sandy red limestone, where it is associated with *A. scarburgensis*. It is very large (L = 130 mm), subtriangular, longer than high (H/L = 0.91), moderately inflated (W/H = 0.27) with a concave posterodorsal margin, prominent well rounded, anteriorly positioned umbones and moderately incurved opisthogyrate beaks. The large sunken escutcheon is unornamented, with a beaded rim. The relatively narrow asymmetrically bipartite area is unornamented, with growth striae only. The marginal carina is beaded in early to middle growth but evanesces later leaving a rounded rim. The posterior two-thirds of the flank are ornamented by 16 curved nodate costae, narrower than the interspaces, that are separated from the marginal rim by an antecarinal space. Anteriorly they are disconnected from oblique rows of beads, in middle to later growth frequently separated by an intercalatory.

Genus *Lebkuechnerella* gen. nov.

LSID:urn:lsid:zoobank.org:act:EB017235-C6D6-4069-AFE1-D1D4B47A7CB9

Etymology: After Richard Lebküchner (1902-1981), documenter of the trigoniids from the Jura of southern Germany.
Type species: *Trigonia trigona* Waagen 1867: 620 (114), pl. 29 (6), fig. 3; by original designation herein.

Diagnosis: Moderately large to very large, trigonally ovate to trigonally elongate; area finely lirate with beaded submedian carina and nodate marginal carina with distinct antecarinal space; posterior flank with short straight strongly opisthocline ribs; midflank with jumbled nodes that may be weak or evanescent; anterior flank with short straight well-spaced subhorizontal nodate ribs. *Aalenian - Lower Callovian.*

Referred species: *Lebkuechnerella caytonensis* (Duff 1978: 89, pl. 10, figs 2, 10, pl. p1, figs 1-2, = *Trigonia rupellensis* Lycett (*non* d'Orbigny 1850) 1872: 28, pl. 8, fig. 4, 1877: 199, pl. 36, figs 1-4, Walker 1972: 124, pl. 8, fig. 20) (Fig. 7 D), *L. couzonensis* (Riche 1904: 162, pl. 5, fig. 40) (Fig. 11 M), *L. cuspidata* (J. de C.

Sowerby 1826: 8, pl. 507, figs 4-5), *L. difficilis* (Tornquist, 1898: 166, pl. 7, fig. 1) (Fig. 11 A), *L. goldfussiana* nom. nov. (= *Lyrodon literatum* Goldfuss 1837: 200, pl. 136, fig. 5b only; *non Trigonia literata* Phillips 1929: 161, pl. 14, fig. 11 (= *Hijitrigonia*); = *Trigonia goldfussii* Agassiz 1840: 24 (*non* Alberti *in* von Zieten 1830, = *Costatoria*), = Schlosser 1901: 553, = Lebküchner 1932: 78, pl. 8, fig. 15, pl. 9, figs 2-6, text-fig. 41); *non Trigonia goldfussii* Quenstedt 1832: 524, pl. 43, fig. 18, = *Costatoria*) (Fig. 11 L), *L. joassi* (Lycett 1874: 82, pl. 20, figs 2-4) (Fig. 11 F), *L. zitteli* (Branco 1879: 115, pl. 8, fig. 1) (Fig. 7 J).

Discussion: A pandemic genus known only from the European (England, France, southern Germany) and Andean (Argentina) provinces. It is distinguished from *Arkelligonia* gen. nov., its likely antecedent, in its generally larger size, straight posterodorsal margin and scattered midflank nodes.

***Lebkuechnerella trigona* (Waagen, 1867)**

Fig. 11 G

1867 *Trigonia trigona* Waagen, p. 620 (114), pl. 29 (6), figs 3a-b.
1932 *Clavotrigonia trigona* (Waagen). - Lebküchner, p. 81, pl. 9, fig. 7.

Type: The lectotype designated herein is the original of Waagen (1867: 620 (114), pl. 29 (6), fig. 3a-b, = Lebküchner 1932: 81, pl. 9, fig. 7) from the Lower Bajocian (zone of *Ammonites sowerbyi*, now the *Witchellia laeviuscula* Zone (Sadki & Dietze 2021) at Gingen/Fils in southwest Germany.

Description: The lectotype is moderately large (L = 97 mm), rounded trigonal, much longer than high (H/L = 0.62), moderately inflated (W/H = 0.28), with a weakly convex vertical anterior margin passing evenly into the long convex ventral margin; the weakly convex respiratory margin is strongly oblique and the long posterodorsal margin gently convex (l/L = 0.55). The low well rounded umbo is inconspicuous, with a weakly incurved (?orthogyrate) beak. The long narrow slightly depressed escutcheon is ornamented only by growth striae, with a beaded rim. The broad area is asymmetrically bipartite, the upper part narrower, with a beaded submedian carina that persists to maturity and growth striae. The straight marginal carina is nodate, the nodes increasing in size and transverse elongation posteriorly, with a well developed antecarinal space that broadens with growth. Following the nepionic stage of beaded commarginal costellae, the flank is ornamented by short bold strongly opisthocline posterior ribs that thicken distally and become longer and straighter posteriorly. These are separated from strongly oblique anterior ribs of smaller fused nodes, narrower than the interspaces, by scattered isolated rounded nodes at midflank.

Discussion: The lectotype of *L. zitteli* (Branco) designated herein, the original of pl. 8, fig. 1a (Fig. 7K), is from Aalenian beds with *Scaphotrigonia navis* (Lamarck) at St Quentin, Metz, France. It is moderately large (L == 92 mm), trigonally ovate (H/L = 0.72), moderately inflated (W/H = 0.30), with a gently curved subvertical anterior margin, long shallowly concave posterodorsal margin and small insignificant near terminal umbo. The area is asymmetrically bipartite with a longitudinal furrow that evanesces in later growth, with commarginal costellae in the nepionic stage followed later only by growth striae. The prominent marginal carina is beaded to middle growth, after which the beads become transversely elongated and the carina rounded

and indistinct. There is no antecarinal space. The flank chevrons comprise 16 straight opisthocline nodate posterior limbs and fine commarginal anterior limbs of uniform thickness separated by 1-3 intercalatories that occupy two-thirds of the flank. The anterior and posterior limbs are separated at midlank by irregular nodes. The broken paralectotype (pl. 8, fig. 1b) is much larger, with coarser flank ornament. It differs from all other *Lebkuechnerella* species in its fine commarginal anterior costae.

Goldfuss (1837) introduced French material as *Lyrodon literatum*, of which the original of pl. 136, fig. 5b is selected herein as lectotype. However *Lyrodon* (Sowerby 1823), incorrectly emended to *Lyriodon* (Cossman 1912), was an unnecessary replacement name for *Trigonia*, under the erroneous belief that it was preoccupied by a plant (Cossman 1912). Unfortunately the name *Trigonia literata* had already been used for a specimen, actually a *Hijitrigonia*, from the Lower Lias of Robin Hood's Bay, Yorkshire (Young & Bird 1828, Phillips 1829). As a result Agassiz (1840) renamed the German species *Trigonia goldfussi*, but this name was preoccupied by *T. goldfussi* Alberti (*in* von Zieten 1830), a species now placed in the genus *Costatoria* (Guo *et al.* 1976 Hayami 1975).

Lebkuechnerella goldfussiana nom. nov. (pro *Trigonia goldfussi* Agassiz 1840: 55; *non* Quenstedt 1832, *nec* Alberti *in* von Zieten 1830) is from the Bajocian of La Miotte, near Belfort, France. The lectotype designation herein (Fig. 11 L) is moderately large (L= 89 mm), trigonally ovate, longer than high (H/L = 0.78), with a thick test, small prominent anteriorly positioned umbo (al/L = 0.17) and opisthogyrate beak. The convex anterior margin curves evenly into the long gently convex ventral margin; the respiratory margin is obliquely subtuncate and the long posterodorsal margin straight (l/L = 0.52). The long narrow slightly depressed escutcheon is smooth, bounded by an irregularly beaded rim. The broad area is asymmetrically bipartite with a longitudinal furrow that eventually becomes a shallow depression. Initially there is a beaded submedian carina but this is lost early leaving the area ornamented only by growth striae. The rounded nodes of the gently curved marginal carina increase in size posteriorly, with a narrow antecarinal space that broadens with growth. Following its nepionic stage of commarginal costellae, the flank is ornamented by acute chevrons with thickened crests, after which the ornament becomes discrepant, with short strong opisthocline posterior limbs separated by irregularly distributed rounded nodes from thin curved anterior costellae of adpressed ellipsoidal beads that cut obliquely downwards across the growth striae and are narrower than the interspaces.

Lycett (1883: 17) considered *T. cuspidata* J. de C. Sowerby (1929: 8, pl. 507, figs 4-5) from the Bathonian Ancliffe Oolite "a minute, dwarfed, and very young form of a Great-Oolite species, probably *T. Moretoni*", but Cox & Arkell (1948) regarded it a very young specimen of *L. goldfussiana*; its hinge teeth were said to be unusually long. Since it is too small for proper identification it is a *nomen dubium*.

The lectotype designated herein of *L. joassi* (Lycett) is the original of his pl. 20, fig. 4 (Fig. 11 F) from the Oxfordian Lower Calcareous Grit Formation of Yorkshire, England. It is moderately large (L = 80 mm), trapezoidal, longer than high (H/L = 0.63), with an incipient posteroventral sinus, long straight posterodorsal margin (l/L = 0.60), and very low insignificant umbo. The wide flattened area is ornamented by commarginally plicae that kink at the feebly beaded submedian carina. The marginal carina is nodate, its nodes becoming transversely elongated posteriorly and finally

obscure. In early growth the flank ornament comprises well spaced very obtuse chevrons with posterior limbs of adpressed nodes and anterior limbs of irregular subcommarginal rows including an intercalatory. At a height of about 30 mm the chevrons become L shaped with short straight thick opisthocline nodate posteriorly limbs and narrow wavy subcommarginal anterior limbs that attenuate and become cord-like, including intercalatories, with the nodes in the middle of the flank irregular in size and distribution. In the larger paralectotype (pl. 20, fig. 3), the anterior limbs flex sharply downwards.

Lebkuechnerella caytonensis (Duff) was based on a specimen from the Lower Callovian at Red Cliff, Kellaways Rock, Cayton Bay, Scarborough, England. The holotype, SMC-J11377 (Fig. 7 D), is medium sized (L = 76 mm, L_{max} = 88 mm), elongate-ovate, longer than high (H/L = 0.66), moderately inflated (W/H = 0.25), with a low small pointed subterminal umbo (al/L = 0.14). The gently curved subvertical anterior margin passes evenly into the strongly convex ventral margin; the curved respiratory margin is obliquely truncated and the long posterodorsal margin shallowly concave (l/L = 0.66). There is a long narrow flat sunken escutcheon with a beaded rim. The flattened area is lirate, with a finely beaded submedian carina that evanesces in later growth and a few commarginal costellae in the nepionic stage. The fine almost straight marginal carina is beaded but evanesces in later growth to leave a rounded rim incised by growth striae and deeper growth halts, with a narrow antecarinal space below. The flank has 13 rows of costae with well rounded nodes, the umbonal 6 simple and subcommarginal, following which the short curved anterior rows are separated from the posterior limbs by subvertical rows of rounded nodes. The posterior three limbs are curved, oblique and nodate, narrower than the interspaces, flexing sharply close to the marginal carina.

Lebkuechnerella couzonensis (Riche) (Fig. 11 M) differs from *L. trigona* in being larger, subtrapezoidal, with a broader area with weak longitudinal furrow bordered by a beaded submedian carina which persists only to middle growth, slightly curved marginal carina with irregular transversely elongated nodes, and far more anterior limbs that are narrower and not so steeply inclined.

Argentinian *L. difficilis* (Tornquist) (Fig. 11 A) is moderately large (L = 85 mm), subovate, with a gently convex subvertical anterior margin, convex ventral margin, narrow obliquely truncate respiratory margin, straight posterodorsal margin and low insignificant subterminal umbo. The narrow asymmetrically bipartite area is lirate, with a beaded submedian carina. The marginal carina is straight with nodes that increase in size and transverse elongation posteriorly, with an antecarinal space below.There are long curved strongly opisthocline well spaced rows of nodes posteriorly, separated at midflank by scattered elliptical nodes, from widely spaced, curved, oblique rows of fused beads.

Genus *Myophorelloides* gen. nov.

LSID:urn:lsid:zoobank.org:act:FCB5DD46-EEC7-47A7-8479-5A57602BB657

Etymology: False *Myophorella*.

Type species: *Trigonia signata* var. *zieteni* (Lycett 1872: 29, pl. 2, figs 1-3, 1883: 2, pl. 1, figs 3-5, 16-17, pl. 4, fig. 7); by original designation herein.

Diagnosis: Small to large, trigonally ovate to elongate-trapezoidal, with concave posterodorsal margin and prominent near terminal umbones; escutcheon rim finely beaded; wide lirate area with beaded submedian carina and narrow depressed dorsal part; marginal carina with nodes becoming larger and transversely more elongate posteriorly, with or without antecarinal space; curved oblique nodate flank costae with posterior third thickened and with large partially fused nodes curving into the anterior two-thirds of rounded beads. *Aalenian – Tithonian.*

Referred species: *Myophorelloides adeli* (Bigot 1893: 315, pl. 13, fig. 5) (Fig. 12 F), *M. clavellatus* (Goldfuss 1837: 200, pl. 136, figs 6a-f) (Fig. 12 O), *M. corallinus* (d'Orbigny 1850: 16, No. 260, Lycett 1874: 45, pl. 3, figs 7-9, 11, pl. 8, fig. 5, Savel'ev 1960a: 85, pl. 6, fig. 2, pl. 13, figs 3-4) (Fig. 11 B), *M. decurtatus* (Lycett 1883: 10, pl. 1, figs 1-2, pl. 4, fig. 3) (Fig. 12 S), *M. hudlestoni* (Lycett, 1877: 194, pl. 34, figs 5-6, pl. 39, figs 1a, 3) (Fig. 12 M), *M. kerfornei* (Bigot 1893: 329, pl. 15, fig. 7) (Fig. 12 E), *M. metzensis* (Strand 1928: 71; = *Trigonia* cf. *leckenbyi* Lycett, Branco 1879: 117, pl. 8, fig. 2) (Fig. 15 D), *M. obscurus* (Savel'ev 1960b: 201, pl. 3, fig. 2) (Fig. 13 N-O), *M? oxoniensis* (Lycett 1883: 12, pl. 1, figs 13-15) (Fig. 12 P), *M. rugulosus* (Lycett, 1883: 8, pl. 2, figs 1-3, pl. 4, figs 2, 4) (Fig. 12 J), *M. smirnovkaensis* (Dykan 1986: 6, fig. 1, Dyckan & Makarenko 1990: 107, pl. 28, figs 13-19) (Fig. 12 D), *M. stutterdi* (Lycett 1883: 9, pl. 2, figs 9-11, pl. 4, figs 1, 5-6) (Fig. 12 A), *M. subsignatus* (Savel'ev 1960a: 81, pl. 14, fig. 1) (Fig. 12 I), *M. suevicus* (Quenstedt 1857: 790, pl. 98, fig. 6, Lebküchner 1932: 66, pl. 6, figs 11-16, pl. 7, figs 1-3, Welhofner 1964: 61, pl. 4, figs 1-5, text-figs 41-42) (Fig. 12 K), *M. trouvillensis* (Strand; = *fischeri* Bigot 1893 (*non* Munier-Chalmas): 326, pl. 15, fig. 8) (Fig. 12 G), *M. uralicus* (Savel'ev 1960b: 200, pl. 3, fig. 1) (Fig. 12 Q-R), *M. ucrainicus* (Yungerman 1962: 106, pl. 1, figs 1-2) (Fig. 8 M-N).

Discussion: A pandemic genus from the Upper Bajocian - Lower Tithonian of the European (England, France, Switzerland, Germany, Poland, Denmark) and Central Asian (Urals, Ukraine) provinces. The bipartite area with narrow sunken dorsal part, and oblique curved flank costae with nodes posteriorly and beads anteriorly distinguish this genus from *Myophorella*. It differs from *Arkelligonia* gen. nov. in that the nodate flank costellae are continuous and curved, not with dislocated posterior (dorsal) and anterior (ventral) portions with different orientation.

Myophorelloides zieteni (Lycett, 1883)

Fig. 12 L

1872 *Trigonia signata* Agassiz. - Lycett, p. 29, pl. 2, figs 1-3.
1883 *Trigonia signata* var. *zieteni* Lycett, p. 2, pl. 1, figs 3-5, 16-17, pl. 4, fig. 7.
1883 *Trigonia signata* var. *rugulosa* Lycett, p. 8, pl. 2, figs 1-3, pl. 4, figs 2, 4.
1883 *Trigonia signata* var. *sutterdi* Lycett, p. 9, pl. 2, figs 9-11, pl. 4, figs 1, 5-6.
1883 *Trigonia signata* var. *decurtata* Lycett, p. 10, pl. 1, figs 1-2, pl. 4, fig. 3.
2000 *Myophorella (Myophorella) signata* (Agassiz). - Francis, p. 156, pl. 11, figs a-d.

Type: The lectotype designated herein, BMNH-L.17517, is the original of the specimen figured by Lycett (1883, pl. 4, fig. 7) and Francis (2000, pl. 11, fig. a) from the Inferior Oolite (Upper Bajocian, *parkinsoni* Zone) of the Rollright quarry near Chipping Norton, Oxfordshire, England.

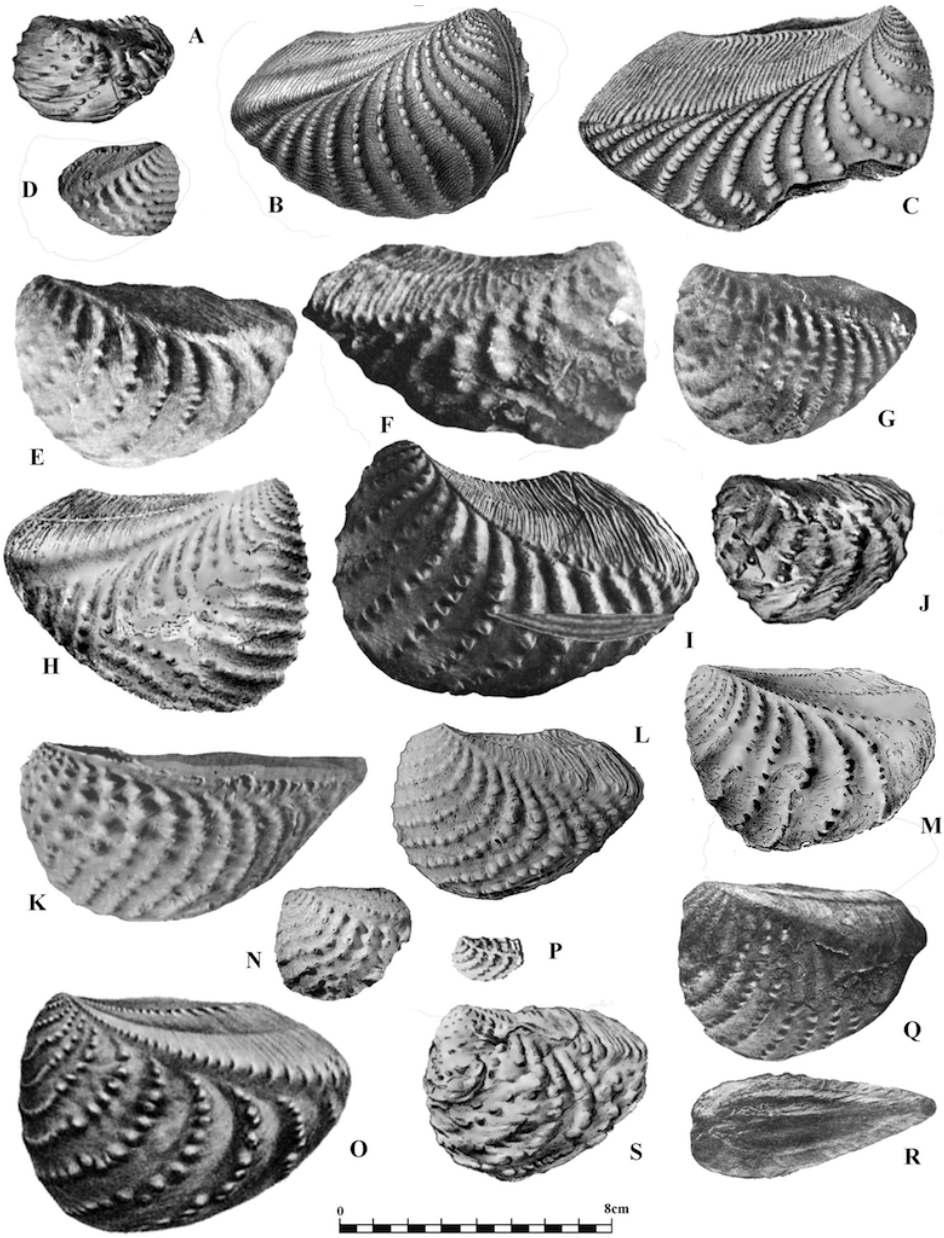

Fig. 12. A. *Myophorelloides stutterdi* (Lycett 1883), the lectotype designated herein, after Lycett (1883). **B-C.** *"Trigonia" signata* Agassiz. B, the lectotype designated herein after Agassiz (1840); C, a hypotype after von Zieten (1830). **D.** *Arkelligonia smirnokoffensis* (Dykan), the holotype after Dykan & Makarenko (1990). **E.** *Myophorelloides kerfornei* (Bigot), the holotype by monotypy after Bigot (1893). **F.** *Myophorelloides adeli* (Bigot), the holotype by monotypy after Bigot (1893). **G.** *Myophorelloides trouvillensis* (Strand), the holotype by monotypy after Bigot (1893). **H.** *Glevenella producta* (Lycett), the lectotype designated herein after Lycett (1874). **I.** *Myophorelloides subsignatus* (Savel'ev), the holotype after Savel'ev (1960a). **J.** *Myophorelloides rugulosus* (Lycett), the lectotype designated herein after Lycett (1883). **K.** *Myophorelloides suevicus* (Quenstedt), a hypotype after Welhofner (1964). **L.** *Myophorelloides zieteni* (Lycett), the lectotype designated herein after Francis (2000). **M.** *Myophorelloides hudlestoni* (Lycett), the lectotype designated herein after Lycett (1877). **N.** *Myophorelloides donbassicus* (Dykan), the holotype after Dykan & Makarenko (1990). **O.** *Myophorelloides clavellatus* (Goldfuss), the holotype by monotypy after Goldfuss (1836). **P.** *Myophorelloides? oxoniensis* (Lycett), the lectotype designated herein, after Lycett (1874). **Q-R.** *Myophorelloides uralicus* (Savel'ev), the holotype after Savel'ev (1960b). **S.** *Myophorelloides decurtatus* (Lycett), the lectotype designated herein after Lycett (1883).

Description: The lectotype (Fig. 12 L) is medium sized (L = 72 mm), elongate ovate, longer than high (H/L = 0.70), with a convex anterior margin, a convex ventral margin that straightens posteriorly, a wide obliquely truncate respiratory margin, and a shallowly concave posterodorsal margin (l/L = 0.57), with a rounded anteriorly positioned umbo (al/L = 0.18) and moderately incurved opisthogyrate beak. The long narrow excavated escutcheon is unornamented, rising towards the commissure, with its rim beaded by the swollen terminations of areal lirae that increase in size and transverse elongation posteriorly. Following its nepionic stage, the broad gabled asymmetrically bipartite area has a finely beaded submedian carina, with the narrower upper area concave and the broader lower part flat. It is ornamented by irregular single and looped lirae that are deflected at the submedian carina. The marginal carina is finely nodate in early growth, the nodes increasing in size and transverse elongation posteriorly, with a narrow antecarinal space below. Following the nepionic stage of commarginal costellae the flank ornament becomes discrepant. Posteriorly there are bold, slightly curved, opisthocline nodate ribs that cover about a third of the flank and connect anteriorly to well spaced almost straight oblique rows of tiny rounded beads.

Discussion: Lycett (1883, pl. 4) selected a number of specimens from Rollright, near Chipping Norton, to illustrate the Oxfordshire varieties of *Trigonia signata* Agassiz that he named *stutterdi* (Fig. 12 A), *rugulosa* (Fig. 12 J), *decurtata* (Fig. 12 S) and *zieteni* (Fig. 12 L). Here, due to page priority and favourable preservation, *zieteni* is selected as having nomenclatural priority over the other names which are therefore likely to be junior synonyms.

The name *Trigonia signata* Agassiz (1840: 18, pl. 3, fig. 8, pl. 9, fig. 5) has been widely applied to Bajocian trigoniids. The lectotype designated herein (Fig. 12 C) is the original of pl. 9, fig. 5, from the Inferior Oolite "calcaire marno-sableux de Goldenthal (Canton de Soleure)", Switzerland. It is remarkable for its elongate (H/L ~ 0.67) and strongly compressed shape, long concave posterodorsal margin (l/L = 0.62) and tiny inconspicuous anteriorly positioned umbo (al/L = 0.12). The ligament pit is narrow and very elongate, surrounded by a smooth escutcheon with a beaded rim formed by the terminal swellings of areal lirae. The latter are prominent and sinuous, deflected at the slight thickening of the gabled submedian carina, and greater thickening for the marginal carina. Both a longitudinal furrow and antecarinal gap are lacking. In early to middle growth the flank is covered with curved oblique rows of rounded nodes that increase uniformly in size anteriorly, and meet the marginal carina at an acute angle that increases posteriorly, while the interspace between ribs increases markedly. In later growth the curved ribs become strongly geniculated close to the ventral margin, forming obtuse chevrons, leaving the remaining 5 ribs to meet the posteroventral margin at a very acute angle. Noteworthy is the uniform increase in size of the rounded nodes to the anterior flank costellae of *T. signata*. This is different to those assigned here by Lycett (1882), Bigot (1893) and Lebküchner (1932, pl. 5, fig. 3) that show the discrepant flank nodation typical of *Myophorelloides* gen. nov. Moreover Agassiz' incomplete lectotype does not preserve the anteroventral portion of the shell that is critical for generic placement. Agassiz (1840: 18) claimed that von Zieten's (1830: 78, pl. 58, figs 3a-c) *Trigonia clavellata* (*non* Sowerby) (Fig. 12 B) was the same as his *T. signata* yet the Württemberg specimen has sinuous flank costae that curve downwards anteriorly, unlike the condition in *Myophorelloides* gen. nov. but very similar to that displayed

by "*Myophorella" woodwardi* (Lycett, 1872: 40, unnumbered text fig.). Complete toptype specimens are required for the satisfactory generic assignment of *"T." signata*.

The lectotype of *M. clavellatus* (Goldfuss) (Fig. 12 O) is moderately large (L = 89 mm), trapezoidal, longer than high (H/L = 0.74) with a long shallowly concave posterodorsal margin (l/L = 0.66). The escutcheon rim and marginal carina are prominently nodate, the nodes becoming increasingly transversely elongated posteriorly, but the submedian carina to the area evanesces early, leaving a longitudinal furrow for much of growth and a narrow antecarinal space. The nodate flank costellae are curved and oblique, the posterior three quarters with enlarged often ellipsoidal nodes and the anterior quarter with subhorizontal rows of rounded adpressed to fused beads.

Myophorelloides adeli (Bigot) is fairly common in the Upper Bajocian of Fresnay-la-Mère, Sérans (Orne), France. The holotype by monotypy (Fig. 12 F) is medium sized (L = 68 mm), trapezoidally very elongate (H/L = 0.61), with a very long gently convex ventral margin straightening posteriorly, a relatively narrow obliquely truncate respiratory margin, a long shallowly concave posterodorsal margin (l/L = 0.64) and a low rounded subterminal umbo. The long narrow escutcheon is fringed by extensions of the carinal beads. The relatively narrow asymmetrically bipartite area is gabled, its concave upper part narrower than the broad flat lower part, with a persistent beaded submedian carina. It is ornamented with bold lirae that are looped or joined singly to the prominent nodes of the marginal carina, and are deflected anteriorly on the upper area. There is a narrow antecarinal space. Following its nepionic stage, the flank is ornamented with well spaced curved oblique rows of nodes, following which they become L-shaped with thickened curved nodate posterior limbs that cover about a third of the flank, the last four of which reach the ventral margin, and well spaced thinner beaded subcommarginal anterior limbs.

Myophorelloides corallinus (d'Orbigny), the lectotype designated by Savel'ev (1960a) being the original of Lycett (1872, pl. 8, fig. 5) (Fig. 11 B) from the Upper Oxfordian Coral Rag Member of the Coralline Oolite Formation at Pickering, northern Yorkshire, England. It is small, elongate-ovate and posteriorly produced with a broad area, well developed antecarinal space, and curved nodate ribs that cover two-thirds of the flank and are poorly connected to their beaded anterior portions.

"Trigonia" perlata Agassiz (1840: 19, pl. 3, figs 9-11) lectotype designated herein the original of his fig. 9 from the Middle Jurassic of Largue, Bàle, Switzerland, is incomplete. It is moderately large (L = 97 mm) with a weakly curved subvertical anterior margin, conspicuously geniculated respiratory margin, and small near-terminal umbo. In later growth it has prominent escutcheon, submedian and marginal carinae, the first two with transversely elongated nodes, and the latter with small rounded nodes and a narrow antecarinal space. The area is asymmetrically bipartite with a narrower upper part, and commarginal lirae that flex sharply forwards at the submedian carina. The flank is ornamented with well-spaced curved oblique costae with discrete rounded nodes that increase in size posteriorly, with a suggestion they are replaced anteriorly by small nodes. The generic placement of this species is uncertain, but the specimens assigned here by Bigot (1893: 321, pl. 14, figs 3-5) from the Middle and Upper Oxfordian of Normandy are typical *Myophorelloides* gen. nov.

Myophorelloides smirnovkaensis (Dykan) (Fig. 12 D) from the Lower Oxfordian of the Ukraine (Kharkov region) is small (L = 35.9 mm), trigonally ovate (H/L = 0.74), with a strongly oblique respiratory margin and long almost straight posterodorsal margin. The escutcheon has a sharp beaded rim, and the moderately wide gabled area has its narrower depressed dorsal part at an angle to the ventral part, with a beaded submedian carina that strengthens with growth. The marginal carina is formed by dense scale-like tubercles that overlap and become larger posteriorly, with an antecarinal gap below that widens with growth. The curved flank costae have their posterior third thickened and subnodate, curving into the anterior two-thirds that are straight and subcommarginal with smaller partially fused nodes and a rare intercalatory.

Upper Oxfordian *M. trouvillensis* (Strand) (Fig. 12 G) closely resemble *M. zieteni* and is doubtfully distinct. Contemporaneous *M. kerfornei* (Bigot) (Fig. 12 E) has a very oblique respiratory margin, curved marginal carina and more widely spaced anterior segments that cover only about a third of the flank.

Myophorelloides suevicus (Quenstedt) (Fig. 12 K) is widely reported from the Upper Oxfordian to Tithonian of England, France, Switzerland, Poland, Germany and Denmarck. It is large (Lmax = 110 mm), trigonally very elongate, much longer than high (H/L = 0.52), with a subterminal umbo and long almost straight posterodorsal margin. The almost straight marginal carina is beaded initially but these become larger and transversely elongated posteriorly, with a prominent antecarinal space. In middle growth the upper part of the flank is ornamented with curved rows of 3-5 round, large, well separated nodes disconnected from straight oblique rows of 5-7 much smaller nodes.

The holotype of Callovian *M. subsignatus* (Savel'ev) (Fig. 8 M) is large (L = 106 mm), trapezoidally elongate (H/L = 0.78), moderately inflated (H/W = 0.28), with a weakly curved subvertical anterior margin, broad gently rounded respiratory margin and relatively short deeply concave posterodorsal margin (l/L = 0.46), with prominent rounded terminal umbones.

The large unornamented escutcheon (l/L = 0.43) is sunken, with a beaded rim, and the broad asymmetrically bipartite area is initially gabled with a submedian angulation and longitudinal furrow that evanesces in later growth. Following the nepionic stage of commarginal costellae, the area is ornamented with dense fine commarginal lirae, single or looped, that kink at the longitudinal furrow, with the dorsal striae being deflected anteriorly. The marginal carina is concave, finely beaded to middle growth, with nodes that increase in size and transverse elongation posteriorly, without an antecarinal space. The flanks have curved oblique nodate costae, much narrower than the interspaces, that meet the marginal carina at an acute angle. In middle to later growth the upper third of the ribs are thick and opisthocline with fused nodes, whereas the lower two-thirds have small discrete nodes that decrease in size antero-ventrally.

The lectotype designated herein of *M. hudlestoni* (Lycett) (Fig. 12 M) is from the Oxfordian of Elsworth Rock, Cambridgeshire, England. It is medium sized (L = 72 mm) although a paralectotype (pl. 39, fig. 2) is much larger (L = 105 mm), longer

than high (H/L = 0.76), and differs from *M. zieteni* (Lycett) in being less produced posteriorly, with fewer more widely spaced flank costae that do not curve forward so markedly.

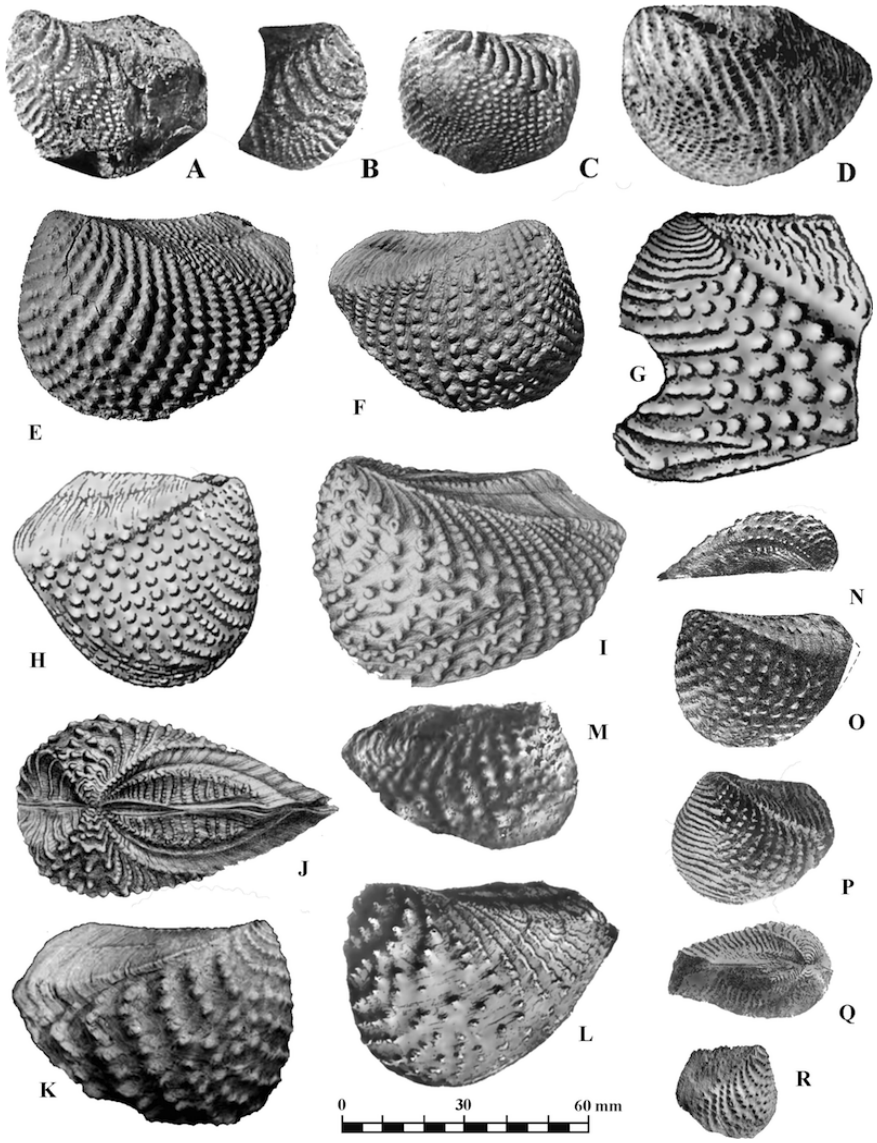

Fig. 13. A-C. *Algonquinella taylori* (Poulton). A, C, paratypes, B the holotype, after Poulton (1980). **D.** *Algonquinella tuxedniensis* (Poulton), a paratype after Poulton (1979). **E.** *Alcobacella muricata* (Goldfuss), a hypotype after Schneider (2009). **F.** *Agassigonia neumayri* (Choffat), the holotype by monotypy, after Schneider (2009). **G.** *Montdorella geographica* (Agassiz), the holotype by monotypy after Agassiz (1840). **H.** *Agassigonia parkinsoni* (Agassiz), the holotype by monotypy after Agassiz (1840). **I-L.** *Alcobacella lusitanica* (Sharpe). I-J, the holotype by monotypy after Sharpe (1850); K-L, hypotypes after Choffat (1885). **M.** *Amaraligonia beirensis* (Choffat), the lectotype designated herein after Choffat (1885). **N-O.** *Myophorelloides obscurus* (Savel'ev), the holotype after Savel'ev (1960b). **P-Q.** *Amaraligonia ribeiroi* (Choffat), the lectotype designated herein, after Choffat (1885). **R.** *Algonquinella* cf. *taylori* (Poulton), a paratype of *Vaugonia? yukonensis* Poulton, after Poulton (1979).

Lower Volgian (*Dorsoplanites panderi* Zone) *M. uralicus* (Savel'ev) (Fig. 12 Q-R) is moderately large (L = 86 mm), longer than high (H/L = 0.77), moderately convex (W/L = 0.17), with an imperceptible near-terminal umbo and slightly opisthogyrate beak. The straight anterior margin curves evenly into the strongly convex ventral

margin, with a shallow sinus posteriorly; the respiratory margin is oblique truncate, and the long posterodorsal margin straight. The unornamented sunken escutcheon is narrow (w/l = 0.14), with the ligament pit 37% of its length. The escutcheon rim and marginal carina are worn and rounded but may have been nodate. The broad bipartite area is markedly asymmetrical with a persistent longitudinal furrow and the dorsal part much narrower than the ventral part; it is ornamented by growth striae and lacks a submedian carina. There is a smooth antecarinal space that broadens posteriorly. The flank has 15 curved strongly oblique nodate costae, narrower than the interspaces, the posterior half with 6 well separated ribs with large ellipsoidal nodes. The anterior ribs have tiny nodes to their distal 15-20%.

Lower Volgian *M. obscurus* (Savel'ev) (Fig. 13 N-O) from the Yatria River, eastern slopes of the Subpolar Urals, is medium sized (L = 58 mm), longer than high (H/L = 0.77), moderately convex (W/H = 0.28), with imperceptible near-terminal umbones and strongly incurved opisthogyrate beaks. The vertical gently convex anterior margin curves evenly into the strongly convex ventral margin; the respiratory margin is obliquely truncated, and the long posterodorsal margin (l/L = 0.68) shallowly concave. The ligament pit is a third the length of the long wide unornamented escutcheon (w/W = 0.36), its rim in early to middle growth with well separated beads, becoming rounded later. The bipartite area is narrow, its upper part slightly narrower than the lower, with a weak longitudinal furrow, a prominent submedian carina with well rounded beads that become transversely elongated posteriorly and persist to middle growth. It is ornamented only by growth striae, with a well rounded marginal rim and prominent antecarinal space that broadens ventrally. The flank has 17 curved oblique rows of nodes, narrower than the interspaces; the posterior half of each rib has large, discrete, triangular nodes whereas the anterior half has rows of small adpressed nodes separated by a short intercalatory.

Myophorelloides ucrainicus (Yungerman) (Fig. 8 M-N) from the Upper Kimmeridgian of the Kharkiv region of northeastern Ukraine, is medium sized (L = 53 mm), trapezoidally elongate and posteriorly produced (H/L = 0.66), moderately inflated (W/H = 0.26), with low indistinct subterminal umbones. The anterior margin is almost straight, curving evenly into the convex ventral margin that straightens posteriorly, and the long posterodorsal margin is straight. The smooth escutcheon (l/L = 0.39) is narrow (w/l = 0.21), rising towards the commissure, with frequent sharp beads to its rim. The flat area has 20 sharp commarginal costellae on its narrower upper part, with a well defined longitudinal groove and narrow antecarinal space. The entire surface of the area is covered by sharp, finely beaded lirae, the distance between which increases with growth and, in maturity, the beads merge and the sharpness of the lirae remains only on the upper part of the area. The gently curved marginal carina is distinct and nodate. Following a nepionic stage of two commarginal costellae, the flank is ornamented by three nodate chevrons with zigzagging and dichotomous anterior limbs and 6-7 long thick curved coarsely nodate posterior limbs covering 40% of the flank, meeting the marginal carina acutely (80°), with the last three reaching the ventral margin. The short oblique anterior limbs are beaded, about as wide as the interspaces, outnumbering the posterior limbs due to bifurcation and intercalation, and meeting the anterior commissure at an acute angle.

Myophorelloides? oxoniensis (Lycett) was, with some hesitation, introduced as a variety of *T. moretoni* (Morris & Lycett) from the lower beds of the Aalenian Salperton Limestone of the Inferior Oolite at Hook Norton, Oxfordshire. The

lectotype designated herein (Fig. 12 P) is very small (L_{max} = 9.5 mm), oblong, much longer than high (H/L = 0.62), with a distinct spinose escutcheon rim, coarse commarginal costellae to the area, a curved marginal carina that straightens posteriorly and flank costellae with 2-3 prominent fused nodes dorsally that connect ventrally with curved rows of smaller nodes.

Myophorelloides metzensis (Strand) (Fig. 15 D-E) is from the Lower Dogger (*S. navis* Zone) of Hayingen, Baden-Württemberg, Germany. It is trigonally elongate and posteriorly produced, moderately inflated (W/H = 0.33), with a gently curved anterior margin curving evenly into the long convex ventral margin. The posterior part of the shell is not preserved. The posteroventral margin is shallowly concave, and the subterminal umbo well rounded, with an opisthogyrate beak and rounded anterolateral shoulders. The area is perpendicular to the flank near the umbo but inclined posteriorly with a beaded marginal carina whose nodes become increasingly transversely elongate posteriorly; it lacks a submedian carina and longitudinal furrow and is ornamented only by growth striae. The flank ornament is discrepant, the chevrons with 14 curved nodate opisthocline posterior limbs which are disconnected from the oblique beaded rows of costellae that, in middle to later growth are separated by an intercalatory.

Genus *Amaraligonia* gen. nov.

LSID:urn:lsid:zoobank.org:act:B5C7458E-89AB-4EAE-963B-7B1711B6956C

Etymology: Amaral - the name of the formation from which the type species was collected.

Type species: *Trigonia ribeiroi* Choffat 1885: 31, pl. 4, figs. 8-9; by original designation herein.

Diagnosis: Like *Munierchalmasia* gen. nov. but with convex anterior margin, broader area with strong crinckled commarginal lirae, lack of antecarinal space; flank chevrons with long curved closely spaced nodate posterior limbs that cover more than half the flank, and with twice as many finer, closely spaced subhorizontal wavy feebly nodate anterior limbs that continue onto the peaked anterior face where they are nontuberculate; conjoined valves gape posteriorly. *Callovian - Kimmeridgian*.

Referred species: *Amaraligonia beirensis* (Choffat 1885: 25, pl. 3, figs. 17-20) (Fig. 13 M).

Discussion: *Amaraligonia* gen. nov. is endemic to the Lusitanian basin of Portugal. It differs most obviously from older *Vaugonia* in its greater inflation, shallow antecarinal depression, coarse commarginal costellae to the area, and flank chevrons whose curved anterior limbs cover half the flank. In the latter character it approaches *Munierchalmasia* gen. nov. but the narrow posterior limbs of *A. ribeiroi* are finely beaded, its area ornamented with wavy commarginal lirae and the valves gape.

Amaraligonia ribeiroi (Choffat, 1885)

Fig. 9 I-J

1885 *Trigonia ribeiroi* Choffat, p. 31, pl. 4, figs. 8-9.

Types: Choffat had 29 specimens from the Late Kimmeridgian Amaral Formation (= Beds with *Lima pseudalternicosta*) of Portugal, of which the original of his pl. 4, fig.

8 is selected here as lectotype, the remaining figured specimens becoming para-lectotypes.

Description: The lectotype (Fig. 9 I-J) is small (L = 42 mm), longer than high (H/L = 0.88), inflated (W/H = 0.35) with low broadly rounded anteriorly positioned umbones, an obtuse umbonal angle and opisthoogyrate beaks. The straight anterior margin passes imperceptibly into the strongly convex ventral margin, the respiratory margin is obliquely truncate and the long posterodorsal margin straight (l/L = 0.56). The narrow escutcheon (w/W = 0.28) is initially concave, becoming fastigiate posteriorly, with a beaded rim. The broad asymmetrically bipartite area has a feeble longitudinal furrow and is covered with strong simple commarginal wrinkles that swell on the marginal rim, the nodes increasing in width posteriorly; an antecarinal space is lacking. The flank ornament comprises subcommarginal ribs in early growth, forming distinct obtuse chevrons in middle growth, but becoming less obviously V-shaped later when the curved nodate posterior limbs only connect with the straight feebly nodate anterior limbs with a slight kink. From middle growth onwards there are two anterior ribs for every posterior one and these continue on the slightly peaked anterior face from which the tubercles are effaced. The conjoined valves gape posteriorly.

Discussion: Choffat (1885) had some 20 specimens of *A. beirensis* from the Couches à *Pholodomya protei*, mostly internal moulds and their counterparts. Here the original of pl. 3, fig. 17 from S. Jorge is selected as lectotype (Fig. 13 M). It is medium sized (L = 55 mm) and differs from *A. ribeiroi* in its trigonally elongate shape, less inflated valves, areal costellae extending onto the escutcheon, marginal carina that evanesces in later growth, and coarser flank ornament.

Genus *Algonquinella* gen. nov.

LSID:urn:lsid:zoobank.org:act:F1142566-C77B-42DC-8DAB-CE57986A9A5C

Etymology: Algonquin – the original inhabitants of Oregon, where the type species was collected; comes from the Algonquin language meaning “beautiful”.

Type species: *Myophorella taylori* Poulton 1980: 193, pl. 30.2, figs 13-16; by original designation herein.

Referred species: *Algonquinella tuxedniensis* (Poulton 1979: 38, pl. 7, figs 9-17, 1980: 193, pl. 30.2, figs 9-12) (Fig. 13 D).

Diagnosis: Medium sized, subovate, slightly longer than high; asymmetrically bipartite area with wavy lirae and beaded escutcheon, submedian and marginal carinae without antecarinal space; following nepionic stage of subcommarginal costellae, posterior one- to two-thirds of flank with curved oblique rows of rounded nodes, sometimes with intercalations of additional rows; anterior third of flank with dorsoventrally oriented, closely spaced, finely beaded costellae, commonly irregular, bifurcating or separated by an intercalatory. *Lower Bajocian*.

Discussion: An endemic genus to the Cordilleran Province (British Columbia, Alaska, Yukon).

Algonquinella taylori (Poulton, 1980)
Figs 13 A-C

1980 *Myophorella taylori* Poulton, p. 193, pl. 30.2, figs 13-16.

Types: The holotype UCMP 16025 and paratype UCMP 16026 are from the Lower Bajocian (upper part of the Murchisonae Zone) of central Oregon, and paratype GSC 62965 from Vancouver Island, British Columbia.

Description: The holotype is small to medium sized (L_{max} = 50 mm), elongate-subovate, moderately inflated, with a prominent rounded terminal umbo (but low and insignificant in a paratype). The subvertical anterior margin curves evenly into the long convex ventral margin; there is a broad obliquely truncate respiratory margin (holotype), and the long posterodorsal margin (l/L = 0.71) is almost straight (paratype) to concave (holotype). The escutcheon is depressed, apparently smooth, and with a beaded rim. The narrow area has very fine growth lines, a feeble longitudinal furrow and a beaded submedian carina. The marginal carina is ornamented with small, evenly spaced, sharp or rounded tubercles, with a very narrow antecarinal space below. Following the nepionic stage of subcommarginal costellae, the flank ornament becomes discrepant with curved oblique rows of nodate costellae posteriorly that, with growth become increasingly widely spaced and are narrower than the interspaces (but in a paratype these limbs a thick with fused nodes). These are clearly separated from an anterior set of dorsoventrally oriented, closely spaced, finely beaded costellae, commonly irregular, bifurcating or separated by an intercalatory, that become the predominant ornament along the posteroventral margin.

Discussion: A paratype of *Vaugonia? yukonensis* (Poulton 1979: pl. 8. fig. 11) (Fig. 13 R) from the Potem Formation of northern California was subsequently identified as *Myophorella* cf. *taylori* (Poulton 1980: 194, pl. 30.1, fig. 11).

Algonquinella tuxedniensis (Poulton) (Fig. 13 D) from the Lower Bajocian of Alaska differs from *A. taylori* in having wavy transverse costellae to the escutcheon, an almost straight marginal carina whose nodes increase in size posteriorly and almost straight subvertical posterior costellae that cover more than half the flank.

Genus *Agassigonia* gen. nov.

LSID:urn:lsid:zoobank.org:act:CDA3C0F8-99BF-4820-84B1-21310AA9D950

Etymology: After the describer of the type species, the famous Swiss born American palaeontologist Jean Louis Rudolphe Agassiz (1807-1873).

Type species: *Trigonia parkinsoni* Agassiz 1840: 56, pl. 10, fig. 6); by original designation herein.

Diagnosis: Medium sized, subovate, slightly longer than high; asymmetrically bipartite area with wavy lirae and faint submedian carina; marginal carina nodate to maturity (primitive) or evanescing in later growth (derived), with or without antecarinal space; following nepionic stage of subcommarginal costellae, posterior

two-thirds of flank with curved oblique rows of well-rounded nodes, sometimes with intercalations of additional rows; anterior third of flank with dorsoventrally oriented, closely spaced, finely beaded costellae, commonly irregular, bifurcating or separated by an intercalatory. *Kimmeridgian - Tithonian*.

Discussion: An endemic genus to the European Province (England, France, Portugal, Switzerland).

Agassigonia parkinsoni (Agassiz, 1840)

Fig. 13 H

1840 *Trigonia parkinsoni* Agassiz, p.56, pl. 10, fig. 6.

Description: The lectotype (Fig. 13 H) from the Portlandian near Besançon, northeast France, is medium sized (L = 60 mm), subovate, slightly longer than high (H/L = 0.81), with an almost straight vertical anterior margin and strongly convex ventral margin, broad obliquely truncate respiratory margin, fairly long straight posterodorsal margin (l/L = 0.53), and small pointed umbo. The escutcheon has a finely beaded rim. The broad asymmetrically bipartite area is ornamented by slightly wavy commarginal lirae interrupted by a longitudinal furrow bordered by a feeble submedian carina formed by the slightly swollen terminations of the areal lirae. There is a beaded marginal carina to middle growth, whereafter it becomes obsolete and is indicated only by a very slightly angulated rim with a few small swollen terminations to the areal lirae. An antecarinal gap is lacking. Following the nepionic stage of commarginal costellae, the flank is ornamented with oblique nodate costellae, narrower than the interspaces to a height of 15 mm, whereafter the posterior two-thirds of the flank is covered by curved rows of well-rounded nodes that meet the marginal rim at an acute angle that increases posteriorly. The nodation is confused by the periodic intercalation of additional rows of nodes. The anterior third of the flank has subcommarginal rows of small closely adpressed nodes.

Referred species: *Agassigonia neumayri* (Choffat 1885: 30, pl. 4, figs 7a-c) (Fig. 13 F).

Discussion: The lectotype of *A. neumayri* (Choffat) (Fig. 13 F) designated herein, from the Kimmeridgian "Couches á *Lima altemicosta*" at Sobral da Lagoa, Portugal, is medium sized (L = 60 mm), longer than high (H/L = 0.78), inflated (W/H = 0.40), with an almost straight anterior margin, shallowly concave posterodorsal margin, relatively prominent well rounded anteriorly positioned umbo (al/L = 0.19), escutcheon rim beaded by the thickened terminations of the coarse wrinkled lirae to the relatively narrow area. The posterior 7 flank costae are strongly curved with small closely spaced to adpressed nodes, and the anterior costae are concave upwards on the broad anterior face.

Genus *Montdorella* gen. nov.

LSID:urn:lsid:zoobank.org:act:18398295-67E9-4BFF-B15C-7D92AB4BDEBC

Etymology: After Mont d'Or, a peak in the Jura mountains that straddle the border between France and Switzerland, where the type species was collected.

Type species: *Trigonia depereti* Riche 1904: 159, pl. 6, fig. 3 a-c; by original designation herein.

Diagnosis: Very large, much longer than high, elongate-oval to trapezoidal, with a broad bipartite area unornamented (primitive) or with coarse wrinkles (derived), beaded escutcheon and marginal carinae restricted to earliest growth, with rounded rims later; following nepionic stage of commarginal costellae, posterior flank with opisthocline radial rows of well rounded nodes that increase in size ventrally; anterior flank with commarginal rows of small nodes that may persist to maturity or are replaced by radial rows of rounded nodes aligned parallel to the posterior rows. *Upper Aalenian - Oxfordian*.

Referred species: *Montdorella geographica* (Agassiz 1840: 25, pl. 6, figs 2-3, pl. 10, fig. 7) (Fig. 13 G), *M. reussi* (Strand 1928: 71; = Deeke 1925: 227, = Reuss 1845: 5, pl. 19, fig. 3), *M. terquemi* (Benecke 1905: 191, pl. 14, fig. 12) (Fig. 15 A).

Discussion: An endemic genus to the European Province (England, France, Luxembourg, Czechoslovakia), easily distinguished by the radial direction of the posterior rows of nodes, parallel to the marginal carina.

Montdorella depereti (Riche, 1904)

Figs 14 A-B

1904 *Trigonia depereti* Riche, p. 159, pl. 6, fig. 3a-c.

Types: The lectotype designated herein is the original of Riche (1904, pl. 6, fig. 3a) (Fig. 14A) from the Upper Aalenian *Graphoceras concavum* Zone of Mont d'Or, Lyon, where the species was said to be reasonably common. The remaining figured specimens (pl. 6, fig. 3b-c) (Fig. 14 B) serve as paralectotypes.

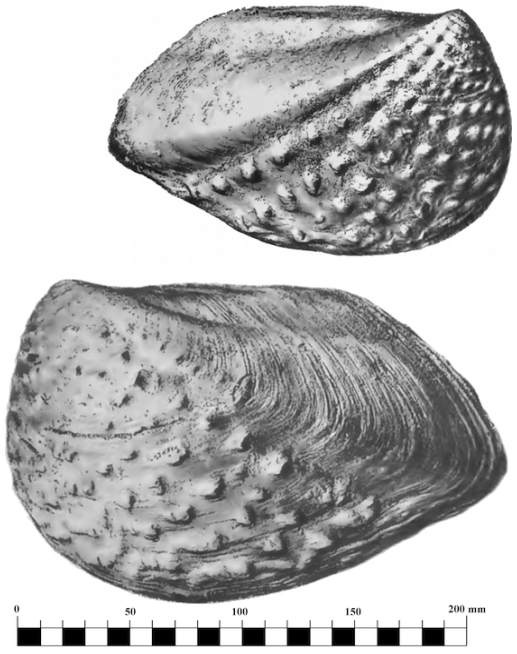

Fig. 14. *Montdorella depereti* (Riche). The lectotype (above) and a paralectotype (below), after Riche (1904).

Description: The lectotype (Fig. 14 A) is very large (L = 186 mm), elongate ovate, much longer than high (H/L = 0.64), with the convex anterior margin grading imperceptibly into the long convex ventral margin with the hint of a broad very shallow posterior sinus. The subtruncate respiratory margin is oblique and the long posterodorsal margin (l/L = 0.52) straight to slightly convex, with a small pointed umbo anteriorly (al/L = 0.12). The unornamented escutcheon is narrow and lanceolate, with an impersistent beaded rim that rounds in middle growth. The broad asymmetrically bipartite area has a shallow longitudinal furrow with commarginal costellae on the nepionic stage that persists longer on the dorsal part, after which it is ornamented only by growth striae. There is a beaded marginal carina in early growth but beyond 60 mm length becomes a broad rounded rim with a narrow antecarinal space below. Following the nepionic stage of 8 commarginal costellae, the flank ornament becomes discrepant. Posteriorly there are four straight divergent opistho-cline radial costae with separated and well rounded nodes that increase in size ventrally. To middle growth these are fronted by well spaced commarginal rows of small nodes, whereafter the nodes enlarge and are arranged into four radial rows to conform to the posterior rows, with the nodes of the anterior rows becoming elongated and, in some cases, fused. Beyond the nepionic stage growth striae are conspicuous. The typical form, with simple and regularly radiating tubercles, is rarer than varieties with fused anterior tubercles.

Discussion: The lectotype of *M. geographica* (Agassiz) (Fig. 13 G) from the Oxfordian of the Swiss Jura differs from *M. depereti* (Riche) in being smaller (L~60 mm), with coarse wavy wrinkles to the area and a submedian carina, distinct marginal carina with nodes that become increasingly transversely elongate posteriorly, and the flanks with anterior ribs that are reduced to nontuberculate and subtuberculate commarginal rows persisting to maturity. The paralectotype (pl. 6, figs. 2-3) is larger (L = 75 mm), subtrapezoidally elongate (H/L = 0.86) and moderately inflated (H/W = 0.33), with a straight posterodorsal margin, narrow antecarinal space, and much reduced nepionic stage.

A juvenile English specimen of *M. geographica* from the Oxfordian Corallian Oolite of Pickering (Lycett 1874: 69, pl. 10, fig. 6) (L = 25 mm) has smaller posterior nodes and an unornamented area, the latter perhaps due to poor preservation.

The holotype by monotypy of *M. terquemi* (Benecke) (Fig. 15 A) from the Rotsandiges Lager, Katzenberg near Esch in Luxembourg is moderately large (L = 94 mm), hemispherical, almost as high as long (H/L = 0.97), with a high gently curved anterior margin that passes imperceptibly into the strongly convex ventral margin; the wide respiratory margin is obliquely truncate, and the short posteroventral margin (l/L = 0.52) almost straight. The escutcheon is not described, but its rim may have been beaded. The wide asymmetrically bipartite area is ornamented with coarse irregular commarginal costellae. The almost straight marginal carina is beaded in early growth but becomes thicker and bolder with growth, and the nodes become transversely elongated and merge into the carina. There is a broad flat antecarinal space. The flank ornament is discrepant, with three radial rows of enlarged rounded nodes posteriorly, the hindmost reaching the ventral margin but the other two shorter. At midflank there are irregularly distributed nodes that only here and there arrange themselves in rows and anteriorly there are short commarginal rows of adpressed beads that sometimes merge into costellae.

The lectotype designated herein of *M. reussi* (Strand) (Fig. 15 C) is medium sized (L = 57 mm), posteriorly produced, much longer than high, with 20-24 well spaced nodate radial costellae over the entire flank, but apparently absent from the anterior face. It is from the pyrope-bearing conglomerates of Meronitz (= Měrunice, Czech. Republic) where it is always pyritized.

Genus *Alcobacella* gen. nov.

LSID:urn:lsid:zoobank.org:act:0121EDCC-B961-42BB-AB77-3B96C3465138

Etymology. After the Alcobaça Formation from which the type species was collected.

Type species: *Trigonia lusitanica* Sharpe 1850: 190, pl. 22, fig. 4a-b; by original designation herein.

Diagnosis. Medium sized to moderately large, trigonally ovate tapering posteriorly, with almost straight vertical anterior margin; escutcheon large, with transverse beaded costellae; area with scattered nodes to upper part; flank chevrons with narrow beaded opisthocline posterior limbs that increase in length posteriorly, up to 9 of which reach the posteroventral margin; anterior flank complexly nodate with curved oblique rows of larger well separated rounded nodes with short irregular intercalated rows and isolated nodes, disconnected anteriorly from short oblique rows of small adpressed nodes that may become thin and wiry on the flattened to rounded anterior face. *Kimmeridgian*.

Referred species: *Alcobacella muricata* (Goldfuss 1837: 201, pl. 137, fig. 1, Choffat 1885: 26, pl. 5, 6, figs 14-17) (Fig. 13 E), *A. torrevedrasi* (Strand 1928: 71; = Deeke 1925: 188; = *Trigonia* aff. *lusitanica* Sharpe, Choffat 1885: 34, pl. 9, fig. 22) (Fig. 7 J).

Discussion. An endemic genus to the Mediterranean Subprovince of Europe (Portugal). In its ornamented escutcheon it approaches Bajocian *Algonquinella tuxedniensis* (Poulton) but the latter has thicker straighter posterior costellae, and the anterior costellae are finely beaded and more numerous. At present the latter is the only feasible antecedent.

Alcobacella lusitanica (Sharpe, 1850)

Fig. 13 I-L

Type. The original of Sharpe (1850), by monotypy, that was said to be abundant in the limestones of the Alcobaça Formation between Torres Vedra and Sobra, Portugal.

1850 *Trigonia lusitanica* Sharpe, p. 190, pl. 22, fig. 4 a-b.
1885 *Trigonia lusitanica* Sharpe. – Choffat, p. 32, pl. 7-8, 9, figs 19-21.

Description. The holotype by monotypy (Fig. 13 I-J) is moderately large (L = 76 mm), trigonally ovate, longer than high (H/L = 0.66), inflated (W/H = 0.38), with a weakly convex subvertical anterior margin passing evenly into a long straight ventral

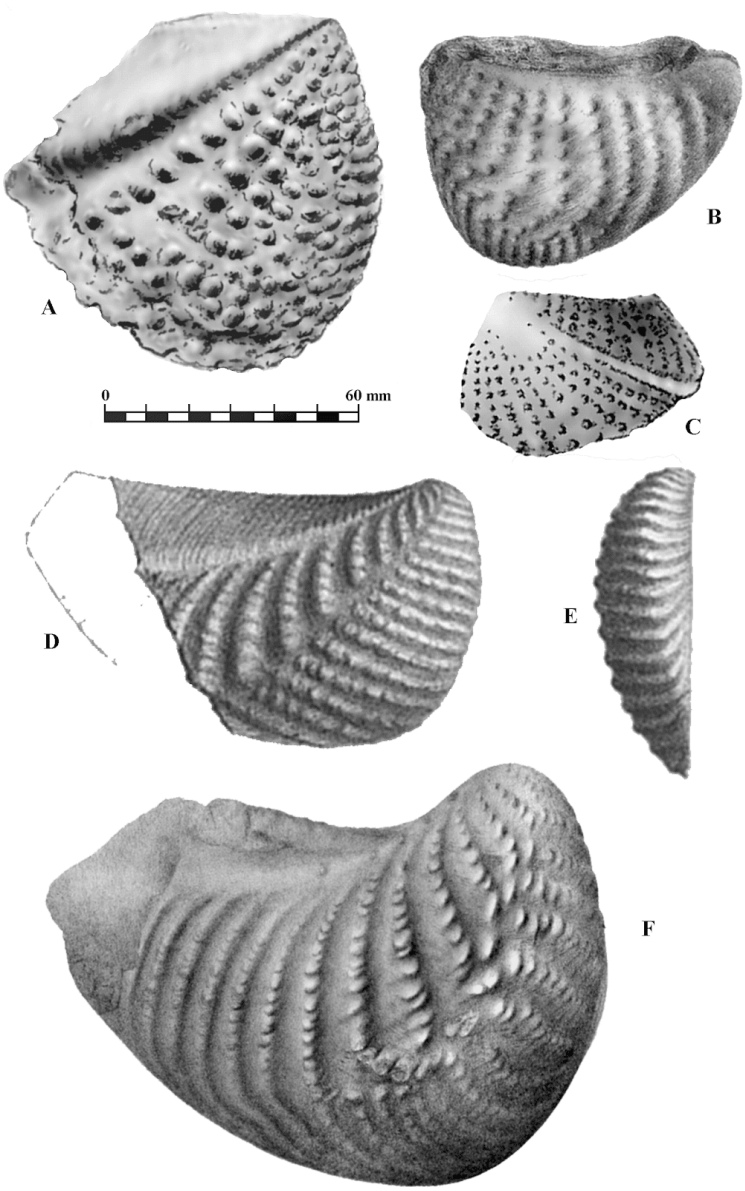

Fig. 15. A. *Montdorella terquemi* (Benecke), the holotype by monotypy, after Benecke (1905). **B.** *Arkelligonia ingens* (Lycett), the lectotype designated herein, after Lycett (1872). **C.** *Montdorella reussi* (Strand), the lectotype designated herein, after Reuss (1845). **D-E.** *Myophorelloides metzensis* (Strand), the holotype by monotypy, after Branco (1879). **F.** *Arkelligonia suprabathonica* (Greppin), the holotype by monotypy, after Greppin (1870).

margin that straightens posteriorly. The rather narrow respiratory margin is obliquely truncate, the long posterodorsal margin (L/L = 0.70) shallowly concave, low rounded subterminal umbones (al/L = 0.15), moderately incurved opisthogyrate beaks and a narrow lanceolate ligament pit. The shallowly sunken cordate anterior face is ornamented with distant thin subhorizontal costellae. The large escutcheon (l/L = 0.69) is moderately wide (w/W = 0.20), with transverse beaded costellae narrower than the interspaces and a beaded rim that evanesces in maturity. The asymmetrically bipartite area has a persistent longitudinal furrow, its narrower upper part with rows of beads, its lower part with growth striae. The marginal carina is an acute nodate rim in early to middle growth, later rounding and indented by striae and growth halts. The flank ornament is complex with oblique rows of nodes with narrow curved beaded stems that increase in length posteriorly so that the last 9 reach the ventral margin.

Anteriorly these stems pass downwards into 4-6 well-separated large rounded nodes that are disconnected from short irregular intercalated rows of small adpressed nodes. The internal commissure has two elongated buttresses corresponding externally in positions to the escutcheon and submedian carinae (Choffat 1885, pl. 9, fig. 20).

Discussion. Choffat (1885) had 500 specimens from different localities, noting a wide range of "intraspecific variation" (Fig. 13 K-L) with no two alike and, significantly, none of his hypotypes matched the holotype, lacking a concave flattened anterior face with angular anterolateral shoulders (Fig. 13 I-J). The latter character is convergent towards much smaller *Orthotrigonia*.

Alcobacella torrevedrasi (Strand) (Fig. 7 J) from the Kimmeridgian (Pterocerien superieur) of Arsena, Torre Vedras, Portugal, was distinguished from closely ribbed varieties of *A. lusitanica* by the large number of ribs meeting the ventral margin and its angular marginal carina. It is also trapezoidal in shape.

Kimmeridgian *A. muricata* (Goldfuss), the holotype by monotypy being the original of Goldfuss's figure, in the palaeontological collections of the University of Bonn, No. 861, from Alco, Portugal. Choffat (1885) had 300 specimens from a number of different localities, and hence horizons, in the upper part of the Couches à *Pholadomya Protei* of the Alcobaça Fornation. The hypotype figured here (Fig. 13 E) closely matches the holotype and is medium sized (L = 68 mm), trapezoidally elongate, with wrinkled lirae to the area, strongly curved nodate posterior costae covering three quarters of the flank, 8 of which reach the ventral margin. The anterior quarter of the flank is covered by well separated slightly oblique rows of up to 7 small rounded nodes with short intercalatories so that they outnumber the posterior limbs 2:1.

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REFERENCES

Agassiz, L. 1840. *Études critiques sur les mollusques fossiles*. Imprimerie de Petitpierre, Nêuchatel.

Alencáster, G. de Cserna. 1963. Pelecipodos del Jurasico Medio del noroeste de Oaxaca y noreste de Guerrero. *Paleontologia Mexicana*, 15: 1-52.

Anderson, F.W. & Cox, L.R. 1948. The "Loch Staffin Beds" of Skye; with notes on the molluscan fauna of the Great Estuarine Series. *Proceedings of the Royal Physical Society of Edinburgh*, 23: 103-122.

Arkell, W.J. 1929-37. A monograph of British Corallian Lamellibranchia. *Palaeontographical Society Monograph*, Part 1: 1-72 (1929), Part 2 (1930): 73-104; Part 3 (1931): 105-132; Part 4 (1932): 133-180; Part 5 (1933): 181-228; Part 6 (1934a): 229-276; Part 7 (1934b): 277-324; Part 8 (1935): 325-350; Part 9 (1936): 351-376; Part 10 (1937): 377-392.

Behrendsen, O. 1922. Contribución a la geología de la pendiente oriental de la Cordillera Argentina. *Actas de la Academia Nacional de Ciencias*, 8: 157-227.

Benecke, E.W. 1905. Die Versteinrungeren der Eisenerzformation von Deutsch-lothringen und Luxemburg. *Abhandlungen zur geologischen Specialkarte von Elsass-Lothringen*, n.f., Heft 6: 1-598.

Benett, E. 1831. *A catalogue of the organic remains of the county of Wilts*. J.L. Vardy, Warminster.

Bigot, A. 1893. Contributions à l'étude de la faune Jurassique de Normandie. Mémoire de trigonees. *Mémoires de la Societé Linnéenne de Normandie*, 17 (2): 262-345.

Blake, J.F. 1880. The Portland rocks of England. *Quarterly Journal of the Geological Society of London*, 36: 189-235.

Branco, W. 1879. Die untere Dogger Deutsch-Lothringens. *Abhandlungen zur geologischen Spezialkarte von Elsass-Lothringen*, 2 (1): 1-160.

Burmeister, H. & Giebel, C. 1861. Die Versteinerungen von Juntas im Thal des Río Copiapó. *Abhandlungen der Naturforschenden Gesellschaft zu Halle*, 6: 113-144.

Butler, B.S., Loughlin, G.F. & Heikes, V.C. 1920. The ore deposits of Utah. *United States Geological Survey, Professional Paper*, 111: 1-672.

Ceccolini, F. & Cianferoni, F. 2021. Five replacement names for fossil bivalve genera (Mollusca: Bivalvia). *Neues Jahrbuch für Geologie und Paläontologie*, 302 (2): 231-234.

Choffat, P. 1885. Description de la faune jurassique du Portugal. Mollusques Lamellibranches. Deuxième ordre, Asiphonidae. *Commission des Travaux Géologiques du Portugal, Mémoires*, 1st livraison, 4: 1-36.

Cooper, M.R. 1991. Lower Cretaceous Trigonioida (Mollusca, Bivalvia) from the Algoa Basin, with a revised classification of the order. *Annals of the South African Museum*, 100: 1-52.

Cooper, M.R. 2015a. On the Pterotrigoniidae (Bivalvia: Trigonioidea); their palaeo-biogeography, evolution, classification and relationships. *Neues Jahrbuch für Geologie und Paläontologie*, 277 (1): 11-42.

Cooper, M.R. 2015b. On the Iotrigoniidae (Bivalvia: Trigonioidea); their palaeobiogeography, evolution and classification. *Neues Jahrbuch für Geologie und Paläontologie*, 277 (1): 49-62.

Cooper, M.R. 2019. On the Quadratotrigoniinae (Trigoniida: Myophorelloidea), their palaeobiogeography, evolution and classification. *Durban Natural Science Museum Novitates*, 39: 1- 48.

Cooper, M.R. 2021. On the Apiotrigoniinae (Bivalvia, Trigoniida), their palaeo-biogeography, evolution and classification. *Neues Jahrbuch für Geologie und Paläontologie*, 300 (2): 145-174.

Cooper, M.R. 2024. On the Orthotrigoniinae subfam. nov. (Trigoniida, Vaugoniidae); their palaeobiogeography, evolution and classification. *Neues Jahrbuch für Geologie und Paläontologie*, 311 (2): 175-190.

Cooper, M.R. & Leanza, H.A. 2019. On the Middle Jurassic - Early Cretaceous Mega- trigoniidae (Bivalvia, Trigoniidae): their biogeography, evolution and classification. *Neues Jahrbuch für Geologie und Paläontologie*, 291 (1): 19-40.

Cooper, M.R. & Leanza, H.A. 2021. On the Buchotrigoniidae (Cretaceous Trigoniida), their palaeobiogeography, evolution and classification. *Neues Jahrbuch für Geologie und Paläontologie*, 301 (2): 119-134,

Cossmann, M. 1912. Essai sur l'évolution des trigonies. *Annales de Paléontologie*, 7: 59-84.

Cossmann, M. 1922. Description de quelques pélécypodes jurassiques receuillis en France. 2e sér., 2e art. *Comptes Rendus de l'Association Françaises pour l'Avancement des Sciences.* Congrès Montpellier 1922: 1-21.

Cox, L.R. 1950. Bathonian *Viviparus*-like gastropods. *Geological Magazine*, 87 (3): 229-230.

Cox, L.R. 1952. Notes on Trigoniidae, with outlines of a classification of the family. *Proceedings of the Malacological Society of London*, 29 (2-3): 45-70,

Cox, L.R. 1969. Trigoniacea Lamarck, 1859. *In*: Moore, R.C. (ed.), *Treatise on invertebrate paleontology. Part N, Mollusca*, 6 (1): N471-489. Geological Society of America, Boulder; University of Kansas Press, Lawrence.

Cox, L.R. & Arkell, W.J. 1948-50. 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 (1905-7). *Palaeontographical Society Monograph*, 102 (444): i□xiii, 1-48; 103 (449): 49-105.

Crickmay, C.H. 1930. The Jurassic rocks of Ashcroft, British Columbia. *California University, Department of Geological Science, Bulletin*, 19 (2): 23-74.
Dall, W.H. 1889. On the hinge of pelecypods and its development, with an attempt toward a better subdivision of the group. *American Journal of Science*, Series 3, 38 (228): 445-462.

Damborenea, S.E. 2002. Jurassic evolution of Southern Hemisphere marine palaeo-biogeographic units based on benthonic bivalves. *Geobios, Mémoire special*, 24: 51-71.

Damon, R. 1860. *Handbook to the geology of Weymouth and the Isle of Portland; with notes on the natural history of the coast and neighbourhood*. E. Stanford, London.

Dechaseaux, C. 1931. L'Oxfordien Supériéur de la bordure et du basin de Paris. *Compte Rendu Sommaire et Bulletin de la Sociéte géologique de France,* (5), 1931: 353-387.

Deeke, W. 1925. *Fossilium Catalogus. I, Animalia. Pars 30: W. Deecke, Trigoniidae mesozoicae (Myophoria exelusa)*. W. Junk, Berlin.

Dollfus, A. 1863. *La faune Kimméridienne du Cap de la Hève, essai d'une révision paléontologique*. F. Savy, Paris.

Douglas, J.A. & Arkell, W.J. 1928. The stratigraphical distribution of the Cornbrash. Part 1. The south-western area. *Quarterly Journal of the Geological Society of London,* 84: 117-178.

Duff, K.L. 1974. *Studies on the palaeontology of the Lower Oxford Clay of southern England*. Unpublished D. Phil. thesis, University of Leicester.

Duff, K.L. 1978. Bivalvia from the English Lower Oxford Clay (Middle Jurassic). *Palaeont-ographical Society Monograph*, 132 (553): 1-137.

Dykan (Dikan), K.V. 1986. New Late Jurassic *Vaugonia*. *Dopovidian Academy of Nauk Ukrainskoi RSR* (Seriya B - Geologichni Khimichni ta Biologichni Nauki), 11: 5-9 [in Ukranian].

Dykan (Dikan), K.V. & Makarenko, D.E. 1990. *Bivalve and gastropod molluscs of the Upper Jurassic of Dniepr-Donets depression*. Naukova Dumka, Kiev [in Ukranian].

Echevarría, J., Damborenea, S.E. & Manceñido, M.O. 2018. Early Jurassic trigoniides from southern South America: their recovery after extinction and its bearing on the evolution of the group. *10th International Congress on the Jurassic System, 2018 Mexico*: 44-45.

Echevarría, J., Damborenea, S.E. & Manceñido, M.O. 2021. Early Jurassic Trigoniida (Bivalvia) from Argentina. *Journal of Paleontology*, 95: 1-55.

Eguiluz-de Antuñano, S., Villaseñor, A.B., Ibarra-Bustos, P.D. & Centeno-Olivares, M. 2021. Record of Aalenian ammonites and bivalves in Canelas, Durango, western Mexico. *Journal of South American Earth Sciences*, 114: 103676.

Efimova, A.F., Kinasov, V.P., Paraketsov, K.V., Polubotko, I.V., Repin, Yu.S. & Dagis, A.S. 1968. *Field atlas of the Jurassic fauna and flora of the northeastern part of the U.S.S.R.* Ministry of Geology RSFSR, Severo-vostochnoye ordena trydovogo krasnogo Znameni geologicheskoe upravlenie, Magadanskoe Knizhnoe-Izdatel'stvo: 1-378 [in Russian].

Eichwald, C.E. von. 1865-68. *Lethaea Rossica ou Paléontologie de la Russie*. 2: 1-640 (1865), 641-1304 (1868). E. Schweizerbart, Stuttgart.

Eichwald, C.E. von. 1871. *Geognostich-Palaeontologische Bemerkungen uber die Halbinsel Mangischlak und der Aleutischen Iseln, von dr. Eduard von Eichwald*. Buckdruckerei der kaiserlichen Akademie der Wissenschaften, St Petersburg.

Enay, R. & Mangold, C. (eds) 1980. Synthèse paléogéographique du Jurassique français. *Document Laboratoire Géologie de Lyon*, H.S., 5: 1-210.

Étallon, A. 1864. Études paléontologiques sur le Jura graylois. *Mémoires de la Société d'Emulation du Département du Doubs*, 3 Série, 8: 221-506.

Fischer, J.-C. 1969. Géologie, paléontologie et paléoécologie du Bathonien au sud-est du massif Arduennais. *Mémoires du Muséum National d'Histoire Naturelle, Paris*, n.s., Série C (Sciences de la Terre), 20: 1-319.

Fleming, C.A. 1987. New Zealand Mesozoic bivalves of the superfamily Trigoniacea. *New Zealand Geological Survey, Palaeontological Bulletin*, 53: 1-104.

Forbes, E. 1851. The Estuary Beds and the Oxford Clay of Loch Staffin, in Skye. *Quarterly Journal of the Geological Society of London*, 7: 104-113.

Francis, A.O. 2000. *The palaeobiology of the European Jurassic Trigoniidae*. Unpublished Ph.D. thesis, University of Birmingham.

Freneix, S. 1958. Deux especes de Trigoniidae de la Haute-Marne. *Mémoires de la Société historique et archéologique de Langres*, 5: 35-39.

Fromherz, K. 1838. *Die Jura-Formationen des Breisgaues geognostisch beschrieben*. Christian Theodor Groos, Karlsruhe.

Gerasimov, P.A. 1955. *The Mesozoic index fossils from the central region of the European part of the USSR. Volume 1. Lamellibranchiata, Gastropoda, Scaphopoda and Brachiopoda of the Jurassic beds*. Ministry for Geology & Mining of the USSR, Moscow [in Russian].

Geyer, O. 1973. Das praekretazische Mesozoikum von Kolumbien. *Geologisches Jahrbuch*, Reihe B, Heft 5: 1-156.

Goldfuss, G.A. 1826. *Petrefacta Germaniæ tam ea., quae in Museo Universitatis Regiae Borussicae Fridericiae*. Arnz & Co., Düsseldorf.

Goldfuss, G.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 Teil: 1-68, pls 72-96, (1833); 69-140, pls 97-121 (1835); 141-224, pls 122-146 (1837); 225-312, pls 147-165 (1841). Arnz & Co., Düsseldorf.

Gottsche, C. 1878. Ueber jurassische Versteinerungen aus der argentinischen Cordillera. *In*: Stelzner, A. (ed.), Beiträge zur Geologie und Paläontologie der Argentinischen Republik. II. Paläontologischer Thiel. *Palaeontographica*, Supplement 3, 2 (3): 1-51.

Greppin, F.G. 1870. Description géologique du Jura bernois et quelques districts adjacents. *Matériaux pour la carte géologique de la Suisse*, 8: 1-357.

Hall, J. & Whitfield, R.P. 1877. Paleontology, Part 2. *United States Geological Exploration of the 40th Parallel*, 4: 199-302.

Hallam, A. 1969. Faunal realms and facies in the Jurassic. *Palaeontology*, 12 (1): 1-18.

Hallam, A. 1978. Eustatic cycles in the Jurassic. *Palaeogeography, palaeoclimatology, Palaeoecology*, 23: 1-32.

Hayami, I. 1961. On the Jurassic pelecypod faunas in Japan. *Journal of the Faculty of Science, University of Tokyo*, Section 2, 13 (2): 243-343.

Hayami, I. 1975. A systematic survey of the Mesozoic Bivalvia from Japan. *University Museum, University of Tokyo, Bulletin*, 10: 1-249.

Hayasaka, I. 1943. On the Jurassic formation of the Philippines with a note on *Trigonia*. *Taiwan Tigaku Kizi*, 14 (1-2): 1-12.

Hesselbo, S.P., Ogg, J.G. & Ruhl, M. 2020. The Jurassic Period. *In*: *Geological Time Scale*: 992-1021. Elsevier B.V. https: doi.org/10.1016/B978-0-12-824360-2.00026-7.

Hyatt, A. 1892. Jura and Trias at Taylorville, California. *Bulletin of the Geological Society of America*, 3: 395-412

Imlay, R.W. 1964. Marine Jurassic pelecypods from central and southern Utah. *United States Geological Survey, Professional Paper*, 483: C1-42.

Imlay, R.W. 1980. Jurassic geology of the conterminous United States and its continental setting. *United States Geological Survey, Professional Paper*, 1062: 1-139.

Ishikawa, H., Maeda, S., Kawabe, T. & Rangel, C. 1983. Some Jurassic trigoniids from Peru. *Bulletin of the Faculty of Education, Chiba University*, 32 (2): 37-45 [in Japanese].

Jaworski, E. 1915. Beitrage zur Kenntnis des Jura in Südamerika. Teil II. Spezieller paläontologischer Teil. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band*, 40: 364-456.

Jaworski, E. 1925. *In*: Jaworski, E. & Groeber, P., *Contribución a la paleontología del Jurásico Sudamericano*. Publicación, 4: 1-168. Ministerio de Agricultura. Dirección General de Minas, Geología e Hidrología, Buenso Aires.

Kelly, S.R.A. 1984. Bivalvia of the Spilsby Sandstone and Sandringham Sands (Late Jurassic - Early Cretaceous) of eastern England. Part I. *Monographs of the Palaeontographical Society, London*, 137 (566): i-xii, 1-94.

Kelly, S.R.A. 1995. New trigonioid bivalves from the Early Jurassic to earliest Cretaceous of the Antarctic Peninsula region: systematics and austral paleobiogeography. *Journal of Paleontology*, 69 (1): 66-84.

Kent, D.V. & Irving, E. 2010. Influence of inclination error in sedimentary rocks on the Triassic and Jurassic apparent pole wander path for North America and implications for Cordilleran tectonics. *Journal of Geophysical Research*, 115: 1-25.

Kobayashi, T. 1954. Studies on the Jurassic trigonians in Japan. Part 1. Preliminary notes. *Japanese Journal of Geology and Geography*, 25 (1-2): 61-80.

Kobayashi, T. 1957. Studies on the Jurassic trigonians in Japan. Part 7. Some trigonians from the Hida Plateau region, central Japan. *Japanese Journal of Geology and Geography*, 28 (1-3): 43-46.

Kobayashi, T. & Mori, K. 1955. The Vaugoniinae from the Kitakami Mountains in north Japan. On the Jurassic trigonians in Japan. Part III. *Japanese Journal of Geology and Geography*, 26 (1-2): 73-88.

Kobayashi, T. & Tamura, M. 1959. The bearing of trigoniids on the Jurassic stratigraphy of Japan. Studies on the Jurassic trigonians in Japan. *Japanese Journal of Geology and Geography*, 30: 273-292.

Konovalov, V.P. & Miroljubov, Y.G. 1978. Some Early Cretaceous trigoniids of the Primorye territory. *In*: Ablaev, A.G., Pojarkov, B.V. & Pojarkova, Z.N. (eds.), *Biostratigraphy of the Far East (Phanerozoic)*: 85-96. Dal'nevostočnyj Geologičeskij Institut, Dal'nevostočnyj Naučnyj Centr, Akademija Nauk SSSR, Vladivostok [in Russian].

Konovalova, I.V. 1979. Peculiar representatives of the genus *Vaugonia* from the Lower Jurassic of the Razdolnaya River Basin (southern Primorye). *In*: Ablaev, A.G., Pojarkova, Z.N. & Pojarkov, B.V. (eds), *Paleontology and stratigraphy of the Far East*: 41-49. Akadmija Nauk SSSR, Dal'novostochnyj Nauchnyj Tsentr, Dal'novostochnyj Geologicheskij Institut, Vladivostok [in Russian].

Krömmelbein, K. 1956. Die ersten marinen Fossilien (Trigoniidae, Lamellibr.) aus der Cayetano-Formation West-Cubas. *Senckenbergiana Lethaea*, 37 (3/4): 331-335.

Krömmelbein, K. 1960. Los primeros fósiles marinos (Trigoniidae, Lamellibr.) procedentes de la formación Cayetano del Oeste de Cuba. *Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey"*, 25 (1): 43-47.

Kulzhinskaya-Voronets, N.S. 1936. Representatives of the genera *Trigonia* and *Inoceramus* from the Jurassic deposits of Yuzhnoussuriysk territory. *Materials on geology and minerals of Far Eastern Territory*, 67: 1-37 [in Russian].

Lambert, L.R. 1944. Algunas trigonias del Neuquen. *Revista del Museo de La Plata*, n.s, Paleontologia, 2: 357-397.

Leanza, H.A. 1985. *Maputrigonia*, un nuevo género de Trigoniidae (Bivalvia) del Berriasiano de Neuquén, Argentina. *Academia Nacional de Ciencias, Boletín*, 56 (3-4): 275-285.

Leanza, H.A. 1993. Jurassic and Cretaceous trigoniid bivalves from west-central Argentina. *Bulletin of American Paleontology*, 105: 1-95.

Leanza, H.A. & Garate, J.I. 1987. Faunas de trigonias (Bivalvia) del Jurasico y Cretacico Inferior de la Provincia del Nequen, Argentina, conservadas en el Museo Juan Olsacher de Zapala. *In*: Volkheimer, W. (ed.), *Bioestratigrafia de los sistemas regionales del Jurasico y Cretacico de America del Sur, Mendoza 1987*, 1: 201-255.

Lebküchner, R. 1932. Die Trigonien des süddeutschen Jura. *Palaeontographica*, 77: 1-120.

Lebrun, P. 2021. Des bivalves pincipalement mésozoïques: les trigonies - celles du Jurassique des France. *Fossiles*, 47: 1-36.

Loriol, P. de & Pellat, E. 1866. Monographie paléontologique et géologique de l'étage Portlandien des environs de Boulogne-sur-Mer. *Mémoire de la Société de Physique et d'Histoire naturelle de Genève*, 19 (1): 1-200.

Lycett, J. 1850. Tabular view of fossil shells from the middle division of the Inferior Oolite in Gloucestershire. *The Annals and Magazine of Natural History*, 2nd Series, 6: 401-424.

Lycett, J. 1853. On some new species of *Trigonia* from the Inferior Oolite of the Cotteswolds, with preliminary remarks upon the genus. *The Annals and Magazine of Natural History*, 2nd Series, 70: 225-339.

Lycett, J. 1863. Supplementary monograph on the Mollusca from the Stonefield Slate, Great Oolite, Forest Marble and Cornbrash. *Palaeontological Society Monograph*, 1863: 1-129.

Lycett, J. 1872-83. A monograph of the British fossil trigoniae. *Palaeontological Society Monographs*, 1-2: 1-52 (1872); 53-92 (1874); 93-148 (1875); 149-204 (1877); Addenda: 205-245 (1879); Supplement 1: 1-3 (1881); Supplement 2: 5-19 (1883).

Maeda, S. 1962. On some species of Jurassic trigoniids from the Tetori Group in central Japan. *Journal of the College of Arts and Sciences, Chiba University*, 3 (4): 515–517,

Maeda, S. 1963. Some Jurassic trigoniids from the Tetori Group in the Kuzuryu district, central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan*, n.s., 49: 1-7.

Maeda, S. & Kawabe, T. 1963. Two Jurassic trigoniid from the Tetori Group in the Arimine district, central Japan. *Journal of the College of Arts and Science, Chiba University* (Natural Science), 4 (1): 55-58.

Mansfield, G.R. 1927. Geography, geology, and mineral resources of southeastern Idaho. *United States Geological Survey, Professional Paper*, 152: 1-453.

McLearn, F.H. 1919. New species of pelecypods from the Cretaceous of northern Alberta. *Canada Department of Mines, Geological Survey, Museum Bulletin*, 29: 9-22.

Meek, F.B. 1864. Description of the Jurassic fossils. Palaeontology. 1. Carboniferous and Jurassic fossils. *Geological Survey of California*, 1864: 39-53.

Meek, F.B. & Hayden, F.V. 1860. Descriptions of new organic remains from the Tertiary, Cretaceous and Jurassic rocks of Nebraska. *Proceedings of the National Academy of Sciences, Philadelphia*, 1860: 175-185.

Meek, F.B. & Hayden, F.V. 1865. Palaeontology of the Upper Missouri: A report upon collections made principally by the expeditions under command of Lieut. G.K. Warren, U.S. Top. Engrs., in 1855 and 1856. Invertebrates. Part I. *Smithsonian Contributions to Knowledge*, 14 (172): ix+1-136.

Möricke, W. 1894. Versteinerungen des Lias und Unteroolith von Chile. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage Band*, 9: 1-100.

Morris, J. & Lycett, J. 1850-54. A monograph of the Mollusca from the Great Oolite. 1: Chiefly from Minchinhampton and the coast of Yorkshire. Part 1. Univalves. *Palaeontographical Society Monograph*, 1-148. Part 2. Supplement: Mollusca from the Stonesfield Slate, Great Oolite, Forest Marble and Cornbrash (by J. Lycett): 1-129.

Munier-Chalmas, E. 1865. Note sur quelques espèces nouvelles du genre *Trigonia*. *Bulletin de la Société Linnéenne de Normandie*, 9: 415-420.

Nikitenko, B., Shurygin, B. & Mickey, M.B. 2008. High resolution stratigraphy of the Lower Jurassic and Aalenian of Arctic regions as the basis for detailed palaeo- biogeographic reconstructions. *Norwegian Journal Geology*, 88: 267-278.

Oppel, A. 1856-1858. *Die Juraformation Englands, Frankreichs und des süd-westlichen Deutschland*: 1-438 [1856]; 439-694 [1857]; 695-857 [1858]. Stuttgart, Ebner & Seubert].

Orbigny, A.d'. 1844-1848. *Paléontologie française. Description zoologique et géologique de tous les animaux Mollusques et Rayonnés fossiles de France*. Masson, Paris.

Orbigny, A.d'. 1850. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés faisant suite au cours élémentaire de paléontologie et de géologie stratigraphique*, 2: 1-427. Masson, Paris.

Packard, E.L. 1921. The trigoniae from the Pacific coast of North America. *University of Oregon Publications*, 1 (9): 1-59.

Page, K. 2003. The Lower Jurassic of Europe: its subdivision and correlation. *Geological Survey of Denmark and Greenland Bulletin*, 1: 3-59.

Page, K. 2008. The evolution and geography of Jurassic ammonoids. *Proceedings of the Geologists Association*, 119 (1): 35-57.

Palmer, T.J. 1979. The Hampden Marly and White Limestone formations: Florida-type carbonate lagoons in the Jurassic of central England. *Palaeontology*, 22 (1): 189-228.

Parkinson, J. 1804-1811. *Organic remains of a former world. An examination of the mineralized remains of the vegetables and animals of the Antediluvian World; generally termed extraneous fossils*. 3 volumes. J. Robson, London.

Pčelincev, V.F. 1937. The Gastropoda and Pelecypoda from the Tethyan Lias and Lower Dogger in the limits of the USSR (the Crimea and Caucasus). *Paleontology of the USSR Monographs*, 48 (1): 1-85 [in Russian].

Pérez, E., Aberhan, M., Reyes, R. & Hillebrandt, A.V. 2008. Early Jurassic Bivalvia of northern Chile. Part III. Order Trigonioida. *Beringeria*, 39: 51-102.

Pérez, E., Biró-Bagoczky, L. & Reyes, R.B. 1987. Nuevos antecedentes sobre *Virgotrigonia* Alleman, 1985 - Bivalvia; Trigoniidae - y presencia de *V. hugoi* Leanza en Chile. *Revista Geológica de Chile*, 30: 35-45.

Pérez, E. & Reyes, R. 1977. Las trigonias Jurásicas de Chile y su valor cronoestratigráfico. *Instituto de Investigaciones Geológicas del Chile, Boletín*, 30: 1-58.

Pérez, E. & Reyes, R.B. 1989. Catalogo analitico de los tipos de trigoniae (Mollusca; Bivalvia) descritos por R.A. Philippi. *Boletin, Servicio Nacional de Geologia y Mineria, Chile*, 41: 5-51.

Philippi, R.A. 1899. *Los fósiles secundarios de Chile. Primera parte*. Gobierno de Chile, Santiago.

Phillips, J. 1829. *llustrations of the geology of Yorkshire; or, a description of the strata and organic remains of the Yorkshire coast: accompanied by a geological map, sections, and plates of the fossil plants and animals*. Printed for the author by T. Wilson, York.

Poulton, T.P. 1976. Some Lower Jurassic trigoniid bivalves from southwestern British Columbia. *Geological Survey of Canada Bulletin*, 256: 41-53.

Poulton, T.P. 1977. Early Cretaceous trigoniid bivalves of Manning Provincial Park, south-western British Columbia. *Geological Survey of Canada Paper*, 76-9: 1-18.

Poulton, T.P. 1979. Jurassic trigoniid bivalves from Canada and western United States of America. *Geological Survey of Canada Bulletin,* 282: 1-82.

Poulton, T.P. 1980. Trigoniid bivalves from the Bajocian (Middle Jurassic) rocks of central Oregon. *Current Research, Part A, Geological Survey of Canada, Paper*, 80-IA: 187-196.

Poulton, T.P. 1991. Hettangian through Aalenian (Jurassic) guide fossils and biostratigraphy, northern Yukon and adjacent northwest territories. *Geological Survey of Canada Bulletin*, 410: 1-95.

Poulton, T.P. & Callomon, J.H. 1977. A new species of trigoniid bivalve from the Boreal Bathonian (Jurassic) of central East Greenland. *Bulletin of the Geological Society of Denmark*, 26: 155-159.

Pugaczewska, H. 1976. Trigoniidae of the Dogger of Lęczyca (central Poland). *Acta Palaeontologica Polonica*, 21 (1): 79-96.

Pugaczewska, H. 1978. Jurassic pelecypods from Cuba. *Acta Palaeontologica Polonica*, 23 (2): 163-186.

Quenstedt, F.A. 1837. *Der Jura*. 3: vi, 1-842. H. Laupp'schen Buchhandlung, Tübingen.

Quenstedt, F.A. 1832. *Handbuch der Petrefactenkunde*. 1st ed. H. Laupp, Tübingen.

Quenstedt, F.A. 1856-1857. Der Jura. *Laupp: Tübingen.* Laupp & Siebeck, Tübingen; pp. 1-208, pl. 1-24 (July 1856), pp. 209-368, pl. 25-48, 1 Übersichtstafel des Lias (December 1856), pp. 369-576, pl. 49-72, 1 Übersichtstafel des Braunen Jura (April 1857), pp. I-vi + 577-842, pl. 73-100,

Quenstedt, F.A. 1867. *Handbuch der Petrefactenkunde*. 3rd ed. H. Laupp, Tübingen.

Quilty, P.G. 1978. Late Jurassic bivalves from Ellsworth Land, Antarctica: their systematics and palaeogeographic implications. *New Zealand Journal of Geology and Geophysics*, 20 (6) (dated 1977): 1033-1080.

Raine, J.I., Beu, A.G., Boyes, A.F., Campbell, H.J., Cooper, R.A., Crampton, J.S., Crundwell, M.P., Hollis, C.J. & Morgans, H.E.G. 2015. Revised calibration of the New Zealand Geological Timescale. *GNS Science Report*, 2012/39: 1-53.

Redlich, K.A. 1894. Der Jura der Umgebung von Alt-Achtla. Ein Beitrage zur Kenntnis der Jura zur Kaukasus-Länder. *Beiträge zur Paläontologie und Geologie Österreich- Ungarns und des Orients*, 9: 55-81.

Reuss, A.E. 1845-1846. *Die Versteinerungen der böhmischen Kreideformation, mit Abbildungen der neuen oder weniger bekannten Arten. Erste Abtheilung*, pp. I-IV, 1-58, pls. 1-13 [1845], Zweite Abtheilung, I. Hälfte, pp. 1-64, pls. 14-26; II. Hälfte, pp. I-IV, 65-148, pls. 27-51 [1846]. E. Schweizerbart'sche Verlagsbuchhandlung und Druckerei, Stuttgart.

Reyes, R.B. & Pérez, E.d'A. 1978. Las trigonias del Tithoniano y Cretácico Inferior de la Cuenca Andina de Chile y su valor cronoestratigráfico. *Instituto de Investigaciones Geologicas de Chile, Boletin*, 32: 1-105.

Reyes, R.B. & Pérez, E.d'A. 1979. Estado actual del conocimiento de la Familia Trigoniidae (Mollusca Bivalva) en Chile. *Revista Geologica Chile*, 8: 13-64.

Reyes, R.B. & Pérez, E.d'A. 1984. Dos nuevos especies del genero *Vaugonia* Crickmay, 1930 (Bivalvia Trigoniidae) del Bathoniano Superior (?) - Caloviano Inferior, norte de Chile. *Revista Geologica Chile*, 22: 35-47.

Riche, A. 1904. Étude stratigraphique et paléontologique sur la Zone a *Lioceras concavum* du Mont-d'Or Lyonnais. *Annales de l'Université de Lyon*, n.s. (Sciences, Médecine), 14: 1-221.

Roemer, F.A. 1839. *Die Versteinerungen des norddeutschen Oolithen-Gebirges. Ein Nachtrag*. Hahn, Hannover.

Rosenkrantz, A. 1934. The Lower Jurassic rocks of east Greenland, Part I. *Meddelelser om Grønland*, 110 (1): 1-122.

Rosenkrantz, A. 1942. The Lower Jurassic rocks of east Greenland, Part II: The Mesozoic sediments of the Kap Hope area, southern Liverpool Land. *Meddelelser om Grønland*, 110 (2): 1-56.

Rouillier, C. & Vossinsky, A. 1849. Études progressives sur la paléontologie de Moscou. Quatrième étude. Cinquième étude. *Bulletin de Ia Société Impériale des Naturalistes de Moscou*, 22 (1-2): 337-355, 356-399.

Sadki D. & Dietze V. 2021. New information on the Early Bajocian types of sonniniids and hammatoceratids (Ammonitina) described by W. Waagen (1867) from Gingen/Fils (SW Germany). *Boletín del Instituto de Fisiografía y Geología*, 91: 1-16.

Sanborn, A.F. 1960. Geology and paleontology of the southwest quarter of the Big Bend quadrangle, Shasta county, California. *California Division of Mines, Special Report*, 63: 18-26.

Savel'ev, A.A. 1960a. *Jurassic Trigoniidae of Mangyshlak and western Turkmenistan*. Gostoptekhizdat (Trudy VNIGRI; Vyp. 148), Leningrad [in Russian].

Savel'ev, A.A. 1960b. On some Upper Jurassic trigoniids from the eastern slope of the subpolar Urals. *Trudy VNIGRI*, Paleontological collection, 2: 196-205 [in Russian].

Schlippe, A.O. 1888. Die Fauna des Bathonien im Oberrheinischen Tieflande. *Abhandlungen zur geologischen Spezialkarte von Elsass-Lothringen*, 4 (4): 1-264.

Schmidt, M. 1905. Über Oberen Jura in Pommern. Beiträge zur Stratigraphie und Paläontologie. *Abhandlungen der preußischen geologischen Landesanstalt*, n.f., 41: 1-222.

Schmidtill, E. 1925. Zur Stratigraphie und Faunenkunde des Doggersandsteins im nördlichen Frankenjura. *Palaeontographica*, 67: 1-82.

Schneider, N. 1927. Étude stratigraphique et paléontologique de l'Aalénien de Gundershoffen (Bas-Rhin). *Mémoires du Service de la carte géologique d'Alsace et de Lorraine*, 3: 1-132.

Schneider, S. 2009. *A multidisciplinary study of Late Jurassic bivalves from a semi-enclosed basin - Examples of adaptation and speciation and their stratigraphic and taphonomic background (Lusitanian Basin, central Portugal)*. Dr. rer. nat. dissertation, Fakultät für Geowissen-schaften der Ludwig-Maximilians-Universität, München.

Seebach, K. von. 1864. *Der Hannoversche Jura*. Hertz, Berlin.

Sharpe, D. 1850. On the secondary district of Portugal which lies on the north of the Tagus. *Quarterly Journal of the Geological Society of London*, 6: 135-201.

Shikama, T. 1943. *A handbook of illustrated fossils from Japanese and their adjacent territories*. Nippon Koubutu Syumi-no-kai, Kyoto [in Japanese].

Shikama, T. 1952. *A handbook of illustrated fossils from Japanese and their adjacent territories*. Nippon Koubutu Syumi-no-kai, Kyoto [in Japanese].

Shurygin, B.N., Nikitenko, B.L., Meledina, S.V., Dzyuba, O.S. & Knyazev, V.G. 2011. Comprehensive zonal subdivisions of Siberian Jurassic and their significance for circum-Arctic correlations. *Геология и геофизика,* 52 (8): 1051-1074 [in Russian].

Sibiriakova, L.V. 1961. A Middle Jurassic mollusc fauna from the Great Balkans and their stratigraphic significance. *The problems of oil and gas content in Central Asia*, 5: 1-171 [in Russian].

Slosser, M. 1901. Die Fauna des Lias und Dogger in Franken und der Oberpfalz. *Zeitschrift der Deutschen geologischen Gesellschaft*, 53 (4): 513-569.

Sowerby, J. de C. 1826-1835. *The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the Earth*. 6: 1-86, pls 504-545 (1826); 87-156, pls 546-580 (1827); 157-200, pls 581-597 (1828); 201-230, pls 598-609; 231-235 (1829); systematical index (1835)]. J. de C. Sowerby, London.

Stanley, S.M. 1977. Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves. *Palaeontology*, 20 (4): 869-899.

Strand, E. (1928, dated 1926): Miscellanea nomenclatoria zoologica et palaeontologica. I-II. *Archiv für Naturgeschichte,* 92A (8): 30-75.

Takahashi, H. 1969. Stratigraphy and ammonite fauna of the Jurassic System of the southern Kitakami massif, northeast Honshu, Japan. *Science Report of the Tohoku University*, (2nd Series, Geology), 41 (1): 1-93.

Tamura, M. 1959. On *Kumatrigonia*, a new subgenus of *Frenguelliella*, and a *Tosapecten* from the Carniac Tanoura Formation in Kyushu, Japan. *Memoir of the Faculty of Education, Kumamoto University*, 7: 212-224.

Tamura, M. 1975. Mesozoic molluscan fossils of Japan, 1 (Early and Middle Jurassic trigonioid bivalves). *Atlas of Japanese fossils*, no. 42-251: 1-4, pl. J-11. Tsukiji Shokan Publishing Co. Ltd, Tokyo [in Japanese].

Terquem, O. & Jourdy, E. 1869. Monographie de l'étage Bathonien dans le département de la Moselle. *Mémoires de la Société géologique de France*, (2) 9: 1-175.

Thevenin, A. 1913. Types du prodrome de paléontologie stratigraphique universalle de d'Orbigny. Tome 1. *Annales de paléontologie*, 8 (2): 73-104.

Tornquist, A. 1898. Der Dogger am Espinazito-Pass, nebst einer Zusammenstellung der jetzigen Kenntnisse von der argentinischen Juraformation. *Paläontologische Abhandlungen*, N.F., 4: 135-204.

Torre, A. de la. 1960. Fauna de la formation Cayetano del Jurasico Medio de Pinar del Rio. *Memorias de la Sociedad Cubana de Historia Natural*, 25 (1): 65-72.

Trechmann, C.T. 1923. The Jurassic rocks of New Zealand. *Quarterly Journal of the Geological Society of London*, 79: 246-312.

Valenzuela, R.C. 1975. *Trigonias*. Laboratoria de Paleontologia, Instituto de Investigaciones Geologicas, Santiago.

Veatch, A.C. 1907. Geography and geology of a portion of southwestern Wyoming. *United States Geological Survey, Professional Paper*, 56: 1-178.

Vörös, A. & Escarguel, G. 2019. Brachiopod palaeobiogeography in the western Tethys during the Early Jurassic diversity maximum: Introduction of a Pontic Province. *Lethaia*, 53 (1): 72-90.

Waagen, W.H. 1867. Über die Zone des *Ammonites sowerby*i. *Geognostisch-paläontologische Beiträge*, 1 (3): 507-688.

Walker**, K.G. 1972.** The stratigraphy and bivalve fauna of the Kellaways Beds (Callovian) around South Cave and South Newbald, East Yorkshire. *Proceedings of the Yorkshire Geological Society***,** 39: 107-138.

Welhofner, P. 1964. Zur Pelecypodenfauna der Neuburger Bankkalke (Mittel-Tithon). *Bayerische Akademie der Wissenschaften Mathematisch-Naturwissenschftliche Klasse Abhandlungen*, n.f., 119: 1-143.

White, C.A. 1880. Contributions to invertebrate paleontology, Nos. 2-8. *In*: Hayden, F.V., A report of progress of the exploration in Wyoming and Idaho for the year 1879. Part 1. *United States Geological Survey of the Territories*, 12 (1): 5-171.

Whitfield, R.P. & Hovey, E.O. 1906. Remarks on and descriptions of Jurassic fossils of the Black Hills. *Bulletin of the American Museum of Natural History*, 22 (23): 389-402.

Wright, T. 1860. On the subdivisions of the Inferior Oolite in the south of England, compared with the equivalent beds of that formation on the Yorkshire coast. *Quarterly Journal of the Geological Society of London*, 16 (for 1859): 1-48.

Yokoyama, M. 1904. On some Jurassic fossils from Rikuzen. *Journal of the College of Science, Tokyo Imperial University*, 18 (6): 1-17.

Young, G. & Bird, J. 1828. *A geological survey of the Yorkshire coast: describing the strata and fossils occurring between the Humber and the Tees, from the German Ocean to the plain of York*. 2nd edition. Clark, Whitby.

Yungerman, A.E. **1962.** On a new species of trigoniid from the Kimmeridgian deposits of north-eastern Ukraine. *Kharkov State University named after M. Gorky*, 15: 106-111 [in Russian].

Zhang, Z.-M., Lu, Y.-J. & Wen, S.-X. 1979. Lamellibranchiata. *In*: Chinese Academy of Sciences (ed.), *Paleontological atlas of northwest China*. Part 1: 225-314. Geological Publishing House, Beijing [in Chinese].

Zieten, C.H. von 1830-1833. *Die Versteinerungen Württembergs, oder naturgetreue Abbildungen der in den vollständigsten Sammlungen, namentlich der in dem Kabinett des Oberamts-Arzt Dr. Hartmann befindlichen Petrefacten, mit Angabe der Gebirgs-Formationen, in welchen dieselben vorkommen und der Fundorte*. Erstes Heft, I-VIII, 1-8 [1830]; Zweites Heft, I-II, 9-16 [1830]; Drittes Heft, I-II, 17-24 [1831]; Viertes Heft, I-II, 25-32 [1831]; Fünftes Heft, I-II, 33-40 [1832]; Sechstes Heft, I-II, 41-48 [1832]; Siebtes Heft, I-II, 49-56 [1832]; Achtes Heft, I-II, 57-64 [1832]; Neuntes Heft, I-II, 65-72 [1833]; Zehntes Heft, I-II, 73-80 [1833]; Elftes Heft, I-II, 81-88 [1833]; Zwölftes Heft, I-II, 89-102 [1833]. Verlag & Lithographie der Expedition des Werkes Unsere Zeit, Stuttgart.

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