


Bivalves from the Changhsingian (upper Permian) Bellerophon Formation of the Dolomites (Italy): ancestors of Lower Triassic post-extinction benthic communities

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Typescript received 25 April 2022; accepted in revised form 24 November 2022

Abstract: Diverse shallow marine fossil assemblages from the Changhsingian Bellerophon Formation (Dolomites) record late Palaeozoic marine life immediately before the end-Permian mass extinction. We classified c. 6500 bivalves from western Dolomites localities, identifying 26 species including one new family (Ladinomyidae), three new genera (*Ladinomya*, *Lovarulucina*, *Gardenapecten*) and 10 new species: *Acharax frenademezi*, *Bakevellia* (*Bakevellia*) *preroman-gica*, *Edmondia hautmanni*, *Etheripecten stuflesseri*, *Ladinomya fosteri*, *Lovarulucina covid*, *Palaeolima badiotica*, *Promytilus merlai*, *Tambanella?* *stetteneckensis* and *Volsellina carinata*. The occurrence of three *Eumorphotis* species with different stratigraphic distributions, leads us to propose an upper Permian ‘Lower *Eumorphotis* Zone’, divided into *E. praecurrens*, *E. striatocostata* and *E. lorigae* subzones, and distinct from the existing Lower Triassic *Eumorphotis* Zone (here renamed ‘Upper *Eumorphotis* Zone’). Palaeoecological analysis produced six biofacies and four ecofacies, based on richness, dominance and ecological lifestyle. The bivalves

inhabited lagoonal to nearshore environments affected by stressed conditions: high temperatures, high salinity, shallow water depths, low oxygen and high terrigenous input. The upper Bellerophon Fm is characterized by increasingly fully marine conditions, although eurytopic taxa still suggest stressed conditions. Bivalve richness of the upper Permian Bellerophon and Lower Triassic Werfen formations was compared to estimate the genus-level extinction rate. The disappearance of almost half (47%) of Bellerophon Fm genera is remarkably low compared with other, coeval bivalve faunas. Pre-extinction bivalve faunas were dominated by stress-adapted taxa (*Unionites*, *Eumorphotis*, *Bakevellia*, *Towapteria*) able to thrive in extreme environmental conditions, survive the end-Permian mass extinction, and become the dominant biotic component of Lower Triassic benthic communities globally.

Key words: Bivalvia, biostratigraphy, palaeoecology, end-Permian mass extinction, Dolomites, disaster taxa.

THE upper Permian Bellerophon Formation (Fm) of the Dolomites (Southern Alps, Italy) records the biodiversity of marginal and shallow-water marine ecosystems immediately before the end-Permian mass extinction. This formation is fossiliferous and characterized by abundant and bivalve-rich assemblages. During the Palaeozoic, bivalve-dominated marine benthic assemblages thrived in stressed and nearshore marine environments while brachiopod-rich assemblages populated more open marine settings (Clapham & Bottjer 2007). The worldwide ecological perturbations triggered by the Siberian Traps Large Igneous Province promoted the spread of bivalve-dominated communities, mainly composed of strongly eurytopic taxa such as *Claraia*, *Unionites*, *Promyalina* and *Eumorphotis* (Wignall & Hallam 1992). A taxonomical, biostratigraphical and palaeoecological analysis of the bivalve

assemblages occurring in a marginal marine setting can contribute to the understanding of the evolutionary processes and adaptive strategies that enabled the bivalves to occupy the ecological niches of the rhynchonelliformean brachiopods and become a dominant component of the modern marine benthic communities (Vermeij 1977, 1987; Gould & Calloway 1980). Despite the numerous palaeontological studies on the Bellerophon Fm (for an extensive review and citations see Posenato 2019), knowledge of the bivalves is mostly based on papers published in the 19th and early 20th centuries. In the early and most important palaeontological monograph on the molluscs and brachiopods of the Bellerophon Fm, Stache (1878) described c. 30 bivalve species, from material mostly collected in the western Dolomites (Badia and Gardena valleys). After minor contributions of

Gortani (1906) and Ogilvie Gordon (1927), the second and last comprehensive systematic monograph was published by Merla (1930), who described 33 bivalve species on material previously collected by Caneva (1906) mostly in the eastern Dolomites (Cadore and Comelico). In all of these systematic papers 41 bivalve genera and 78 species were described, but the species were based on poorly preserved and incomplete specimens, often lacking the internal characters, such as hinge dentition and muscle impressions, and general information on the stratigraphic setting.

Following extensive field work, which has lasted more than a dozen years, on the Bellerophon Fm of the western Dolomites (Adige, Badia and Gardena valleys), 6515 bivalve specimens have been collected and identified, more than in any historical collection. The systematic identification of these specimens has been supported by the examination of type material published by the previous authors and kept in various European museums. The precise stratigraphic setting of the newly collected material has permitted us to evaluate both their biostratigraphic and environmental distribution. The comparison of the bivalve biodiversity of the Bellerophon Fm (upper Permian) and lower Werfen Fm (Lower Triassic) is discussed to evaluate the bivalve extinction rate during the end-Permian mass extinction.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The upper Permian sedimentary succession of the eastern Southern Alps consists of the Gröden/Val Gardena Sandstone, Bellerophon Fm and lowermost Werfen Fm. The Gröden/Val Gardena Sandstone (Grödner Sandstein/Arenarie di Val Gardena) is characterized by continental redbeds, which are laterally and vertically interdigitated with the Bellerophon Fm (Wuchiapingian–Changhsingian). This unit records an overall marine transgression phase interrupted by short regressive events. The marine ingression moved from east to west and reached the Adige Valley at the end of the Permian (Fig. 1). The Bellerophon Fm consists of sulphate evaporites, marly dolostones, marlstones and neritic limestones, which record sedimentary environments ranging from a coastal sabkha to a shallow shelf marine setting. The lowermost Werfen Fm (uppermost Permian) is represented by oolitic limestones, marlstones, carbonate mudstones and microbialites (e.g. Massari & Neri 1997; Neri 2007). The thickness of the Bellerophon Fm ranges from zero in the westernmost area (Adige Valley) to 500 m in the depocentre area (Comelico and Cadore) (Assereto *et al.* 1973; Massari *et al.* 1994). Massari *et al.* (1994) and Massari & Neri (1997) divided the Lopingian succession of the Dolomites into six third-order

depositional sequences. Posenato (2010) indicated the first five sequences with the prefix ‘Lo’ for Lopingian and the sixth with ‘In1’ for Induan.

Sequence Lo3

The stratigraphically oldest bivalves have been found in the lower part of sequence Lo3, which in the western Dolomites is mainly characterized by sulphate evaporites and marly dolostones with typical sabkha cycles (Bosellini & Hardie 1973), also known as Fiammazza Facies (Accordi 1956) or Rio Barbide Member (Farabegoli & Tonidandel 2012). At the Balest section, where the Lo3 sequence is complete, the Fiammazza Facies is *c.* 160 m thick. These sabkha cycles were deposited in a highly stressed environment of a hypersaline restricted lagoon (Bosellini & Hardie 1973). At *c.* 70 m from the base of the Fiammazza Facies, a subtidal dolomitic bed (Ff1) contains abundant *Bakevella* specimens. The upper part of the sequence Lo3 is characterized by 2–5-m-thick marly dolostones with a species-rich mollusc fauna containing nautiloids (Prinot & Posenato 2007) and bivalves. Broglio Loriga *et al.* (1988) named this horizon the ‘Nautiloid and Bivalve Assemblage’ and Posenato & Prinot (2004) and Prinot & Posenato (2007), the ‘Nautiloid Horizon A’ (Fig. 2). This fossiliferous interval represents the maximum flooding surface of the Lo3 sequence. It was tentatively referred to the early Changhsingian (Posenato 2010). The regressive tract of Lo3 sequence is represented by the ‘Val Gardena Sandstone Tongue’ (Broglio Loriga *et al.* 1988; Posenato *et al.* 2014; Posenato 2016) or ‘Rio Bavaro Member’ (Farabegoli *et al.* 2007). In the Balest section this unit is *c.* 15 m thick and consists of green to yellowish sandstones.

Sequence Lo4

The following Lo4 and Lo5 sequences correspond to the Casera Razzo Member of Farabegoli *et al.* (1986) and to the Badiota Facies of Accordi (1956), respectively. These sequences yield the algal assemblage and the ostracod assemblage of Broglio Loriga *et al.* (1988).

Of the studied sections, the whole Lo4 sequence crops out only in the Balest succession where it reaches a thickness of *c.* 60 m. The lower part of the sequence consists of sandy and marly dolostones, which are interbedded with sandstones and dolomitic sandy marlstones. The first appearance of black bioclastic limestone (with calcareous algae and dolostone alternations) occurs at *c.* 50 m from the base. These alternations have been interpreted as subtidal–peritidal shallowing upwards cycles deposited on a homoclinal ramp gently dipping to the

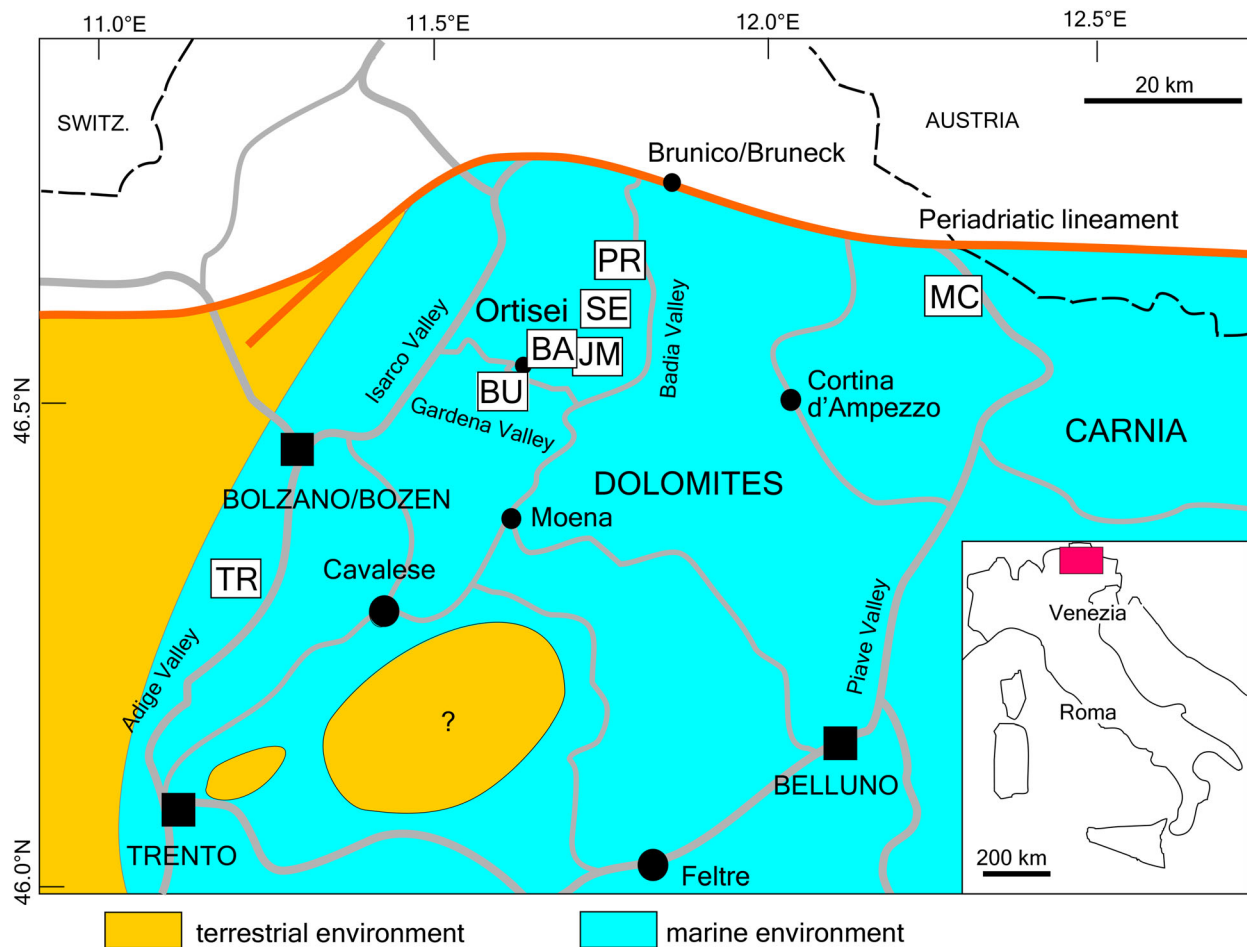


FIG. 1. Palaeogeographical setting of the investigated stratigraphic successions. *Abbreviations:* BA, Balest; BU, Bulla II; JM, Jmueia da Insom; MC, Monte Croce di Comelico/Kreuzberg; PR, Preroman; SE, Seres; TR, Termeno/Tramin. Palaeogeography at the Bulla Mb time sequence In1 (modified from Posenato (2019); emerged land in ochre, marine environment in light blue).

east (Massari *et al.* 1994). At *c.* 10 m above the base, a yellowish dolostone layer (BA231) contains a species-rich bivalve fauna.

Approximately 5 m below the top of Lo4, a 2-m-thick group of beds composed of dark sandy limestone and yellowish sandy limestone yields a species-rich mollusc fauna with abundant bellerophonitids and bivalves. Nautiloids and brachiopods are also present (Posenato & Prinoth 2004; Prinoth & Posenato 2007). This fossiliferous unit, named Nautiloid Horizon B and containing the richest bivalve fauna of the whole Bellerophon Fm, has been interpreted as the maximum flooding surface of the sequence Lo4 (Posenato 2010). This fossiliferous horizon also occurs at the Jmueia da Insom (Gardena Valley) (beds JM27–30) and Preroman (Badia Valley) sections (beds PR59–PR61). The Nautiloid Horizon B is considered late Changhsingian in age (Farabegoli *et al.* 2007; Posenato 2010, 2019).

Sequence Lo5

At the Bulla II, Balest and Jmueia da Insom sections, sequence Lo5 is *c.* 35 m thick and consists of subtidal black limestone and intra-supratidal vuggy dolostone alternations. In all of the studied sections, at *c.* 10–15 m above the Lo5 base, there is a *c.* 1-m-thick group of thin limestone beds intercalated with grey marls and marly siltstone (BA599–601, JM187–195, SE 48–56, PR140–152) with abundant bivalves.

A very fossiliferous bivalve bed, here indicated as the Gardena Valley Bivalve Bed (GVBB), occurs in the whole Gardena Valley, cropping out in the Bulla II (BU 112), Balest (BA634) and Jmueia da Insom (JM222) sections. The shell accumulation is contained in a black limestone bed, *c.* 40 cm thick. The fossil assemblage contains bivalves, rare bellerophonitids and nautiloids. This fossiliferous bed is followed by cherty limestone with thin black chert lenses.

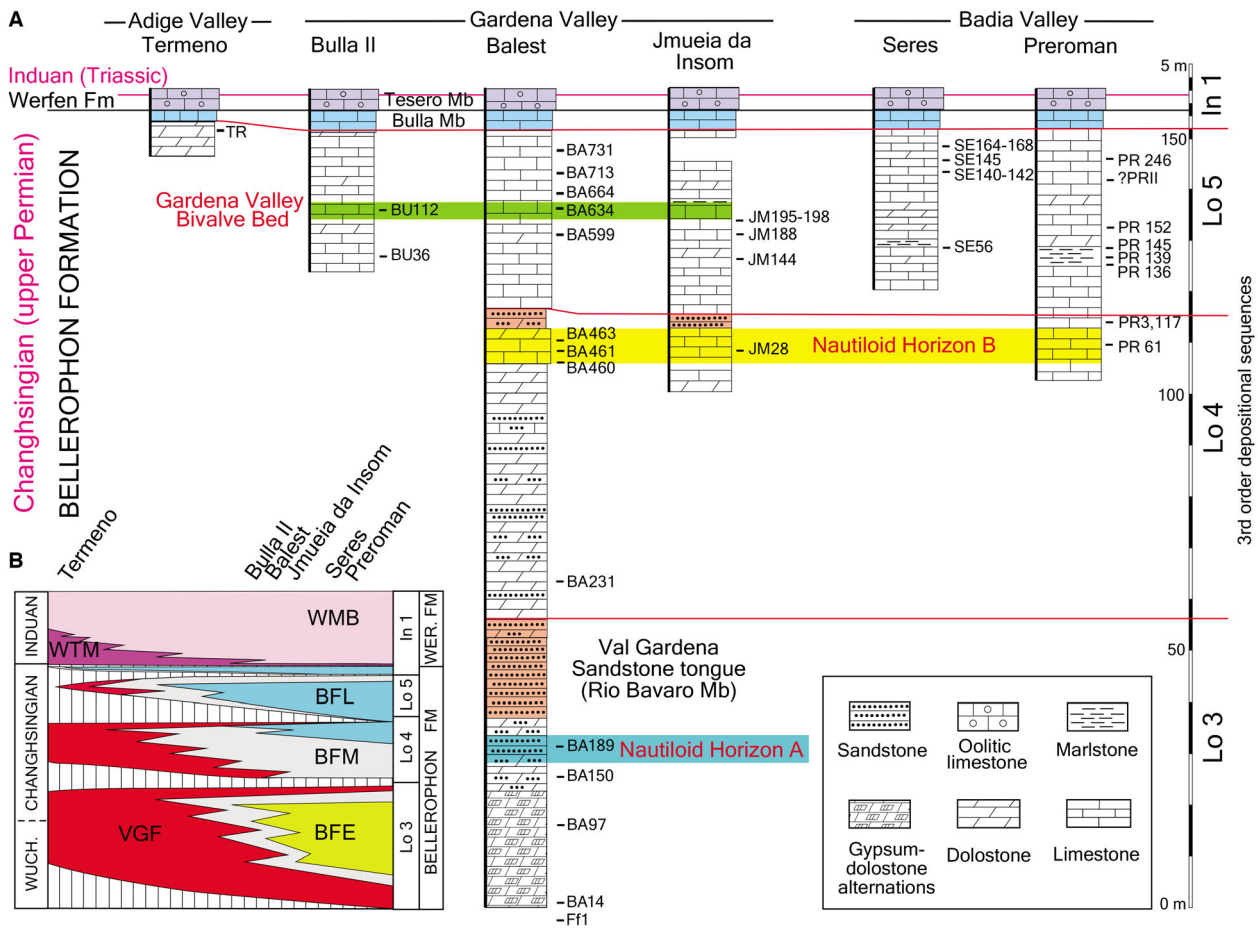


FIG. 2. A, stratigraphic logs of studied key-sections of the western Dolomites and bivalve-bearing beds. B, sequence stratigraphic framework of the studied successions (modified from Posenato 2019). *Abbreviations:* BFE, Bellerophon Fm evaporites; BFM, Bellerophon Fm marlstone and marly dolostone; BFL, Bellerophon Fm limestone; VGF, Gröden/Val Gardena Formation; WMB, Werfen Fm, Mazzin Mb; WTM, Werfen Fm, Tesero Mb; WUCH, Wuchiapingian.

The upper part of this sequence consists of *c.* 15-m-thick limestone and dolostone alternations. It crops out in the Bulla II and Seres sections, but is covered by debris in the Jmueia da Insom and the Preroman sections. The uppermost regressive part of Lo5 is mostly composed of dolostones and marlstones. It contains benthic communities of a salinity-stressed marine environment with ostracods, bivalves and foraminifera (Ostracod Assemblage or Ostracod unit of Broglio Loriga *et al.* 1988 and Farabegoli *et al.* 2007). The upper Changhsingian ammonoid *Paratirolites* sp. discovered in the debris from the Jmueia da Insom probably came from the Ostracod unit (Posenato & Prinoth 1999).

In the San Giacomo/St Jakob section (*c.* 260 m south of Balest above the San Giacomo/St Jakob Church), a small outcrop of marlstone contains a species-rich bivalve fauna. It is located at *c.* 7 m below the top of Lo5 and correlates with bed BA713 of the Balest, bed BU204 of the Bulla II (located 6.8 m below the Bulla Mb) and bed

SE178 of the Seres sections. In the Balest section, at *c.* 3 m below the top of the sequence, another rich bivalve horizon (BA731) occurs. In the Balest (BA750) and Jmueia da Insom (JM258) sections, in the marls immediately below the sequence top, few bivalve species have been collected. In the Termeno/Tramin (TR) section, situated near the shoreline, the uppermost part of the Ostracod unit is represented by yellowish dolomites that contain bivalve shells in the uppermost 20 cm (Bernardi *et al.* 2018). This bivalve bed can be correlated with the Balest beds BA748–750 or Jmueia da Insom bed JM258.

Sequence In1

The In1 sequence contains the Bulla Member of the Bellerophon Fm and the Tesero, Mazzin and Andraz members of the Werfen Fm. The Bulla Member, *c.* 1.5 m thick in the Bulla section, is composed of black bioclastic

limestones with intercalations of thin black marls. This member, latest Changhsingian in age (*H. praeparvus* Zone), is mainly characterized by the occurrence of large brachiopods of the genus *Comelicania* while bivalves are very rare. The Permian–Triassic boundary in the Bulla section is located in the lower Tesero Mb at c. 130 cm from the base of the Werfen Fm, which records the peak of the end-Permian mass extinction (e.g. Farabegoli *et al.* 2007; Posenato 2019).

MATERIAL AND METHOD

The bivalves described here have been collected during the fieldwork connected with the PhD thesis of Herwig Prinoth from 2009 to 2012 under the supervision of Renato Posenato (Prinoth 2012) and as part of a research project of the Azienda Musei Provinciali-Betrieb Landesmuseen, from 2017 to 2021. The fossils from Termeno were collected as part of a research project in the Tyrol – South Tyrol – Trentino Euroregion. All of the sections have been logged in detail with respect to lithological and sedimentological features. The specimens were collected bed by bed until no additional new taxon was found or the outcrop accessibility limited further sampling. Some beds were sampled repeatedly until well-preserved specimens of some taxa were obtained. Standard mechanical preparation techniques were applied to extract the fossils. In total, 2360 fossil-bearing samples with 6515 specimens were collected. The bivalves preserved as internal and external moulds have been reproduced with plaster casts using VPS Hydro Putty impression material. Almost all of the figured specimens have been whitened with magnesium oxide with few exceptions. Most specimens belonging to the historical collections of Stache (1878) and Merla (1930) have been reproduced with plaster moulds from which the positive replica were obtained. All of the specimens are stored at the Museum Ladin Ciastel de Tor (MLCS).

The following historical collections stored in Italian, Austrian and German museums were visited: (1) Stache (1877, 1878), deposited at the Museum of the Austrian Geological Service ‘Geologische Bundesanstalt Wien’ in Vienna (MGBW); (2) Caneva (1906), studied by Merla (1930), deposited at the Museum of the Department of Geosciences of the University of Padua; and (3) Gortani (1906), only a part of which was discovered at the Geological Museum Giovanni Capellini of the University of Bologna.

The studied specimens have been collected from six stratigraphic sections of the Bellerophon Fm from Alto Adige/Südtirol (western Dolomites). The sections are located along a transect, c. 60 km long, from the landwards Termeno/Tramin section (46°20′35.39″ N/11°14′4.48″ E) in the Adige Valley (Bernardi *et al.* 2018) to the seawards

Preroman section near San Martino/St Martin in Thurn (Badia Valley) (Figs 1, 2).

The Termeno/Tramin section (Bernardi *et al.* 2018), measured here only in the uppermost bivalve-bearing part (3.6 m), is located c. 40 km from the Bulla II section (46°34′11.06″N/11°38′7.22″E), which occurs 500 m east of the well-known Bulla road section (e.g. Farabegoli *et al.* 2007; Brandner *et al.* 2009; Posenato 2019), where the Bellerophon Fm is better exposed and can be examined for a thickness of c. 30 m. The Balest section (46°34′38.98″N/11°41′52.34″E) near Ortisei/St Ulrich, previously described by Ogilvie Gordon (1927), was measured for c. 160 m. The Jmueia da Insom section (Gardena Valley) (46°34′30.73″N/11°43′33.92″E), situated on the southern slope of the Pic Mountain (San Cristina/St Christina), has a thickness of c. 55 m but its upper part is covered by the debris. The GVBB also occurs in some smaller outcrops in Gardena Valley: Culatsch, a hill located on the opposite side of the Bulla gorge to Bulla/Pufels (46°33′41.76″N, 11°38′54.4″E), Ruf da Piz, a streamlet that flows from the Alpe di Siusi/Seiser Alm to Gardena Valley (46°33′40.55″N, 11°40′50.51″E), San Giacomo/St Jacob (46°34′26.60″N, 11°41′43.88″E) and probably Plan near Selva/Wolkenstein.

The Seres (Mischi) section (Badia Valley) (46°38′24.02″N/11°50′36.34″E) (Farabegoli & Perri 2012; Farabegoli & Tonidandel 2012), is known under different names. Bosellini (1964) named it Mischi section, Cirilli *et al.* (1998), the Val Seres section, Sephton *et al.* (2002) and Koeberl *et al.* (2004), the Val Badia section and Kraus *et al.* (2013), the Mischi (Seres) section. It was measured for 37 m. It is situated c. 5.7 km from the Preroman section near San Martino/St Martin in Thurn (46°40′23.34″N/11°54′3.97″E), which was measured for c. 55 m.

Palaeoecological analysis

For each assemblage, alpha diversity was measured using taxonomic richness (*S*) and the Simpson index of diversity (1–*D*). Diversity metrics are not independent of abundance, given that *S* provides information on the rare tail of the taxon abundance distribution (i.e. a rare taxon and an abundant taxon have an equal weighting on *S*) and Simpson’s *D* reflects the abundant end of the distribution (i.e. abundant taxa have a bigger impact on *D* than rare taxa). These were used simultaneously to understand how abundance contributes to changes in alpha diversity in a broad sense. Species richness and Simpson’s diversity were calculated in PAST (Hammer *et al.* 2001).

The palaeoecological analysis was limited to bivalves and abundance data and was calculated using the estimates of the minimum number of individuals (MNI) (Prinoth & Posenato 2023, appendix S1, S2), following

Patzkowsky & Holland (2012): where a complete, articulated specimen represents a single individual and two opposing disarticulated valves were counted as one individual. The MNI dataset was then standardized by calculating the relative abundances and log-transforming them to deemphasize the influence of the most dominant species. The cluster analysis using an unweighted pair-group average cluster model (Clarke & Warwick 2001) and the similarity profile test (SIMPROF), was applied to recognize those species that tend to co-occur in samples and to group together samples of similar composition using the Bray–Curtis similarity matrix. Here, 999 permutations were applied to calculate a mean similarity profile, with a significance level of 0.05. The resulting clusters of samples were analysed with a similarity percentages routine (SIMPER) to determine which species were responsible for the greatest similarity within groups (Clarke 1993). This method enabled the identification of groups of samples that contain a similar suite of species in similar proportions (i.e. ‘biofacies’ *sensu* Ludvigsen *et al.* 1986). The matrix shade plots were generated using a two-way cluster analysis, using the above-described method to recognize biofacies and the unweighted pair-group average cluster model to recognise relationships between different species. The same protocol was applied to samples based on their functional composition. Cluster analyses and shade plots were generated using the software PRIMER 7 (Clarke & Gorley 2015).

Abbreviations & terminology. α , angle between dorsal margin and umbonal ridge; β , angle that delimits the shell body; Fm, formation; GVBB, Gardena Valley Bivalve Bed; H, shell height; L, shell length, LV, left valve; NH A, Nautiloid Horizon A; NH B, Nautiloid Horizon B; max. L, maximum shell length; Mb, member; RV, right valve.

Localities: BA, Balest; BU, Bulla II; CU, Culatsch; JM, Jmueia da Insom; MC, Monte Croce di Comelico/Kreuzberg; PL, Plan; PR, Preroman; RP, Ruf da Piz; SE, Seres; TR, Termeno/Tramin.

Institutions: GBA, MGBW, Geological Survey of Austria (Geologische Bundesanstalt Wien); MLCS, Museum Ladin Ćiastel de Tor, Italy; NHMW, Natural History Museum Vienna, Austria.

The ligament demipad in *Acharax* is used as defined by Bailey (2011, p. 18). The terms ‘retrorescent’, ‘infracrescent’ and ‘prorescent’ are used according to Newell & Boyd (1995).

In synonymy lists, ‘v’ indicates that the cited specimens have been examined, and ‘v*’, that the nomenclatural types of species have been seen.

SYSTEMATIC PALAEOLOGY

We used the systematic classification proposed by Carter *et al.* (2011), following Hautmann (2008) for *Stutchburia*, and Geyer *et al.* (2005) for *Unionites*. For measurements of all

figured specimens see Prinoth & Posenato (2023, appendix S3). We followed Aberhan *et al.* (2004), Hofmann *et al.* (2013a, 2015) and Stanley (1972) for the palaeoecological attribution. The taxa in the new taxonomic categories from the Bellerophon Fm are assumed to have adopted a lifestyle similar to related genera and species.

Phylum MOLLUSCA Linnaeus, 1758

Class BIVALVIA Linnaeus, 1758

Subclass PROTOBRANCHIA Pelseneer, 1889

Order SOLEMYOIDA Dall, 1889

Family SOLEMYIDAE Gray, 1840

Genus ACHARAX Dall, 1908

Type species. *Solemya johnsoni* Dall, 1891.

Remarks. The specimens discussed here from the Bellerophon Fm have a shell shape and internal characters of the family Solemyidae. They are characterized by external nymphs that supported an external parivincular convex-upward primary ligament, and well-developed external radial ornamentation. According to Cox’s (1969) classification, these specimens have similarities to *Solemya* (*Solemya*), *Solemya* (*Janeia*) and *Acharax*. Pojeta (1988) proposed to avoid the name *Solemya* (*Janeia*) because valid systematic criteria are lacking, while Bailey (2021) referred the species previously attributed to this subgenus mostly to *Acharax*. The main difference between *Solemya* (*Solemya*) and *Acharax* is the ligament position, internal and attached on nymphs in *Solemya* (*Solemya*), external and supported by nymphs in *Acharax*. On the basis of this taxonomical character the Dolomites specimens are referred to *Acharax*.

Acharax frenademezi sp. nov.

Figure 3A–K

v1878 ?*Allorisma* sp.; Stache, p. 126, pl. 1, fig. 26.

1927 ?*Cleidophorus* sp.; Ogilvie Gordon, p. 14, pl.1, fig. 9a.

LSID. <https://zoobank.org/nomenclaturalacts/D5769B25-7264-4417-A85F-876D3EE0011C>

Derivation of name. The species is dedicated to Mr Roberto Frenademez from San Cassiano/St Kassian/San Ciascian who discovered the holotype.

Holotype. MLCS1720, PR61b.12a, steinkern of two articulated valves with partially preserved external mould (Figs 3I–M, 4).

Other material. 54 specimens. 8 LVs and 8 RVs from BA460; 7 LVs and 7 RVs from BA461; 8 LVs and 6 RVs from PR61; 7 LVs and 3 RVs from JM28.

Type locality & stratum. Preroman near San Martino/St Martin in Thurn, (Badia Valley); bed PR61b, NH B. Upper Permian, Bellerophon Fm, Changhsingian.

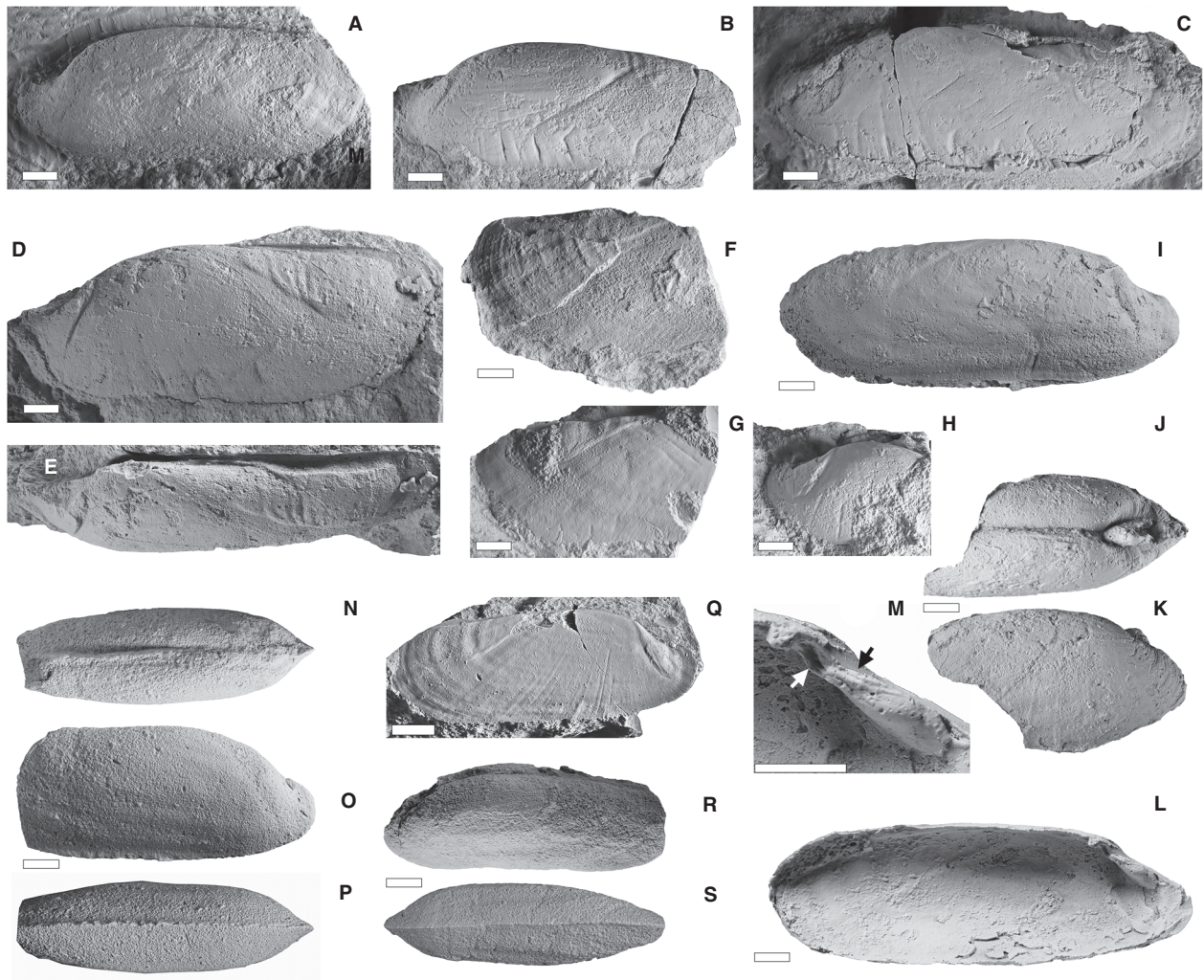


FIG. 3. *Acharax frenademezi* sp. nov., Bellerophon Fm, NH B at Balest (BA), Jmueia da Insom (JM) and Preroman (PR). A, MLCS1549, PRdebris.30a, RV, composite mould. B, MLCS1719, JM28.04, RV, steinkern. C, MLCS409, BA461.15, RV, steinkern. D–E, MLCS756, BA463b.03, RV, steinkern, in: D, lateral, E, dorsal view. F, MLCS325, BA460.21, LV, anterior part of specimen with shell partially preserved in calcite. G, MLCS1721, BA461.155, LV, steinkern of anterior part of shell with anterior composite scar. H, MLCS1722, BA460.90, RV, steinkern of posterior part of shell. I–M, MLCS1720, PR61b.12ab, articulated specimen, holotype: I, steinkern of LV, J, dorsal view, plaster cast of external mould of posterior part of shells with external convex-upward primary ligament; K, lateral view; L, RV, plaster cast, internal view; M, detail of L, internal posterior hinge region; black arrow, nymph; white arrow, anterior groove for the attachment of the anterior part of external primary ligament. N–P, MLCS1083, PR61a.52ab, partially preserved articulated specimen, composite mould, in: N, dorsal view with LV overlapping RV; O, LV, lateral view; P, ventral view with closed ventral margin. Q, MLCS400, BA461.06, LV, steinkern. R–S, MLCS1103, PR61a.72ab, articulated specimen, composite mould: R, RV, lateral view; S, dorsal view with closed dorsal margin. Scale bars represent 5 mm.

Diagnosis. *Acharax* with large and deeply impressed anterior composite muscle scar with oblique ridges in central part; small subvertical groove on posterior subumbonal shell margin; demipad present on RV.

Description. (Morphological terminology according to Bailey 2011; Fig. 4.) Shell medium sized (max. L = 58.8 mm), thin, elongated ovoid, equivalve, inequilateral and strongly elongated anteriorly (longiaxis/breviaxis ratio 5 and L/H ratio *c.* 2.6). Dorsal and ventral margins subparallel; anterior margin obliquely

rounded, connected to dorsal margin by rounded corner. Posterior shell region short, narrow and subrostrate with narrowly rounded posterior margin; ventral margin straight to slightly convex. Beak low, weak and not protruding, located near posterior extremity at about one-fifth of shell length. RV with small pad-like thickening (demipad) (Fig. 4B) anterior of beak. Muscle scars strongly anisomyarian; anterior adductor muscle impression larger than posterior one; posterior muscle scar near dorsal margin, deeply impressed, subtriangular, with dorsal part consisting of small pedal retractor muscle scar and ventral part of larger

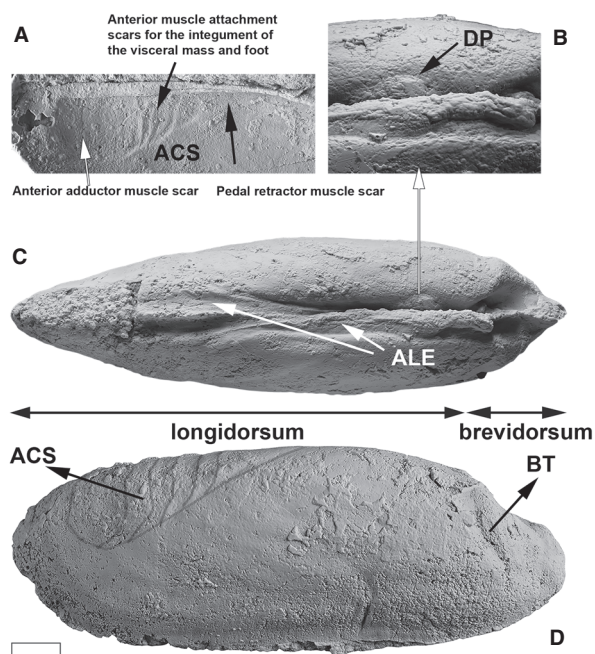


FIG. 4. A–D, MLCS1720, PR61b.12ab, the morphological terminology of *Acharax* from the Bellerophon Fm adopted herein follows Bailey (2011). Abbreviations: ACS, anterior composite scar; ALE, anterior ligamental extension; BT, buttress; DP, demi-pad. Scale bar represents 5 mm.

posterior adductor muscle scar; anteriorly bounded by long oblique and rounded buttress. Anterior composite scar large, deeply impressed, subtriangular and divided into three parts: anterior, large and subtrapezoidal; central, with up to four short oblique undulating ridges representing anterior muscle scars for integument of visceral mass and foot; and posterior, possibly representing pedal retractor muscle scar (Fig. 4A). Dorsal margin of the posterior subrostrate shell region with longitudinal external nymph, bearing convex-upward external parivincular (opisthodontic) primary ligament (Fig. 3J). Internal ventral side of nymph thickened with narrow subumbonal groove (Fig. 3M). Anterior region with radial ridge extending from distinct dorsal groove to anterior margin and hosting adapical part of anterior outer-layer ligamental extension. Pallial line consisting of obscure commarginal band with faint radial striations.

Ornament of up to five strong and regularly spaced commarginal folds, fine growth lines and broad oblique and shallow radial plicae. Internal shell surface with faint oblique radial ribs. LV of articulated specimens dorsally overlapping RV.

Remarks. Stache (1878, pl. 1, fig. 26) described as *Allorisma* sp. the anterior part of a shell belonging to the new species proposed here, to which also *Cleidophorus* sp. described by Ogilvie Gordon (1927, pl. 1, fig. 9a) can be attributed.

Acharax radiata (Meek & Worthen, 1860) from the late Palaeozoic of USA has a similar shell shape and an external primary ligament as the Bellerophon Fm specimens. However, *A. radiata* lacks the posterior rostrum, which is well developed

in our specimens. It has a less elongated shell ($L/H = 2$) than the specimens from the Bellerophon Fm ($L/H = 2.6$) and is lacking the subumbonal ridge for the attachment of the anterior part of the external primary ligament.

Acharax primaeva (Phillips, 1836), considered by Bailey (2011) as a probable senior synonym of *Solemya parallela* Beede & Rogers, 1899, has a shell shape and radial ornamentation similar to those of the specimens discussed here. The new species, however, is less elongated ($L/H = 2.6$) and has a higher longiaxis/breviaxis ratio (5) than that of *A. primaeva*, which has an L/H ratio of 3.0 and a longiaxis/breviaxis ratio of 3.5.

The shell shape of *Acharax* (*Nacrossolemya*) *trapezoides* (Meek, 1874) is similar to our specimens, but it has a less elongated outline ($L/H = 2.3$). The main differences can be seen in the attachment of the external primary ligament on the nymphs. In the specimens from the Bellerophon Fm the posterior part of the ligament is anchored into a subumbonal groove that is missing in *A. (N.) trapezoides*. Major similarities to *Acharax holmwoodensis* (Dickins, 1963) from the lower Permian of Australia, which has a convex-upward external parivincular ligament, are seen. This species was originally classified as *Solemya* based on the hinge structure, but it is here placed in *Acharax* as proposed also by Bailey (2021). The shell of this species is less elongated ($L/H = 2.3$), the posterior part is not subrostrate and the antero-dorsal muscle impression is less developed and impressed than in our specimens.

Palaeoecology. Infaunal, chemosymbiotic deposit feeder.

Subclass AUTOLAMELLIBRANCHIATA Grobden, 1894

Infraclass PTERIOMORPHIA Beurlen, 1944

Order MYTILOIDA Férussac, 1822 in Férussac 1821–1822

Family MYTILIDAE Rafinesque, 1815

Genus PROMYTIUS Newell, 1942

Type species. *Promytilus annosus* Newell, 1942.

Remarks. According to Newell (1942) *Promytilus* differs from *Modiolus* Lamarck, 1799 in having a terminal beak. Later, Waterhouse (2008) broadened the definition of *Promytilus* to include species with subterminal beaks. We agree with Hautmann *et al.* (2013) who criticized this extended definition because it hinders a clear differentiation between *Promytilus* and *Modiolus*. The studied specimens have a very small and narrow terminal beak and the anterior lobe is located immediately behind and ventral to the beak. Therefore, we place them in *Promytilus*.

Promytilus merlai sp. nov.

Figure 5

v1930 *Modiola megaloba* M'Coy; Merla, pp. 118–119, pl. 11, fig. 19.

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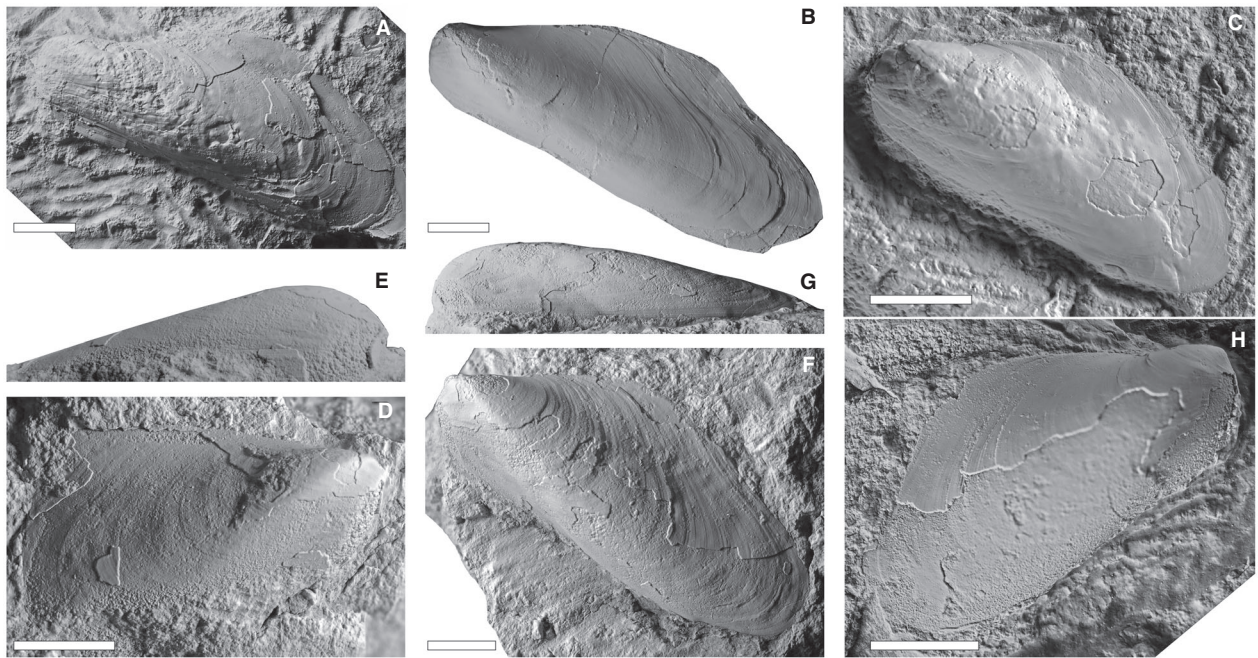


FIG. 5. *Promytilus merlai* sp. nov., Bellerophon Fm, NH B at Preroman (PR). All specimens partially or completely preserved as shells replaced by calcite. A, MLCS1269, PR61a.239, LV. B, MLCS1033, PR61a.02, holotype, LV. C, MLCS1128, PR61a.97, LV. D–E, MLCS1895, PR61a.288, RV, in: D, lateral, E, ventral view. F–G, MLCS1036, PR61a.05, LV, in: F, lateral, G, ventral view. H, MLCS1270, PR61a.240, RV. Scale bars represent 5 mm.

Derivation of name. The new species is named after Giovanni Merla for his contribution to the knowledge of the bivalves from the Bellerophon Fm.

Holotype. MLCS1033, PR61a.02, an LV with the shell replaced by calcitic cement (Fig. 5B).

Other material. 51 specimens. 2 LVs from BA461; 25 LVs and 24 RVs from PR61.

Type locality & stratum. Preroman near San Martino/St Martin in Thurn/San Martin de Tor (Badia Valley), bed 61a, upper Permian, Bellerophon Fm, Changhsingian.

Diagnosis. *Promytilus* with very narrow shell; length up to 2.5-fold the width; dorsal part of posterior margin slightly concave at adult growth stage.

Description. Shell thin, roughly triangular, narrow and elongated. Umbo small, narrow, slightly protruding over hinge line. Beak terminal and prosogyrate. Umbonal ridge broad, slightly sinuated and forming with posterior margin a *c.* 30° angle (α). Anterior lobe small, placed ventral to umbo and separated from it by a faint oblique sulcus, extending posteriorly up to one-third of shell length and vanishing before reaching the ventral margin. Ventral margin long with slight byssal sinus at about one-third of shell length from anterior extremity. Posteroventral corner narrowly rounded. Dorsal part of posterior margin oblique, slightly convex until *c.* 3 cm shell length; slightly concave in adult growth stages.

Dorsal margin straight and connected to posterior margin by broadly rounded corner. Outer surface with fine concentric growth lines, forming slight steps at cyclical intervals.

Remarks. Merla (1930) assigned the specimen MDGP 24880 from the Bellerophon Fm of Cadore, which is conspecific with our specimens, to *Modiola megaloba* M'Coy, 1844. M'Coy (1844) and Hind (1896) described this species from the Carboniferous of England. *Modiola megaloba* differs from our specimens by the subterminal beak, which identifies it as belonging to *Modiolus*. None of the already known *Promytilus* species has such a narrow shell with a slightly concave dorsal part of the posterior margin in the adult growth stage as the specimens described here and a new species is, therefore, proposed.

Palaeoecology. Stationary (byssate), semi-infaunal suspension feeder.

Genus VOLSELLINA Newell, 1942

Type species. *Pleurophorus subellipticus* Meek, 1867.

Volsellina carinata sp. nov.

Figure 6

v1930 *Leiopteria* cfr. *obtusa* Bittner; Merla, pp. 100–106, pl. 11, fig. 11.

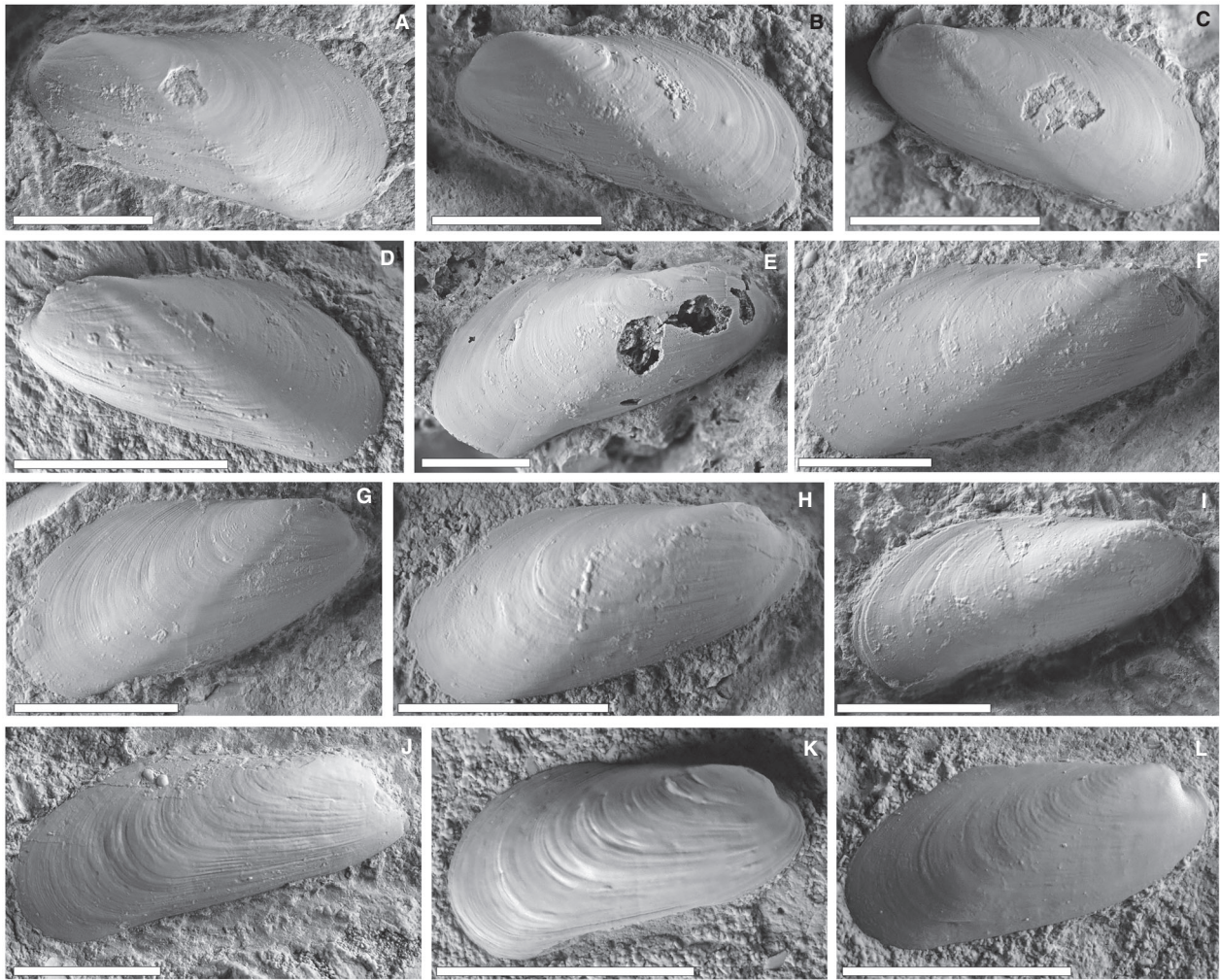


FIG. 6. *Volsellina carinata* sp. nov., Bellerophon Fm, GVBB at Culatsch (CU) and Balest (BA). All specimens preserved as shells replaced by calcite. A, MLCS976, CUGVBB.03, LV. B, MLCS1607, CUGVBB.16, LV. C, MLCS1624.01, CUGVBB.33, LV. D, MLCS1608, CUGVBB.17, holotype, LV. E, MLCS1616, CUGVBB.25, RV. F, MLCS1613, CUGVBB.22, RV. G, MLCS1619, CUGVBB.28, RV. H, MLCS1622, CUGVBB.31, RV. I, MLCS743, SG.21, RV. J, MLCS1775, BA231.135, RV. K, MLCS1770, BA231.130, RV. L, MLCS1773, BA231.133, RV. Scale bars represent 5 mm.

v1930 *Modiolopsis* sp. ind.; Merla, p. 117, pl. 11, fig. 21.

LSID. <https://zoobank.org/nomenclaturalacts/9ABA8961-112E-439B-B22B-4A9F7A6CE1A7>

Derivation of name. From the strong umbonal carina which characterizes this species.

Holotype. MLCS1608, CUGVBB.17, an RV from GVBB of Culatsch near Bulla in Gardena Valley (Fig. 6D).

Other material. 643 specimens. 9 LVs and 13 RVs from BA14; 25 LVs and 28 RVs from BA231; 8 LVs and 5 RVs from BA599; 6 LVs and 10 RVs from BA634; 13 LVs and 15 RVs from BA713; 3 LVs

and 3 RVs from BA731; 3 LVs and 4 RVs from BU112; 48 LVs and 44 RVs from CUGVBB; 1 LV and 1 RV from PR61; 1 RV from PR11; 40 LVs and 57 RVs from PR3,117; 4 LVs and 1 RV from PR139; 7 LVs and 4 RVs from RPGVBB; 3 LVs and 1 RV from SE56; 3 LVs and 1 RV from SE140; 2 LVs and 7 RVs from SE142; 6 LVs and 3 RVs from SE145; 9 LVs and 9 RVs from JM188; 20 LVs and 15 RVs from JM195; 113 LVs and 98 RVs from JM198.

Type locality & stratum. Culatsch near Bulla in Val Gardena/Gröden, GVBB. Upper Permian, Bellerophon Fm, Changhsingian.

Diagnosis. *Volsellina* with sharp, narrowly rounded umbonal carina delimited ventrally by a shallow and variably developed radial groove.

Description. Shell small (max. L = 18 mm), modioliform (L/H up to 2.4), thin, strongly inflated, with maximum inflation at about one-third from anterior margin and posteriorly expanding ($\alpha = \leq 18^\circ$). Dorsal margin straight, extending about two-thirds of shell length and gradually connected, with a c. 150° angle, to an obliquely rounded posterior margin; ventral margin from slightly convex in juveniles to nearly straight in adults. Beak small, prosogyrate, slightly protruding beyond hinge line and placed a little posterior to the narrowly rounded anterior margin. Umbonal carina generally with shallow anterior ventral radial groove (Fig. 6A–H), barely recognizable in stratigraphically older specimens (Lo4; Fig. 6J–L). External ornament with faint growth lines.

Remarks. *Volsellina carinata* has a broad intraspecies variability mostly regarding the shell inflation and development of the umbonal carina, which is generally separated from the ventral surface by a radial sulcus, barely detectable in stratigraphically older populations of the sequence Lo4. *Volsellina? equatorialis* (Thomas, 1928) from the Carboniferous of Peru is longer, narrower (L/H = 3.14), less expanded posteriorly, has a weaker umbonal ridge and a less developed anterior lobe than the specimens from Bellerophon Fm. *Volsellina ornatissima* Johnston, 1887 from the Permian of Australia is considerably larger (up to 42 mm in length) and bears a reticulated ornamentation pattern of concentric growth lines and radial riblets, not present in the Bellerophon Fm specimens. *Volsellina subelliptica* (Meek, 1867) from the Carboniferous and Permian of the USA has a sharper umbonal ridge. *Volsellina yunnanensis* (Reed, 1927) from the Permian of China is considerably narrower anteriorly, more expanded posteriorly and has a less conspicuous umbonal ridge. *Volsellina transparens* (Waagen, 1881) from the upper Permian of the Salt Range (Pakistan) differs from the Bellerophon Fm species by a more angulated umbonal ridge and a more convex dorsal part of posterior margin. *Volsellina areiensis* Neves *et al.* 2014a from the lower Permian of Brazil has a weaker umbonal ridge and a less inflated shell.

Palaeoecology. A stationary (byssate), epifaunal suspension feeder.

Order ARCIDA J. Gray, 1854
Superfamily ARCOIDEA Lamarck, 1809
Family PARALLELODONTIDAE Dall, 1898
Genus GRAMMATODON Meek & Hayden, 1861
Subgenus COSMETODON Branson, 1942

Type species. *Parallelodon rugosus* Buckman in Murchison *et al.*, 1845.

Remarks. Newell (in Cox *et al.* 1969) divided, on the base of tooth orientation, the family Paralleodontidae into two subfamilies: Paralleodontinae and Grammatodontinae. *Grammatodon* is divided into the following subgenera: *Grammatodon* (*Grammatodon*), with well-defined posterior umbonal carina and closely spaced riblets and *Grammatodon* (*Cosmetodon*), similar to *Parallelodon* but with the posterior hinge teeth intersecting the ventral margin of hinge plate and the dorsal hinge teeth longer than the

ventral ones. In the only available specimen with preserved dentition from the Bellerophon Fm, the posterior hinge teeth are *Cosmetodon*-like and the shell is longer than in *Grammatodon* (*Grammatodon*). These specimens are, therefore, assigned to the subgenus *Grammatodon* (*Cosmetodon*).

Grammatodon (*Cosmetodon*) *obsoletiformis*
(Hayasaka, 1925)
Figure 7

- *1925 *Parallelodon obsoletiformis* Hayasaka, p. 18, pl. 8, figs 15, 16, 16a.
- 1977 *Parallelodon* (*Parallelodon*) *obsoletiformis*; Hayami & Kase, pp. 85–86, pl. 9, fig. 11a, b.
- 1985 *Grammatodon* (*Cosmetodon*) *obsoletiformis*; Yancey, p. 1288, figs 1–3.
- 2007 *Grammatodon* (*Cosmetodon*) *obsoletiformis*; Nakazawa, p. 197, pl. 13, figs 5–8.

Material. 15 specimens. 2 LVs and 3 RVs from BA460; 6 LVs and 4 RVs from PR61.

Description. Shell inequilateral, (L/H = 2.3), scaphiform in juveniles to slightly parallelodontiform in adults (Amler 1989), anteriorly strongly inflated and slightly flattened posteriorly. Posterior part of dorsal margin straight; anterior part of dorsal margin very short, forming a c. 80° angle with the anterior margin. Umbo blunt, wide, prosoto orthogyrate and slightly elevated above hinge margin. Beak small, at about one-fifth anteriorly of shell length. Umbonal ridge broad and rounded. Median radial sulcus shallow, extending from beak to ventral margin at about one-third anteriorly of shell length, forming a small byssal sinus there. Ornament of slight concentric folds and faint radial riblets, stronger on posterior part of shell. Hinge cosmetodontid with four elongated posterior teeth, diminishing in length ventrally. Four short anterior teeth; first tooth longest and subparallel to hinge line; other three teeth shorter, more inclined and fourth tooth almost perpendicular to hinge line (Fig. 7E).

Remarks. The specimens from the Bellerophon Fm have a shell shape nearly identical to *Grammatodon* (*Cosmetodon*) *obsoletiformis* from the middle Permian Akasaka Limestone of Japan (Hayasaka 1925; Nakazawa 2007) and from the lower Permian of Malaysia (Yancey 1985). *Grammatodon* (*C.*) *obsoletiformis* has five oblique anterior hinge teeth and five to six very small oblique teeth posterior to the beak. The only specimen of the Bellerophon Fm with preserved dentition (Fig. 7C–E) has four oblique anterior teeth and four posterior hinge teeth. This specimen is only 29 mm long versus the 45 mm length of the holotype of *G.* (*C.*) *obsoletiformis*. A lower number of teeth can, therefore, be related to the smaller size of the Dolomites specimens. The only remarkable difference between some Dolomites specimens and the holotype of *G.* (*C.*) *obsoletiformis* is the occurrence of a faint radial ornamentation in juvenile individuals from the Bellerophon Fm. This radial ornamentation is also present in specimens assigned to *G.* (*C.*) *obsoletiformis* from the lower Permian of Malaysia

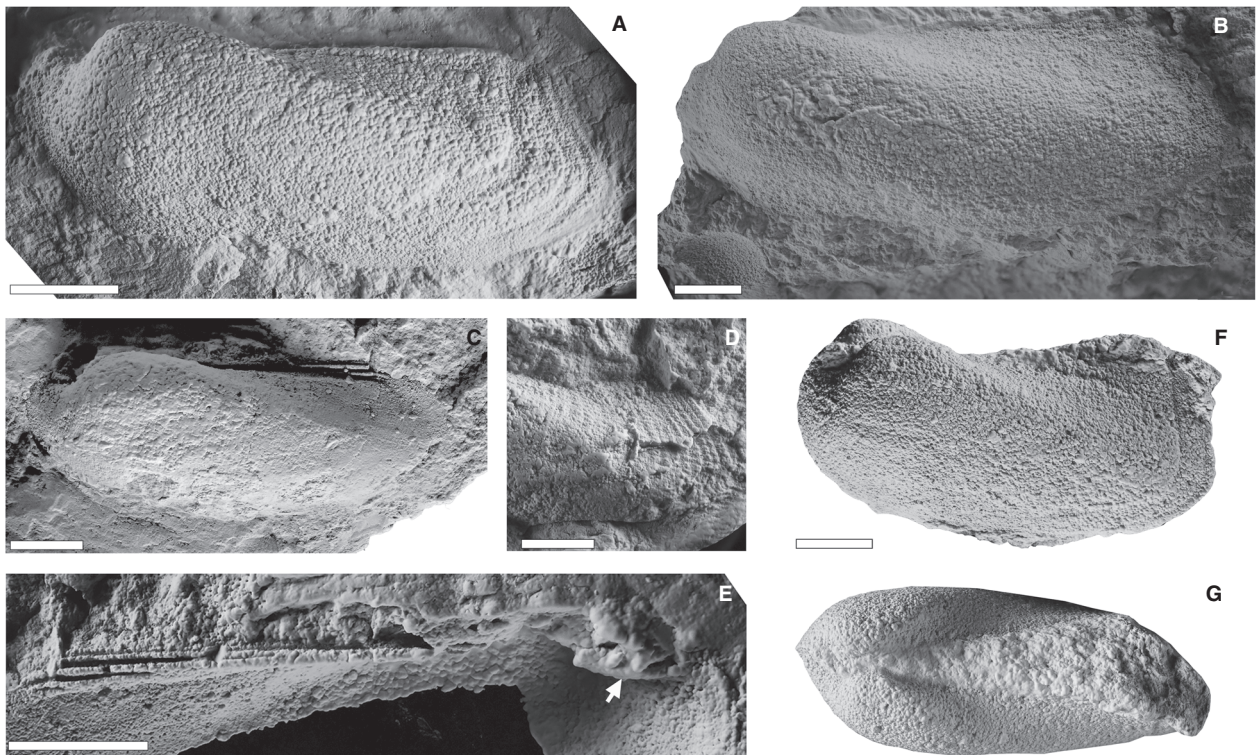


FIG. 7. *Grammatodon (Cosmetodon) obsoletiformis* (Hayasaka, 1925), Bellerophon Fm, NH B at Balest (BA) and Preroman (PR). A, MLCS1281, PR61a.251, LV, steinkern. B, MLCS1184, PR61a.153, LV, steinkern. C–E, MLCS315, BA460.11: C, LV, steinkern; D, posterior part of shell, plaster cast of external mould; E, plaster cast of hinge region with anterior and posterior hinge teeth (white arrow). F–G, MLCS1729, BA460.92ab, articulated specimen, in: F, LV, lateral, G, dorsal view. Scale bars represent 5 mm.

(Yancey 1985) and in juvenile specimens of the Permian Akasaka Limestone from Japan (Nakazawa 2007), and is probably eroded in the considerably larger holotype.

Palaeoecology. Facultatively mobile (byssate), low-level epifaunal suspension feeder.

Order OSTREIDA Férussac, 1822 in Férussac 1821–1822

Suborder MALLEIDINA J. Gray, 1847

Superfamily PTERIOIDEA J. Gray, 1847

Family BAKEVELLIIDAE King, 1850

Genus BAKEVELLIA King, 1848

Type species. *Avicula antiqua* Münster in Goldfuss, 1836.

Subgenus BAKEVELLIA King, 1848

Bakevellia (Bakevellia) binneyi (Brown, 1841)

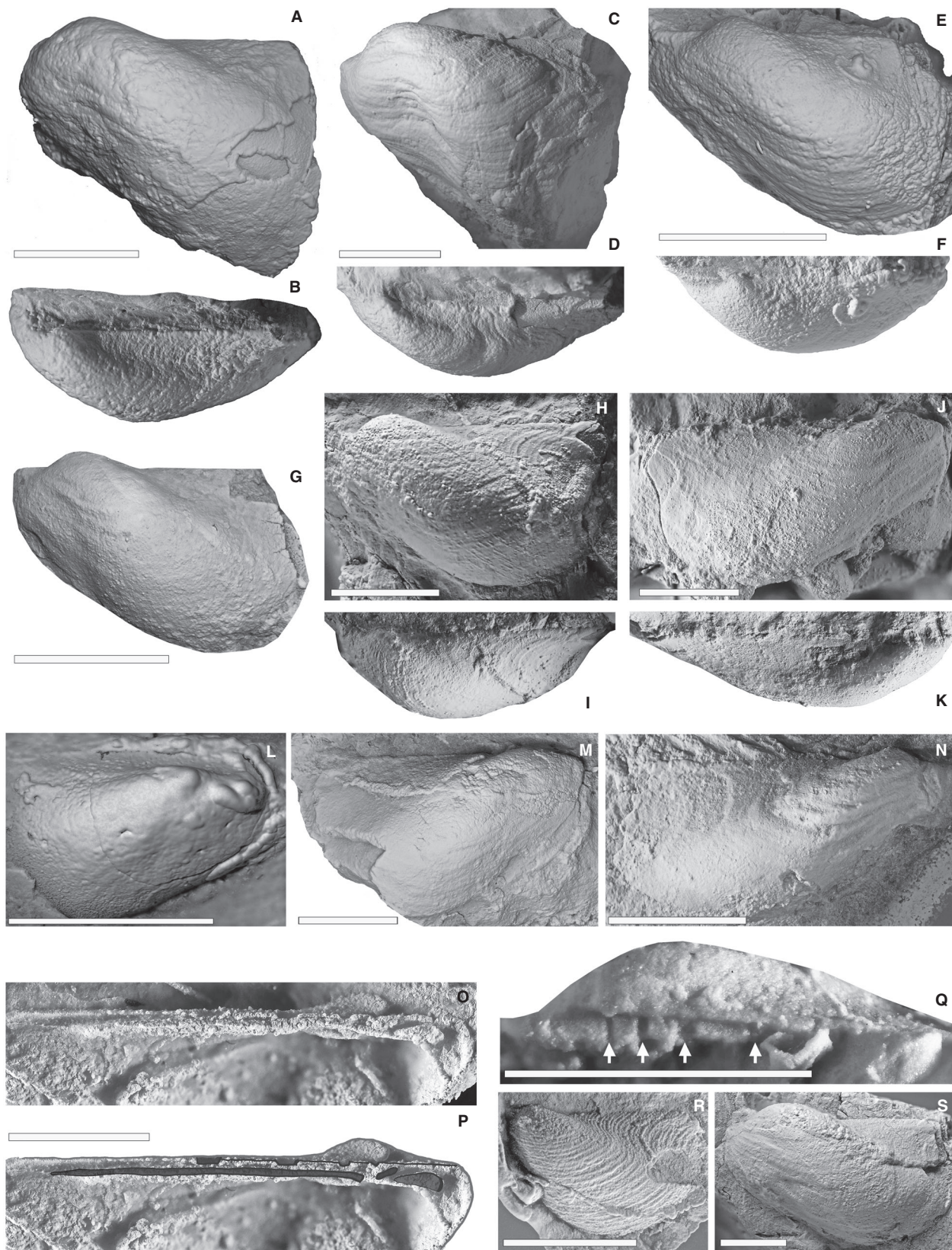
Figure 8

- *1841 *Avicula binneyi* Brown, p. 65, pl. 6, fig 27.
- 1927 *Bakewellia Kingi* Kittl; Ogilvie Gordon, p. 14.
- 1995 *Bakevellia (B.) binneyi*; Muster, p. 31, figs 22–23, pl. 3, figs 5–7; pl. 4, figs 1–7 [cum syn.]
- 2003 *Bakevellia binneyi*; Szente & Vörös, p. 126, pl. 1, figs 16–19.

Material. 151 specimens. 100 LVs and 51 RVs from bed Ff1.

Description. Medium-sized (max. L = 23.6 mm), inequivalve, posteriorly elongated and subtrapezoidal shell.

FIG. 8. *Bakevellia (Bakevellia) binneyi* (Brown, 1841), Fiammazza Facies of the Bellerophon Fm at Balest (Ff1). All specimens except L, O, P, Q and R are preserved as shells replaced by gypsum. A–B, MLCS1914, Ff1.18, LV, in: A, lateral, B, dorsal view. C–D, MLCS1916, Ff1.20, LV, in: C, lateral, D, dorsal view. E–F, MLCS1915, Ff1.19, LV, in: E, lateral, F, dorsal view. G, MLCS1944, Ff1.46, LV. H–I, MLCS1940, Ff1.42, LV, in: H, lateral, I, dorsal view. J–K, MLCS1941, Ff1.43, RV, in: J, lateral, K, dorsal view. L, MLCS1917, Ff1.21, RV, steinkern with muscle impressions. M, MLCS1919, Ff1.23, RV. N, MLCS1918, Ff1.22, RV. O–P, MLCS1900, Ff1.04.02, LV: O, plaster cast of hinge region, P, same specimen with traced dentition and ligament grooves. Q, MLCS1942, Ff1.44, RV, plaster cast of hinge region, arrows indicate the ligament grooves. R, MLCS1943, Ff1.45, LV, plaster cast with growth lines. S, MLCS1931, Ff1.35, LV. Scale bars represent 5 mm.



LV disc strongly inflated with maximum inflation in anterior median part. Umbo strongly prosogyrate; beak flattened and incurved, slightly protruding beyond hinge line, anteriorly placed at about one-fifth of shell length. Angle α c. 40°, disc angle (β) c. 125°. Left anterior auricle short, small with broadly rounded anterior margin, separated from disc by oblique sulcus, originating a slight byssal sinus on the ventral margin. Posterior auricle slender, elongated and pointed, sometimes protruding beyond posterior margin and clearly distinguishable from the disc by a deep radial sulcus. Ornament of crowded, regularly spaced and raised commarginal folds. RV disc weakly inflated with small prosogyrate beak, slightly protruding over hinge line. Disc angle (β) > 135°. Anterior and posterior auricular sulci weaker than those of LV. Ornament of regularly spaced growth lines, better preserved in juvenile specimens (Fig. 8R). Ligamental area with up to four U-shaped grooves in adult specimens. Anterior ligamental groove, narrow and directly beneath beak; posterior ligamental grooves wider, regularly spaced and extending to about three-fifths of hinge length.

Two short anterior teeth on LV hinge, beneath and anterior to beak, from subparallel to slightly inclined to hinge margin. Posterior lateral tooth long and subparallel to hinge margin. Hinge of RV with single and slightly rounded anterior tooth, followed by shallow socket. Posterior hinge dentition with two elongated teeth. Anterior hinge plate with three shallow and small grooves (Fig. 8L) probably representing anterior and posterior pedal retractor muscle scars. Adductor scars not observed.

Remarks. The studied shells have biometric parameters that fall in the variability range of *B. binneyi* as suggested and plotted by Muster (1995). *Bakevellia binneyi* has a ratio of the diagonal line (D) and the width of the shell body (D/B) ranging from 1.5 to 2, while the ratio of D and the length of the posterior auricle (D/PAL) ranges from 1 to 1.5. These specimens have a D/B ratio of 1.5–1.9 and a D/PAL ratio of c. 1.2–1.3.

Palaeoecology. Stationary (endobyssate), semi-infaunal suspension feeder.

Bakevellia (Bakevellia) ceratophaga (Schlotheim, 1816)

Figure 9

- *1816 *Mytulites keratophagus* Schlotheim, p. 30, pl. 5, fig. 2a–c.
- v1878 *Bakevellia* cf. *ceratophaga* Schlotheim; Stache, p. 113, pl. 1, fig. 15a, b.
- 1906 *Avicula (Oxytoma) Vinassai* Gortani, p. 103, pl. 4, fig. 13.
- 1927 *Avicula stachii* Ogilvie Gordon, p. 12, pl. 1, fig. 5.
- v1930 *Bakewellia ceratophaga* Schlotheim; Merla, pp. 107–108, pl. 11, fig. 16.
- 1967 *Bakevellia (Bakevellia) ceratophaga* (Schlotheim); Logan, p. 35, pl. 4, figs 12–19 [cum syn.]
- 1995 *Bakevellia (Bakevellia) ceratophaga* (Schlotheim); Muster, p. 34, pl. 4, fig. 8a–b [cum syn.]
- v2005 *Bakevellia* cf. *ceratophaga*; Posenato *et al.*, p. 221, pl. 1, fig. 11.

2011 *Bakevellia* sp.; Hautmann *et al.*, p. 77, fig. 4 (7–9).

2015 *Bakevellia ceratophaga* (Schlotheim); Hautmann *et al.*, p. 16, fig. 9D, E.

2019 *Bakevellia ceratophaga* (Schlotheim); Foster *et al.*, p. 623, fig. 7A–C.

Material. 206 specimens. 1 LV from BA460; 83 LVs and 19 RVs from BA461; 27 LVs and 2 RVs from BA463; 7 LVs and 2 RVs from PR61; 49 LVs and 16 RVs from JM28.

Description. Shell pteriiform, medium sized, very oblique, inequivalve and posteriorly expanding. Shell length c. 1.5-fold longer than height.

LV highly convex with maximum inflation on anteromedian part. Umbo small, beak strongly prosogyrate and incurved, slightly protruding beyond hinge line and located anteriorly at about one-sixth of shell length. Hinge line long, straight, forming a 26°–28° angle with umbonal ridge. Posterior auricle elongated, pointed and sometimes protruding beyond posterior margin. Anterior auricle small, short, subtriangular and separated from disc by slightly oblique sulcus, ventrally originating weak byssal sinus.

LV ornament of strong concentric folds, faint and slightly protruding commarginal riblets and multiple growth lines. Auricles with faint commarginal ribs. Anterior auricle with large and deeply impressed anterior adductor and small, probably anterior protractor, muscle scars; possible small retractor muscle scar on anteroventral part of beak tip (e.g. Logan 1967). Posterior adductor muscle scar not observed. Hinge dentition with short anterior lateral tooth placed along the anterior auricle, and long posterior lateral tooth subparallel to posterior margin.

RV beak smaller, more prosogyrate, narrower and more flattened than in LV, not or only slightly protruding over hinge line. Right disc less inflated than left one; ornamented with few and weak commarginal folds and regularly spaced growth lines. Muscle scars of RV are the same as in LV.

Remarks. Muster (1995) recognized the following three Permian species of the subgenus *B. (Bakevellia)* as valid: *B. (Bakevellia) binneyi* (Brown, 1841), *B. (Bakevellia) bicarinata* King, 1848 and *B. (Bakevellia) ceratophaga* (Schlotheim, 1816), which mostly differ in shell obliquity and elongation. *Bakevellia. (B.) ceratophaga* is the most elongated and oblique species. In the figured LVs of *B. (Bakevellia) ceratophaga* and its synonym *B. sedgwickiana* the ratio of the diagonal line (D) to the width of the shell body (B) ranges from 2.0 to 3.4 with a mean of 2.5 (Prinot & Posenato 2023, appendix S4). The Dolomites shells (LVs) have a D/B ratio ranging from 1.9 to 2.4 and a mean of 2.2. Although slightly less elongated, the Dolomites shells have a D/B ratio that falls within the range of *B. (Bakevellia) ceratophaga*. This species has a wide geographic and stratigraphic distribution, ranging from the lower Permian to the Lower Triassic (e.g. Muromtseva & Guskov 1984; Hautmann *et al.* 2011; Foster *et al.* 2019). Despite its numerous occurrences, the internal characters are rarely preserved and described. Of the Dolomites specimens, only the hinge area and muscle scars have been observed. The multivincular ligament of *B. ceratophaga* was detected and figured only by King (1850, pl. 14, fig. 26), on which the generic assessment of the species is based.

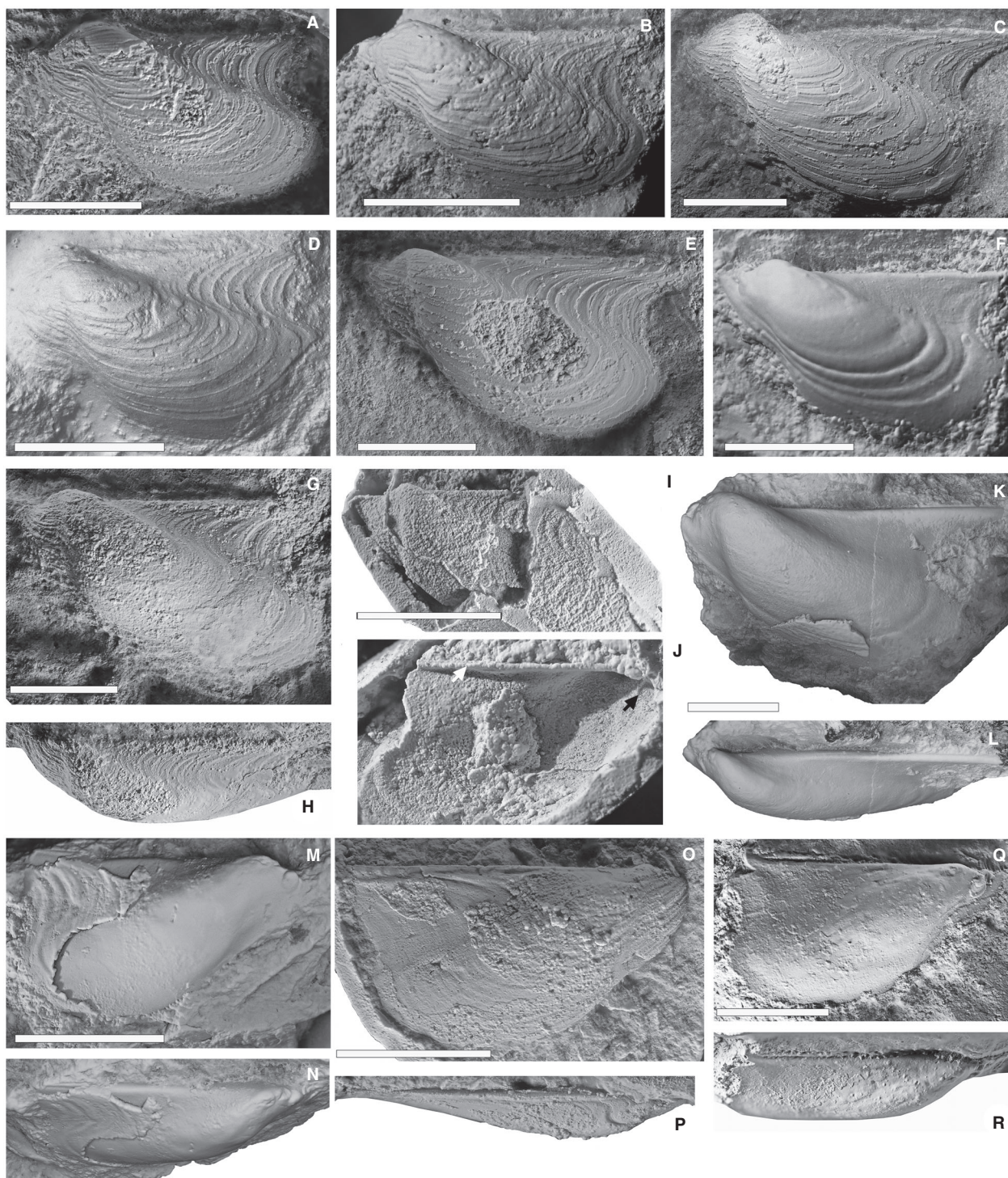


FIG. 9. *Bakevellia (Bakevellia) ceratophaga* (Schlotheim, 1816), Bellerophon Fm at Balest (BA) and Culatsch (CU). A–E and G–H are preserved as shells replaced by calcite; F, K–L and Q–R are steinkerns. A, MLCS556, BA463.61.05, LV. B, MLCS1796, BA463.80, LV. C, MLCS1789, BA463.72, LV. D, MGBW, N1878/1/14, holotype, LV. E, MLCS1795, BA463.79, LV. F, MLCS403, BA461.09, LV. G–H, MLCS1793, BA463.77, LV, in: G, lateral; H, dorsal view. I–J, MLCS1876, CUdebris.01, LV, plaster cast, in: I, lateral; J, internal lateral view, white arrow indicates the posterior lateral tooth, black arrow indicates the deeply impressed anterior adductor scar. K–L, MLCS430, BA461.36, LV, in: K, lateral; L, dorsal view. M–N, MLCS417, BA461.23, LV, in: M, lateral view with traces of shell replaced with calcite; N, dorsal view. O–P, MLCS1875, PR61b.15, RV, plaster cast of external mould, in: O, lateral; P, dorsal view. Q–R, MLCS1874, BA461.173, RV, in: Q, lateral; R, dorsal view. Scale bars represent 5 mm.

Stache (1878) determined two pteriiform specimens from the Bellerophon Fm as *Bakevellia* (*B.*) cf. *ceratophaga* (Schlottheim 1816). The open nomenclature was adopted because the shells have denser growth lines than *B. ceratophaga*. The same classification was also adopted by Merla (1930). Ogilvie Gordon (1927) allocated some pteriiform bivalves from the Gardena Valley to her new species *Avicula stachii*, which is characterized by curved and strongly prosogyrate beaks. Considering the broad intraspecific variability of the bakevellids (e.g. height of shell body, auricle length, beak shape, ornamentation) highlighted by Muster (1995), the differences of Dolomites individuals noted by the previous authors are here considered as intraspecific variability of the Schlottheim species.

Palaeoecology. Stationary (endobysate), semi-infaunal suspension feeder.

Bakevellia (*Bakevellia*) *preromangica* sp. nov.

Figure 10

?1927 *Bakevellia* cf. *ceratophaga* Schlottheim sp.; Ogilvie Gordon, p. 14, pl. 1, fig. 8.

LSID. <https://zoobank.org/nomenclaturalacts/3CEF35E7-B52C-42B2-AF51-D3D53A17206F>

Derivation of name. From Preromang (Badia Valley), the ancient name of the locality Preroman where the holotype was found.

Holotype. MLCS1878, PR145.07.02, LV preserved as shell replaced by calcite (Fig. 10A).

Other material. 418 specimens. 3 LVs and 1 RV from BA231; 2 LVs from BA599; 9 LVs and 4 RVs from BA713; 3 LVs from BA731; 7 LVs and 3 RVs from PR11; 20 LVs and 9 RVs from PR3117; 8 LVs and 4 RVs from PR136; 2 LVs and 1 RV from PR139; 62 LVs and 16 RVs from PR145; 14 LVs and 13 RVs from SE142; 2 LVs and 1 RV from SE145; 28 LVs and 16 RVs from TR; 1 LV from JM188; 41 LVs and 17 RVs from JM195; 96 LVs and 35 RVs from JM198.

Type locality & stratum. Preroman in Badia Valley near San Martino/St Martin in Thurn/San Martin de Tor, Bed PR145. Upper Permian, Bellerophon Fm, Changhsingian.

Diagnosis. *Bakevellia* with long, small and slender retroscrescent shell; ventral margin almost parallel to dorsal margin; hinge area short, with one or two ligamental grooves beneath beak.

Description. Shell small (max. L = 14.5 mm but generally shorter than 10 mm), narrow, inequivalve, strongly retroscrescent, slightly backwards expanding; L/H = ≥ 2.2 .

Shell with height $> c.$ 3.5 mm, mainly growing in posterior direction; dorsal and ventral margins almost subparallel. Posterior auricle long, narrow ($\alpha c.$ 19°), flattened with shallow auricular sinus and occasionally with slight longitudinal sulcus

ventral to dorsal margin. Posterior margin deeply rounded. Outer surface with sparse and irregular concentric folds and regularly spaced weak and narrow commarginal riblets, forming an S-shaped pattern on the posterior auricle and shell body. Ligamental area narrow, located with one, or rarely two shallow grooves below the beak. Umbonal cavity with anterior adductor scar and smaller pedal muscle scar. Posterior adductor large and rounded but only rarely detectable on steinkerns.

LV umbo small, prosocline, at about one-fifth of shell length from anterior margin, slightly protruding over hinge line with gently prosogyrate beak. Umbonal angle $\beta c.$ 117° and $\alpha c.$ 24°–27°. Shell body of LV broadly inflated and strongly oblique. LV anterior auricle short, flattened and subtriangular with obliquely rounded anterior margin and straight dorsal margin; with short and straight anterior tooth, subparallel to dorsal margin. Posterior lateral tooth weak, long and subparallel to dorsal margin, extending about two-thirds of posterior auricle length.

RV umbo small, narrow with faint carina on posterodorsal side. Beak smaller than in LV, slightly prosogyrate and protruding a little beyond the hinge line. Shell body oblique, narrow, slightly inflated. Shallow but broad sulcus extending from umbo to ventral margin and delimiting posteriorly the anterior auricle.

Dorsal margin of posterior auricle with shallow longitudinal sulcus.

RV dentition as in LV.

Remarks. The mean D/B ratio of *B. (B.) preromangica* is 2.8, which falls within the range of *B. ceratophaga* (2.0–3.4) (Prinath & Posenato 2023, appendix S4). However, they differ in shell shape. The new species is posteriorly more elongated and has a ventral margin almost parallel to the dorsal margin. In addition, the posterior wing is less pointed and has a very shallow posterior auricular sinus. A specimen from St Jakob/San Giacomo classified by Ogilvie Gordon (1927) as *Bakevellia* cf. *ceratophaga* could belong to the proposed new species. This is confirmed only by her good drawing of the specimens, because the original material, stored in the Paläontologisches Museum München, could not be found. *Bakevellia (B.) preromangica* shows similarities to *Bakevellia ladina* (Leonardi, 1932) from the overlying Werfen Fm. However, the latter species has a shorter posterior auricle and a slightly concave ventral margin.

Palaeoecology. Stationary (endobysate), semi-infaunal suspension feeder.

Genus TAMBANELLA Nakazawa & Newell, 1968

Type species. *Tambanella gujoensis* Nakazawa & Newell, 1968; Permian; Japan.

Remarks. The specimens from the Dolomites share most of the characters that Nakazawa & Newell (1968) listed for *Tambanella* but they differ in having a higher number of ligamental grooves (up to six) and in the occurrence of an internal radial ridge on the beak. Therefore, they are assigned with reservation to *Tambanella*, a genus that was tentatively referred by Nakazawa &

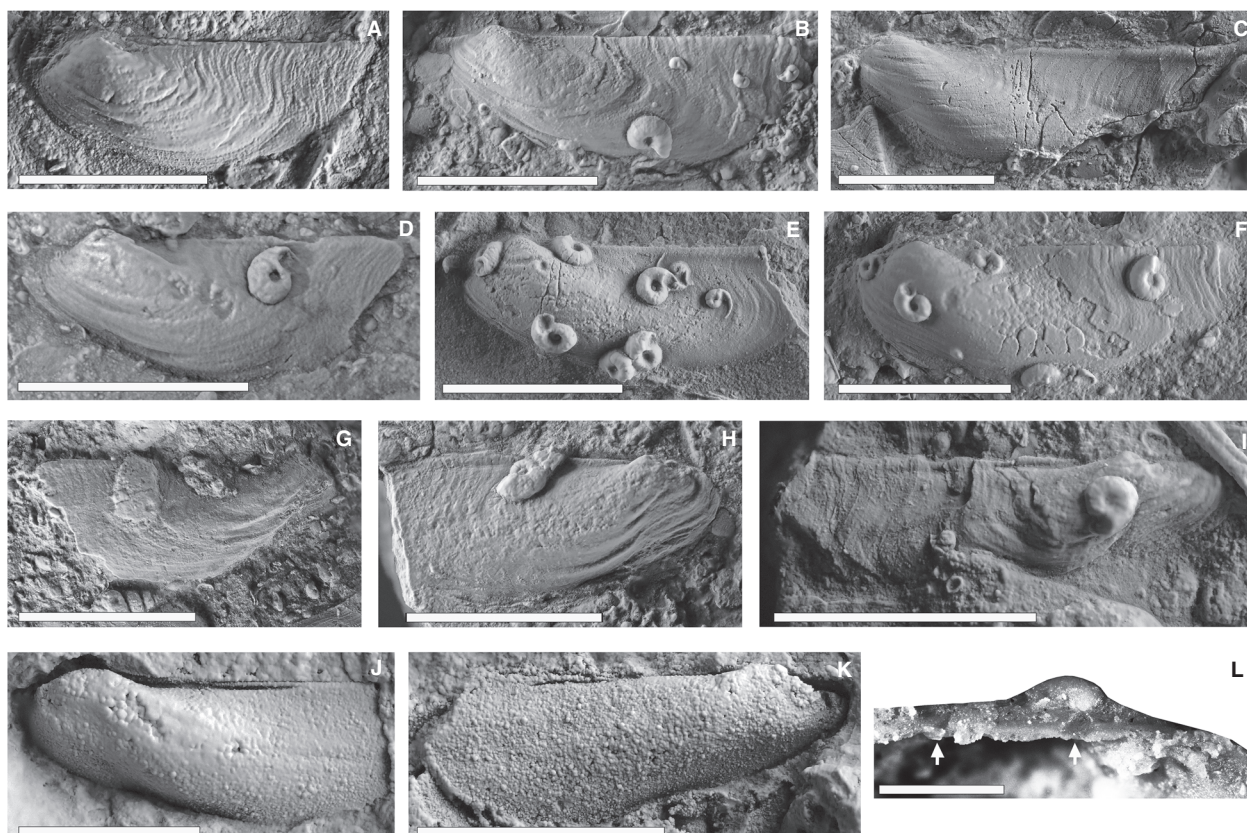


FIG. 10. *Bakevellia (Bakevellia) preromangica* sp. nov., Bellerophon Fm at Preroman (PR), Jmueia da Insom (JM), Preroman II (PRII) and Tramin (TR). J–K are steinkerns, other specimens (except L) are preserved as shells replaced by calcite. A, MLCS1878, PR145.07.02, holotype, LV. B, MLCS1878, PR145.07.01, LV. C, MLCS1879, JM197.06, LV. D, MLCS1877, PR145.06a.05, LV. E, MLCS1880, JM198.03.01, LV. F, MLCS1881, JM198.04.01, LV. G, MLCS1877, PR145.06a.03, RV. H, MLCS1877, PR145.06a.04, RV. I, MLCS1877, PR145.06a.06, RV. J, MLCS940, PRII.21.01.09, LV. K, MLCS968, PRII.49.02, RV. L, MLCS1885, TR.02.01, LV, plaster cast with ligament pits indicated by white arrows. Scale bars represent: 5 mm (A–K); 1 mm (L).

Newell (1968) to the family Isognomonidae. This family is characterized by the presence of hinge teeth in the early growth stages only and by both narrowly spaced and deep ligamental grooves. These characters are, however, observed neither in the *Tambanella* specimens from Japan nor in the specimens from the Dolomites. For this reason, the proposal of Fang (1987) and Yang *et al.* (2016) to include *Tambanella* in the Bakevelliidae is followed here.

Tambanella? stetteneckensis sp. nov.

Figure 11

1878 *Aucella* cf. *Hausmanni* Goldfuss; Stache, p. 115, pl. 1, fig. 18.

LSID. <https://zoobank.org/nomenclaturalacts/E4921BD0-961A-4C40-BF61-3266B63E3AA1>

Derivation of name. From Stetteneck, a castle ruin near the type locality in the Gardena Valley.

Holotype. MLCS190, BA231.18, steinkern of LV (Fig. 11A).

Other material. 48 specimens. 1 LV and 1 RV from BA14; 19 LVs and 26 RVs from BA231; 1 LV from CUGVBB.

Type locality & stratum. Balest, a mountain near Ortisei/St Ulrich, bed BA231. Upper Permian, Bellerophon Fm, Changhsingian.

Diagnosis. Sublanceolate, elongated, slightly inequivalve shell with terminal umbo and without anterior auricle; dorsal part of anterior margin slightly inflexed with byssal sinus. Beak small, prosogyrate with internal surface bipartite by radial ridge; ligamental area with up to six grooves; RV with small procline anterior cardinal tooth and two lamellar posterior lateral teeth; LV with one posterior lateral tooth.

Description. Medium-sized shell (max. L = 27 mm), subromboidal in juveniles to sublanceolate in adults; strongly inequilateral, retrocurved and posteroventrally expanded. LV slightly more inflated than RV. Dorsal part of anterior margin a little inflexed with shallow byssal sinus. Dorsal margin straight. Beak terminal,

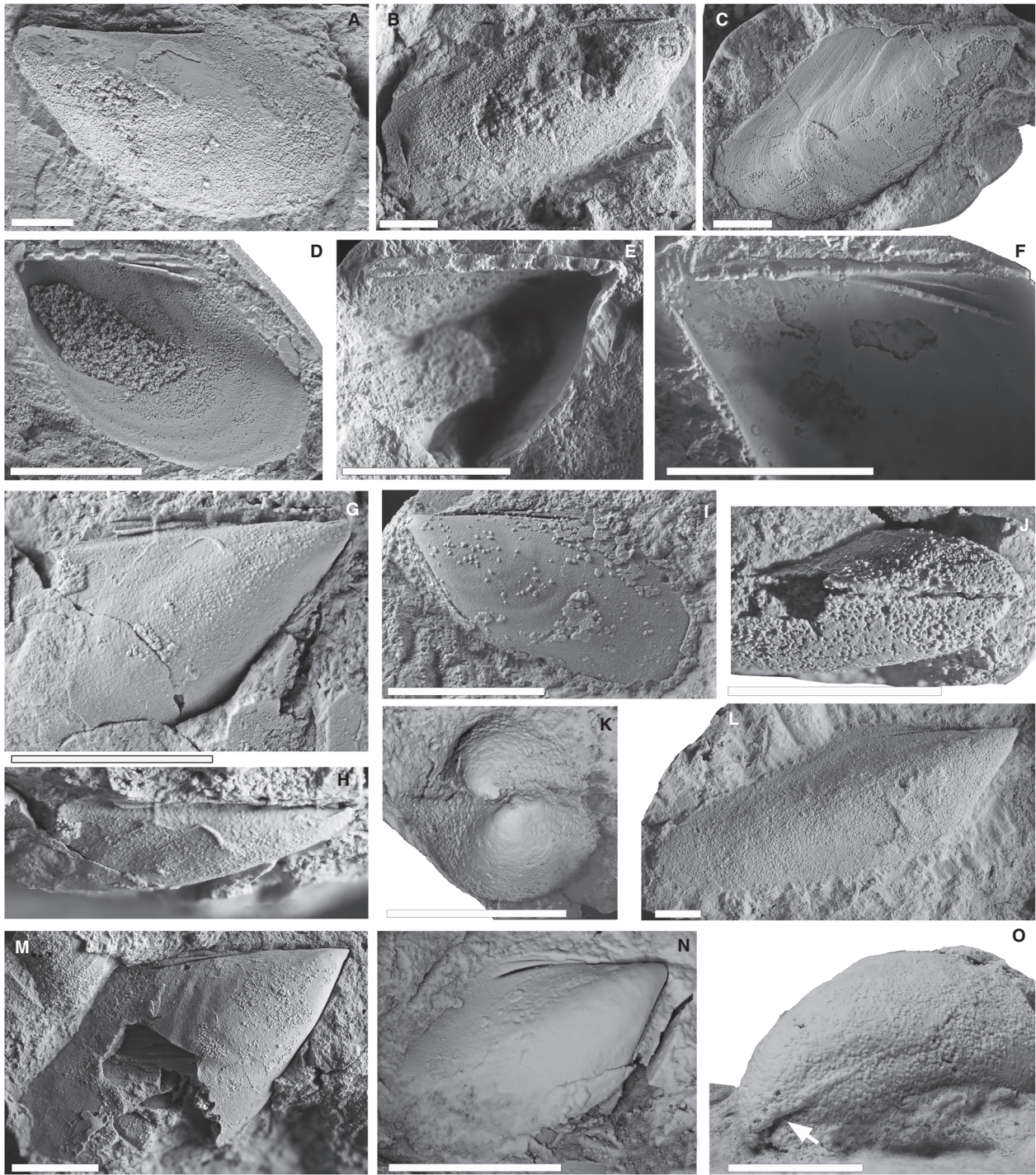


FIG. 11. *Tambanella? stetteneckensis* sp. nov., Bellerophon Fm at Balest (BA). A–B, G–I, L–O are steinkerns. A, MLCS190, BA231.18, holotype, LV. B, MLCS193, BA231.23, RV. C, MLCS275b, BA231.103b, RV, plaster cast of external mould. D, MLCS193, BA231.21, RV, plaster cast, internal view. E, MLCS1863, BA231.174, LV, plaster cast of hinge region, internal view. F, MLCS1864, BA231.175, RV, plaster cast of hinge region, internal view. G–H, MLCS1865, BA231.176, RV, in: G, lateral; H, dorsal view. I, MLCS1866, BA231.177, LV. J, MLCS275b, BA231.103b.05, dorsal view, plaster cast of external mould of beaks of articulated specimen. K, MLCS275, BA231.103d, anterior view, plaster cast of external mould of beaks of articulated specimen. L, MLCS1867, BA231.295, RV. M, MLCS1868, BA231.296, RV. N, MLCS188, BA231.16a.05, RV. O, MLCS189, BA231.17, LV, steinkern, anteroventral view of beak with radial sulcus (white arrow) representing the internal radial ridge on beak. Scale bars represent 5 mm.

acuminate, prosogyrate, internally divided by transverse ridge (Fig. 110). Umbonal ridge blunt, forming with dorsal margin a c. 30° angle. Posterior auricle narrow, subtriangular and separated from the disc by a shallow sulcus. Posterior auricular margin long, oblique and slightly concave. Anterior auricle absent. Ornament of growth lines and commarginal folds. Midpoint of umbonal ridge bearing a shallow, suboval adductor muscle scar.

Ligament area narrow with up to six shallow subrectangular ligamental grooves occupying, in adult specimens, less than half the hinge line. RV with small prosocline anterior cardinal tooth and two lamellar posterior lateral teeth; LV with one posterior lateral tooth.

Remarks. The specimens from Bellerophon Fm can be distinguished from *T. gujoensis* Nakazawa & Newell, 1968 in having a less perpendicular and more inflated shell. Moreover, the specimens from the Dolomites have a higher number of ligamental grooves and an internal ridge on the beak, absent in *T. gujoensis*. The late Permian species *T. guanshanensis* Fang, 1987, *T. shaodongensis* Zhang in Zhang *et al.*, 1977, *T. yunnanensis* Guo, 1985 and *T. alta* Guo, 1985 all have upright shells with an umbonal angle (between the dorsal and anterior margins) of c. 90°, decidedly different to the Dolomites specimens.

Boyd & Newell (1979) assigned only with reservation some specimens from the late Permian Djebel Tebaga Biohermal complex of Tunisia to *Tambanella*, because they are lacking a cardinal tooth and have an apical internal ridge. The Tunisian specimens are similar to the Dolomites ones, but the apical internal ridge is horizontal and not oblique as in the new species here proposed.

Palaeoecology. Stationary (byssate), epifaunal suspension feeder.

Genus TOWAPTERIA Nakazawa & Newell, 1968

Type species. *Towapteria nipponica* Nakazawa & Newell, 1968, by original designation.

Remarks. Nakazawa & Newell (1968) established the genus *Towapteria* for middle Permian bivalves from Japan characterized by a small, pteriiform, inequivalve, inequilateral, multivincular and radially ornamented shell. *Towapteria* is very similar to *Marmaronia* Larghi, 2002 from the middle Permian of Chios (Greece). The specimens from the Dolomites share with *Marmaronia* the little-developed anterior auricle and ornamentation, but for their more elongated shell, smaller beak and minor inflation of the RV we assign them to *Towapteria*. This genus also has some similarities to *Cassiavellia* Tëmkin & Pojeta, 2010 such as shell shape, dentition and mainly the presence of a commarginal impression on the internal side of the LV, which was produced by the shell margin of the smaller RV when they are fitting together incongruently.

Towapteria peracuta (Stache, 1878)

Figure 12

- v*1878 ?*Gervillia peracuta* Stache, p. 113–114, pl. 1, fig. 20a, b.
1878 *Bakevellia ladina* cf. *bicarinata* King; Stache, pp. 112–113, pl. 2, fig. 5a, b.

- v1903 *Avicula (Oxytoma) wachneri* Kittl, pp. 687–688, pl. 22, figs 9, 10.
1906 *Avicula (Oxytoma) Silveri* Gortani, p. 104, pl. 4, fig. 17.
v1930 *Myophoria* cfr. *inaequicostata* Klipstein; Merla, pp. 122–124, pl. 11, fig. 26.
v1988 *Towapteria wachneri* (Kittl); Broglio Loriga *et al.*, p. 17, pl. 1, fig. 2.

Material. 550 specimens. 205 LVs and 59 RVs from BA14; 1 LV from BA97; 25 LVs and 8 RVs from BA150; 24 LVs and 7 RVs from BA461; 3 LVs from BA463; 151 LVs and 39 RVs from BA713; 4 LVs from PR61; 2 LVs from PR11; 9 LVs from PR3,117; 3 LVs and 1 RV from SE142; 2 LVs from SE145; 7 LVs from JM28.

Description. Shell small (max L = 14 mm), strongly inequivalve, pteriiform, retroscrescent and L/H = 1.5. LV more inflated and slightly larger than RV. Little discordant valves with LV shell margin overlapping that of RV (Fig. 12E). LV with commarginal impression of RV margin on internal shell surface (Fig. 12B). Ventral margin of LV folded, ventral margin of RV entire. Umbonal ridge of both valves slightly concave and sharp, forming with dorsal margin a c. 35° angle.

LV anterior auricle little developed, small, subtriangular, anteriorly acuminate, separated from the disc by a deep and smooth radial furrow, bearing occasionally radial riblets and forming a byssal sinus on the ventral margin. Anterior auricle with up to eight scaly ribs, stronger than those on disc. Large, well-inflated and backwards-expanding disc, with seven radial ribs in juveniles and up to 15 thin, scaly radial ribs in adults, usually arranged in two orders. Left beak acuminate, prosogyrate to orthogyrate, at about the anterior one-fifth of shell length and protruding over hinge line. Posterior auricle large, wing-like expanded, acuminate, reaching or slightly exceeding posterior margin and with a moderately deep auricular sinus. Auricle ornament of growth lines and radial ribs. Disc with strong and scaly growth lines.

Anterior auricle of RV separated from disc by shallow, narrow and subvertical radial furrow, forming a slight byssal sinus on ventral margin. Anterior auricle with concentric folds; disc with slight commarginal riblets; posterior auricle with slight radial ribs and commarginal riblets. Posterior auricle of RV large, wing-like and ornamented by growth lines and radial ribs, weaker than on LV. RV beak considerably smaller than LV beak and only slightly protruding over hinge line.

Internal surface of both valves with thickened tooth-like umbonal ridge, long in RV (Fig. 12I) and short in LV (Fig. 12B). Anterior part of RV hinge plate with socket and small anterior tooth fused to auricular septum, anteriorly delimiting the pedo-byssal retractor muscle scar (Fig. 12I). Anterior hinge plate of LV with short and strong anterior tooth, subparallel to dorsal margin.

LV with one long posterior lateral tooth (or exceptionally up to three) subparallel to dorsal margin. RV with only one long and well-developed posterior lateral tooth, reaching two-thirds of posterior auricle length.

Left anterior auricle with rounded and deeply impressed adductor scar (Fig. 12B); tip of beak with two small muscle scars

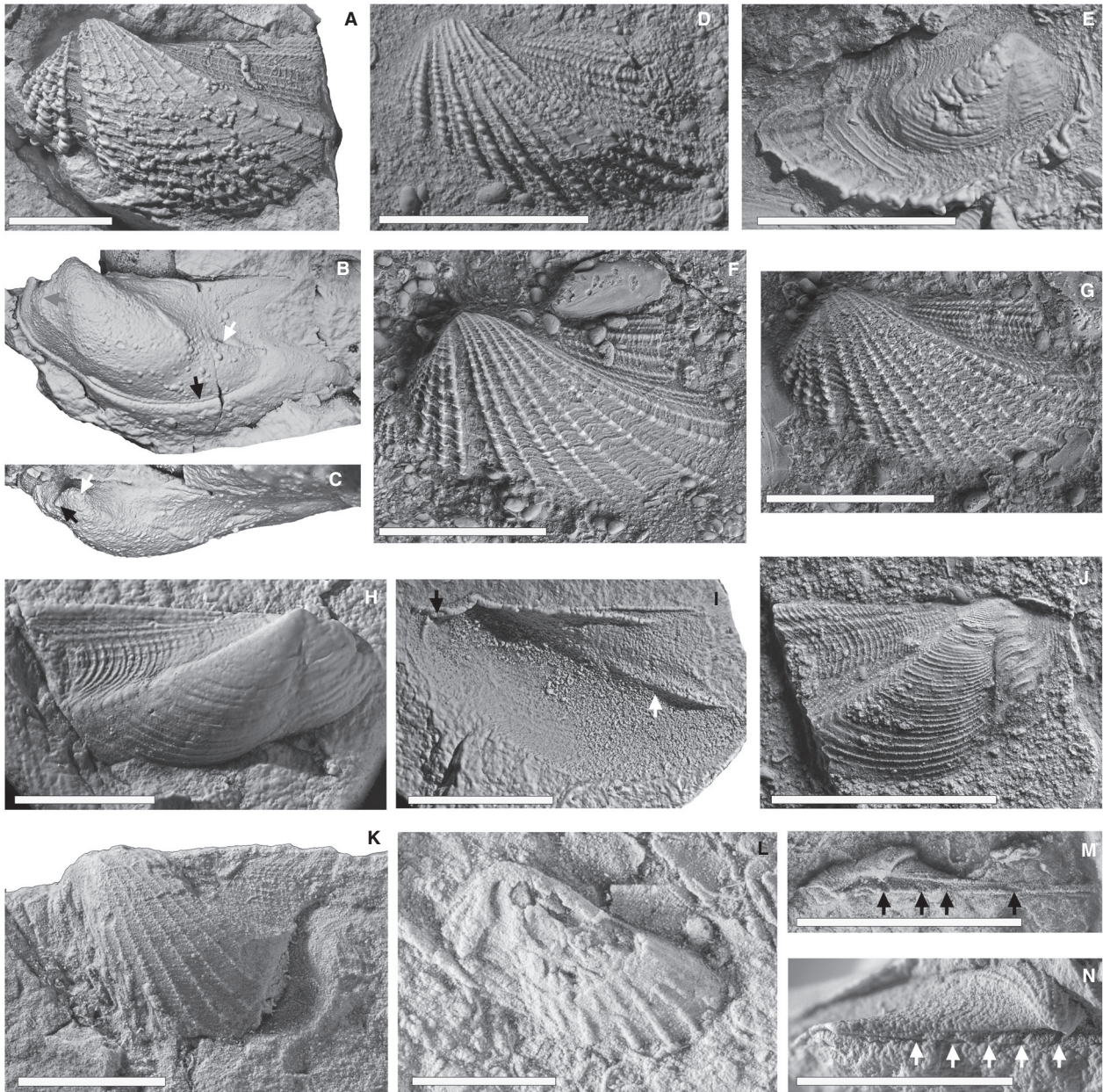


FIG. 12. A–J, M–N, *Towapteria peracuta* (Stache, 1878), Bellerophon Fm at Balest (BA) and Preroman (PR). K–L, syntypes of *Towapteria waehneri* (Kittl, 1903) from Han Orahovica, Sarajevo, Bosnia. D–G, J–L are preserved as shells replaced by calcite. A–C, MLCS98, BA150.0, LV: A, plaster cast of external mould; B, steinkern, lateral view, note the commarginal impression of the RV margin (black arrow), the short rib on the umbonal ridge marked as a short furrow (white arrow) and the anterior adductor scar (grey arrow); C, dorsal view with anterior retractor scars (black and white arrows). D, MLCS1317, PR117.02, LV. E, MLCS716, BA713.30, articulated specimen, RV view, note the crenulate margin of the LV overlapping the entire ventral margin of the RV. F, MLCS1331, PR3.117.16.02, LV. G, MLCS1870, PR3.117.29, LV. H, MLCS105, BA150.08, RV, plaster cast of external mould. I, MLCS113, BA150.16, RV, internal view of plaster cast of steinkern with rib on umbonal ridge (white arrow) and anterior hinge tooth (black arrow). J, MLCS1871, PR3.117.30, RV. K, NHMW 1998z0011/0001, syntype 1 of *T. waehneri* (Kittl, 1903), articulated specimen. L, NHMW 1998z0011/0016, LV, syntype 2 of *T. waehneri* (Kittl, 1903). M, MLCS2401, BA150.33, RV, plaster cast of external mould of hinge plate with ligament grooves (black arrows). N, MLCS2402, BA150.34, LV, plaster cast of external mould of hinge plate with ligament grooves (white arrows). Scale bars represent 5 mm.

(Fig. 12C), probably representing anterior retractor scars. RV posterior auricle with posterior adductor scar; adductor scar not observed on posterior auricle of LV. Ligament multivincular with up to five small ligamental grooves (Fig. 12M, N).

Remarks. Stache (1878) described ?*Gervillia peracuta* and ‘*Bakevelia ladina* cf. *bicarinata* King’ as two separate species, both from the Bellerophon Fm of San Martino (Preroman). The holotype of ?*G. peracuta* is a highly damaged LV. ?*Gervillia peracuta* can be attributed to the genus *Towapteria* because of the characteristic radial ornamentation and the dentition. The finding of new articulated specimens shows that ‘*B. ladina* cf. *bicarinata* King’ represents the RV of *Towapteria peracuta*, having the same shape and ornamentation and must, therefore, be included in Stache’s species.

When Nakazawa & Newell (1968) described *Towapteria nipponica* from the middle Permian of Japan, they noted significant similarities to *Avicula (Oxytoma) waehneri* Kittl, 1903 from the Bellerophon Fm from Sarajevo, which is known only from LVs. *Towapteria nipponica* has an LV with a minor obliquity and a greater number of ribs on the disc than *A. (O.) waehneri*. Nakazawa & Newell (1968) did not include *A. (O.) waehneri* in *Towapteria* mainly because of the distinctly separated trigonal anterior auricle figured in Kittl’s drawings. By examining the syntypes of *A. (O.) waehneri* (Fig. 12K, L), we could see that the anterior auricle is as poorly developed as in *Towapteria*. Therefore, also *A. (O.) waehneri* can be attributed to *Towapteria*. For the nearly identical shell shape and ornamentation *A. (O.) waehneri* can be considered a junior synonym of *T. peracuta*.

Palaeoecology. Stationary (endobyssate), epifaunal suspension feeder.

Order PECTINIDA Gray, 1854

Suborder ENTOLIIDINA Hautmann, 2011

Superfamily ENTOLIOIDEA Teppner, 1922

Family PENOPECTINIDAE Newell, 1938

Genus PENOPECTEN Winchell, 1865

Type species. *Aviculopecten limaformis* White & Whitfield, 1862.

Remarks. The comparison between *Pernopecten* and *Entolium* Meek, 1865 has been discussed by Newell (1938) and Yin (1982). *Pernopecten* is characterized by acuminate auricles on the LV projecting above the hinge line, slightly asymmetrical disc, well-developed lateral furrows and a byssal notch, whereas in *Entolium* the auricles of the LV and RV are not projecting above the hinge line, the disc is symmetrical and the lateral furrows are missing. The specimens from the Bellerophon Fm have all of the characters of *Pernopecten* and are referred to this genus.

Pernopecten tirolense (Stache, 1878)

Figure 13

v*1878 *Pecten (Entolium) tirolense* Stache, pp. 101–102, pl. 1, fig. 1 [indicated as *Pecten (Entolium) tirolensis* in figure caption].

Material. 34 specimens. 4 LVs from BA460; 21 LVs and 6 RVs from PR61; 2 LVs and 1 RV from JM28.

Description. LV medium-sized (max. H = 43 mm), subequilateral, orbicular and infracrescent. Beak acuminate, slightly shifted posteriorly from midpoint of hinge line. Umbonal angle 107°–130°. Anterior and posterior disc flanks short, anterior slightly concave and less inclined and shorter than posterior one. Shell smooth with slight and dense growth lines and weak radial striations. Some specimens with ‘filosus’ structure (*sensu* Waller 2006).

LV disc with central inflation, laterally limited by two radial furrows, anterior narrower than posterior one. Radial furrows of RV missing or only slightly developed. Auricles acuminate extending beyond hinge line. Anterior auricle slightly higher and narrower than posterior one, with small byssal sinus at base; posterior margin of posterior auricle a little inclined and slightly rounded. Anterior auricle angle c. 55° and posterior c. 67°.

RV disc weakly inflated and smooth. Auricles not protruding above hinge line. Anterior auricle narrower and smaller than posterior one and with a small byssal sinus. Posterior auricle with slightly inclined posterior margin.

Remarks. Stache’s holotype (Fig. 13A) is a tectonically laterally compressed specimen from Kreuzberg/Monte Croce. On the same slab this deformation is detectable also on *Cardium* (?*Conocardium*) sp. indet. (Stache (1878, table 4, fig. 14), here classified as *Eumorphotis praecurrens* Merla, 1930) and on the living chamber of *Tirolonautilus crux* and therefore the description of *P. tirolense* is here emended.

Pernopecten tirolense is very similar to *Pernopecten symmetricus* Newell, 1940, from the middle Permian (Capitanian) of the USA and the upper Permian (Wuchapingian and Changhsingian) of China. The specimens from the USA are, however, narrower and their auricles are less projected above the hinge line than those from the Bellerophon Fm.

Palaeoecology. Facultatively mobile, epifaunal suspension feeder.

Superfamily HETEROPECTINOIDEA Beurlen, 1954

Family HETEROPECTINIDAE Beurlen, 1954

Genus ETHERIPECTEN Waterhouse, 1963

Type species. *Etheripecten striatura* Waterhouse, 1963.

Remarks. Some pectinoids from the Bellerophon Fm have a fan-like shape and an ornamentation pattern consisting of faint, numerous, narrowly spaced and irregular ribs arranged in four orders of strength. A similar shell morphology is present in *Eumorphotis*, but in this genus the right posterior auricle is almost merging with the disc whereas it is well divided in the specimens described here. Similarities also exist with *Euchondria* Meek, 1874 with regard to the shell shape and ornamentation, but this genus has a pseudotaxodont hinge (Newell & Boyd 1987, 1995) not present in our specimens. Close similarities also occur with *Aviculopecten* M’Coy, 1851, *Heteropecten* Kegel &

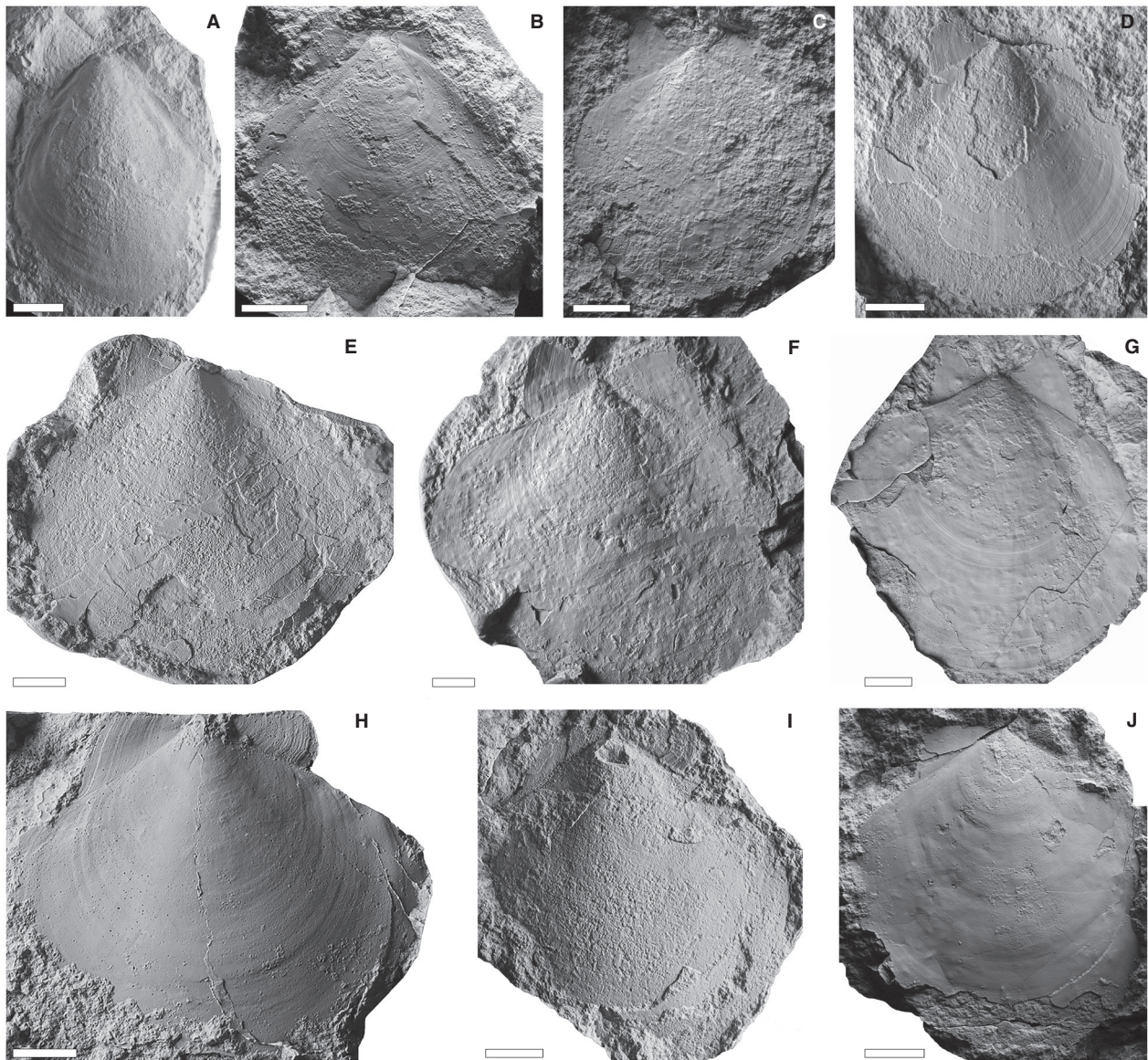


FIG. 13. *Pernopecten tirolense* (Stache, 1878), Bellerophon Fm at Preroman (PR) and Jmueia da Insom (JM). All specimens, except I, are preserved as shells replaced by calcite. A, GBA1878/001/00002, holotype from Monte Croce/Kreuzberg, tectonically compressed LV. B, MLCS1725, PR61a.278a, LV. C, MLCS1182, PR61a.151.02, LV. D, MLCS1061, PR61a.30.1, LV. E, MLCS1723, JM28.05, LV. F, MLCS1055, PR61a.24a, LV, plaster cast of external mould. G, MLCS1060, PA61a.29, LV preserved as shell replaced in calcite and combined with plaster cast. H, MLCS1724, JM28.06, RV, plaster cast of external mould. I, MLCS1726, PR61a.279, RV, steinkern. J, MLCS1197, PR61a.167, RV. Scale bars represent 5 mm.

Costa, 1951 and *Etheripecten*. The ornamentation pattern of *Aviculopecten* consists of simple and not graded (*sensu* Neves *et al.* 2014b) plicae on the RVs and LVs that grow by bifurcation in the RVs (Fang & Morris 1999). *Heteropecten* and *Etheripecten* cannot be distinguished based on RVs because they both have intercalated ribs. In the LVs of *Heteropecten* the primary ribs are broad and separated by narrower interspaces compared with *Etheripecten*, where the primary ribs are smaller and divided by broader interspaces (Waterhouse 2008; Neves *et al.* 2014b). The specimens from the Bellerophon Fm have an ornamentation consisting of narrow primary ribs separated by relatively wide

interspaces, which bear up to five minor order riblets. On the base of this ornamentation pattern these pectinoids are assigned to *Etheripecten*.

Etheripecten stuflesseri sp. nov.

Figure 14A–G

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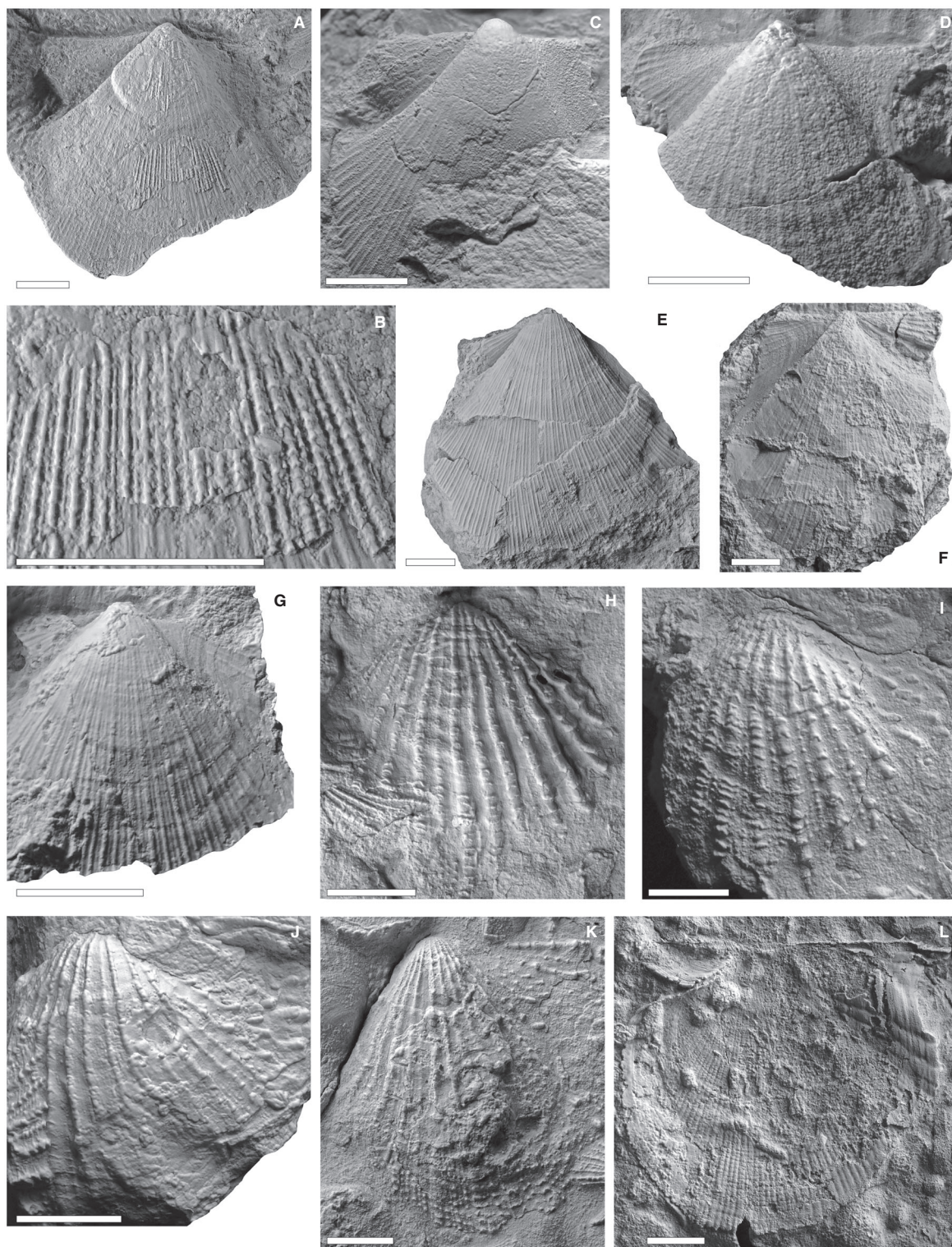


FIG. 14. A–G, *Etheripecten stuflesseri* sp. nov., Bellerophon Fm at Preroman (PR); all specimens except A and B are steinkerns. A–B, holotype, LV, MLCS1195, PR61a.164: A, lateral view with traces of shell replaced in calcite, B, detail of ribs with hyote scales. C, MLCS1289, PR61a.259, LV. D, MLCS1288, PR61a.258, LV. E–F, paratype, articulated specimen: E, MLCS1942, PR61b.290.01, LV; F, MLCS1942, PR61b.290.02, RV. G, MLCS1063, PR61a.32, LV. H–L, *Eumorphotis lorigae* Posenato *et al.*, 2005, Bellerophon Fm at Balest (SG) and Plan (PL). All specimens are preserved as shells replaced by calcite. H, MLCS699, SG13.05, LV. I, MLCS705, SG19.07, LV. J, MLCS718, SG32.01, LV. K, MLCS687, SG02.01, LV. L, MLCS1499, PL01, RV, internal view. Scale bars represent 5 mm.

Derivation of name. This species is named after Sofia Stuflesser da Digon for her help in the fieldwork at Preroman.

Holotype. MLCS1195, PR61a.164, LV with traces of shell replaced by calcite (Fig. 14A, B).

Paratype. 1 articulated specimen: LV, MLCS1942, PR61a.290.01 and RV, MLCS1942, PR61a.290.02 (Fig. 14E, F).

Other material. 8 specimens. 6 LVs, 1 articulated specimen and 1 RV from PR61.

Type locality & stratum. Preroman in the Badia Valley near San Martino/St Martin in Thurn/San Martin de Tor, bed PR61a. Upper Permian, Bellerophon Fm, Changhsingian.

Diagnosis. *Etheripecten* with up to 90 scaly ribs arranged in up to four orders. Between first-order ribs are intercalated up to five ribs of minor orders.

Description. Shell medium-sized (max H = 23 mm), infracrescent, slightly longer than high. LV disc subtriangular, slightly inflated and more convex in umbonal region, nearly flat close to ventral margin. Beak acuminate and slightly protruding beyond hinge line. Umbonal angle 70°–85°. Auricles subequal; anterior auricle long, subtriangular, with rounded anterior margin and clearly separated from disc by radial groove, sharper and deeper than that of posterior auricle. Anterior disc flank slightly concave, posterior straight. Posterior auricle acuminate with wide and deep auricular sinus. Anterior auricle with *c.* 10 radial ribs, stronger than those on posterior auricle. External alivincular ligament with strong steep bourrelets and triangular resilifer.

Disc ornament of 60–90 radial ribs divided into four orders and increasing by intercalation. At shell height of *c.* 10 mm, interspaces between primary ribs with up to five ribs of lower order. Ribs with hyote scales and subtriangular in cross-section. Auricle ornament with ribs of second and third order.

RV subtriangular and nearly flat. Umbo pointed and not protruding beyond straight hinge line. Anterior disc flank short, slightly concave, posterior disc flank much longer and straight. Ventral margin deeply rounded. Disc ornament of very fine, narrowly arranged and undifferentiated radial riblets, increasing by intercalation.

Auricles well-delimited from disc. Anterior auricle long, narrow, anteriorly expanding, obtuse at anterior margin, with up to seven radial ribs and separated from disc by deep and narrow auricular sinus. Posterior auricle subtriangular, extending ventrally to about half shell height with faint radial ribs.

Remarks. Only a few *Etheripecten* species have a high number of weakly differentiated radial ribs with small hyote scales similar to the specimens from the Bellerophon Fm (Fig. 14B). A similar shell shape and scaly ribs are present in *Etheripecten trichotomus* (Kegel & Costa, 1951) from the middle Pennsylvanian of Brazil, but this species has broader and fewer ribs than those from the Dolomites. *Etheripecten cf. mutabilis* (Licharew, 1927) from the upper Permian of Spitzbergen has hyote scales restricted only to the primary ribs of LVs (Nakazawa 1999). *Aviculopecten hataii*

Murata, 1964 and *Aviculopecten cf. hataii* described by Nakazawa & Newell (1968) from the middle Permian of Japan have the characteristic ornamentation pattern of *Etheripecten* and should therefore be placed in the latter genus. They are ornamented with up to four orders of radial ribs with hyote scales, similar to the Bellerophon Fm specimens. However, the Dolomites specimens have a larger number of ribs on the disc, weaker and thinner primary ribs, and auricles more separated from the disc and therefore a new species is here proposed.

Palaeoecology. Stationary (epibyssate), epifaunal suspension feeder.

Genus EUMORPHOTIS Bittner, 1901a

Type species. *Pseudomonotis telleri* Bittner, 1898.

Remarks. According to Bittner (1901a), *Avicula cingulata* Stache, 1878, *A. striatocostata* Stache, 1878, *Hinnites crinifer* Stache, 1878 and *Conocardium* sp. Stache, 1878 from the Bellerophon Fm could be included in his *Pseudomonotis telleri* and *Pseudomonotis multiformis* group, for which he proposed the name *Eumorphotis*. The new and abundant collected material from the Dolomites has all the characters of *Eumorphotis* reported in the literature (e.g. the left anterior auricle is considerably smaller than the posterior one and sharply divided from the disc by a steep anterior margin; posterior auricle is instead very large and slightly differentiated from the disc; Newell 1969) and adds to the knowledge on Stache's and Merla's species and their classification in Bittner's genus.

Eumorphotis lorigae Posenato et al., 2005

Figure 14H–L

v*2005 *Eumorphotis lorigae* Posenato et al., pp. 222–223, pl. 1, figs 1–9.

v2009 *Eumorphotis lorigae* Posenato et al.; Posenato, pp. 157, 162, figs 6.1–6.5.

Material. 12 specimens. 11 LVs from BA713; 1 RV from PL1.

Description. LV medium-sized (max H = 21 mm), well inflated with small and broad umbo, beak slightly protruding beyond hinge line. Posterior auricle wing-like expanded and moderately separated from disc by wide and slight depression. Anterior auricle not observed. Ornament of *c.* 12 narrow and raised first-order ribs with rounded crest. Minor order ribs added by intercalation. Disc and posterior auricle with strong hyote scales at intersection of growth lines with radial ribs. RV almost flat, with anterior auricle small and sharply separated from anterior disc flank by narrow byssal sinus. Posterior auricle much longer than anterior one, tapering to a point at the scaly dorsal margin and ornamented with growth lines, auricular sinus moderately deep. Disc ornament of faint radial ribs and growth lines, with exception of four stronger radial ribs near the posterior disc flank.

Remarks. *Eumorphotis lorigae* was first described from the uppermost marly beds of the Gerennavár Limestone, Bükk Mountains (Hungary), which are located in the stratigraphic interval recording the mass extinction event and c. 20 cm below the Permian–Triassic boundary (Posenato *et al.* 2005).

This species probably also occurs in the Tesero Member (Werfen Fm) of Bulla (Posenato 2009). The specimens described here from the upper Bellerophon Fm occur at c. 10 m below the Permian–Triassic boundary. They also have some similarities to the Lower Triassic *E. hinmitidea* Bittner, 1898, which is characterized by two orders of spondyloid radial ribs (Broglia Loriga & Mirabella 1986). However, in well-preserved specimens from the Bellerophon Fm, riblets of the third order are also present, the ribs are stronger and most hyote scales are concentrated on the posterior auricle, which differentiates them from Bittner's species. Therefore, we assign the Bellerophon Fm specimens to *E. lorigae*.

Palaeoecology. Stationary (epibyssate), epifaunal suspension feeder.

Eumorphotis praecurrens Merla, 1930

Figure 15

- v1878 ?*Conocardium* sp.; Stache, p. 124, pl.1, fig. 14.
- v*1930 *Eumorphotis praecurrens* Merla, pp. 94–95, text fig. 3.
- v1930 *Pseudomonotis (Eumorphotis) striato-costata* Stache; Merla, pp. 90–94, pl. 11, fig. 4.
- v1986 *Pseudomonotis (Eumorphotis) striatocostata* (Stache); Broglia Loriga & Mirabella, pp. 255–256, fig. 7b.
- v1986 *Eumorphotis praecurrens* Merla; Broglia Loriga & Mirabella, p. 255, fig. 6.

Material. 24 specimens. 1 LV from Ff1; 5 LVs and 1 RV from BA97; 1 LV and 2 RVs from BA150; 13 LVs and 1 RV from BA189.

Description. LV medium-sized (max. H = 40 mm), well-inflated, slightly retrocrescent and little longer than high. Anterior disc flank short and steep with slightly concave step (Fig. 15B). Beak small, tapering to a point at about the anterior one-third of hinge line length and slightly protruding beyond it. Umbo well inflated with umbonal angle of c. 80°. Disc ornament of 8–12 rounded, narrow but prominent first-order radial ribs separated by wide interspaces with considerably smaller second and third-order riblets. First-order ribs with hyote scales at regularly spaced intervals. Posterior auricle large, not distinctly separated from disc and with deep auricular sinus; ornamented with 3–4 faint second-order ribs. Anterior auricle small, narrow, ranging from triangular to subrectangular with radial riblets. Anterior auricular angle c. 48°.

RV flat and slightly retrocrescent; dorsal margin straight, anterior disc flank slightly concave, posterior disc flank merging with posterior auricle, ventral margin broadly rounded. Small and pointed beak behind the midpoint of hinge and not protruding over thick and scaly ribbed hinge margin. Umbonal angle c. 100°. Anterior auricle narrow, long, subtriangular with six scaly riblets and separated from the disc by a deep and

narrow byssal notch; anterior auricular angle c. 47°. Posterior auricle expanding and acuminate with deep auricular sinus; posterior auricular angle c. 34°. Posterior auricle ornamentation with about three first-order spiny ribs intercalated by riblets of second and third order. Disc with c. 40 faint ribs and irregular strong concentric growth lines.

Remarks. Merla (1930) proposed the new species *E. praecurrens* based on an RV steinkern with shell fragments from Monte Croce di Comelico/Kreuzberg in the eastern Dolomites. Merla (1930) also described an LV from the same locality as *Pseudomonotis (Eumorphotis) 'striato-costata'* Stache. However, this LV differs from the holotype of *E. striatocostata* (Stache, 1878) in that it has a subrectangular and longer anterior auricle and stronger radial ornamentation. *Eumorphotis* specimens from the lower Bellerophon Fm (Lo3) of the western Dolomites, consisting both of LVs and RVs, have the same morphological characters as the material described by Merla (1930) from the eastern Dolomites. Therefore, the LV, previously determined by Merla as *E. striatocostata*, is here considered as an LV of *E. praecurrens*. *Eumorphotis striatocostata* is common in the upper Bellerophon Fm of the western Dolomites. The internal surface of the holotype of *E. praecurrens*, preserved in limestone, is smooth, while it has radial ornamentation in the specimens embedded in dolostones from the western Dolomites. This difference is due to the different preservation state of the inner aragonite layer, which has been replaced by calcite in the holotype while it underwent an early diagenetic dissolution in the other specimens.

Eumorphotis praecurrens differs from *E. cingulata* (Stache, 1878) in having a wider, less inflated umbo, a steeper anterior dorsal margin and narrower, higher ribs, intercalated with considerably smaller riblets. *Eumorphotis striatocostata* is characterized by a triangular anterior auricle and wider, flattened primary ribs, intercalated with narrower secondary riblets. *Eumorphotis lorigae* bears narrow scaly and spiny ribs and riblets.

Palaeoecology. Stationary (epibyssate), epifaunal suspension feeder.

Eumorphotis striatocostata (Stache, 1878)

Figure 16

- v*1878 ?*Avicula striatocostata* Stache, p. 110, pl. 1, fig. 13.
- v1878 *Hinnites crinifer* Stache, p. 100, pl. 1, fig. 10.
- ?1898 *Pseudomonotis bocharica* Bittner, pp. 717–718, pl. 15, fig. 1.
- ?1908 *Pecten duronicus* Wittenburg, p. 268, pl. 1, figs 7, 8.
- ?1930 *Pterinopecten cf. granosus* Hind; Merla, pp. 97–98, pl. 11, fig. 3.
- ?1981 *Eumorphotis* sp. aff. *bokharica* Bittner; Nakazawa, pp. 102–103, pl. 9, figs 22–25.

Material. 136 specimens. 7 LVs from BA460; 6 LVs and 2 RVs from BA461; 13 LVs and 5 RVs from BA463; 23 LVs from BA599; 1 LV from BA634; 1 LV from BA664; 2 LVs and 1 RV

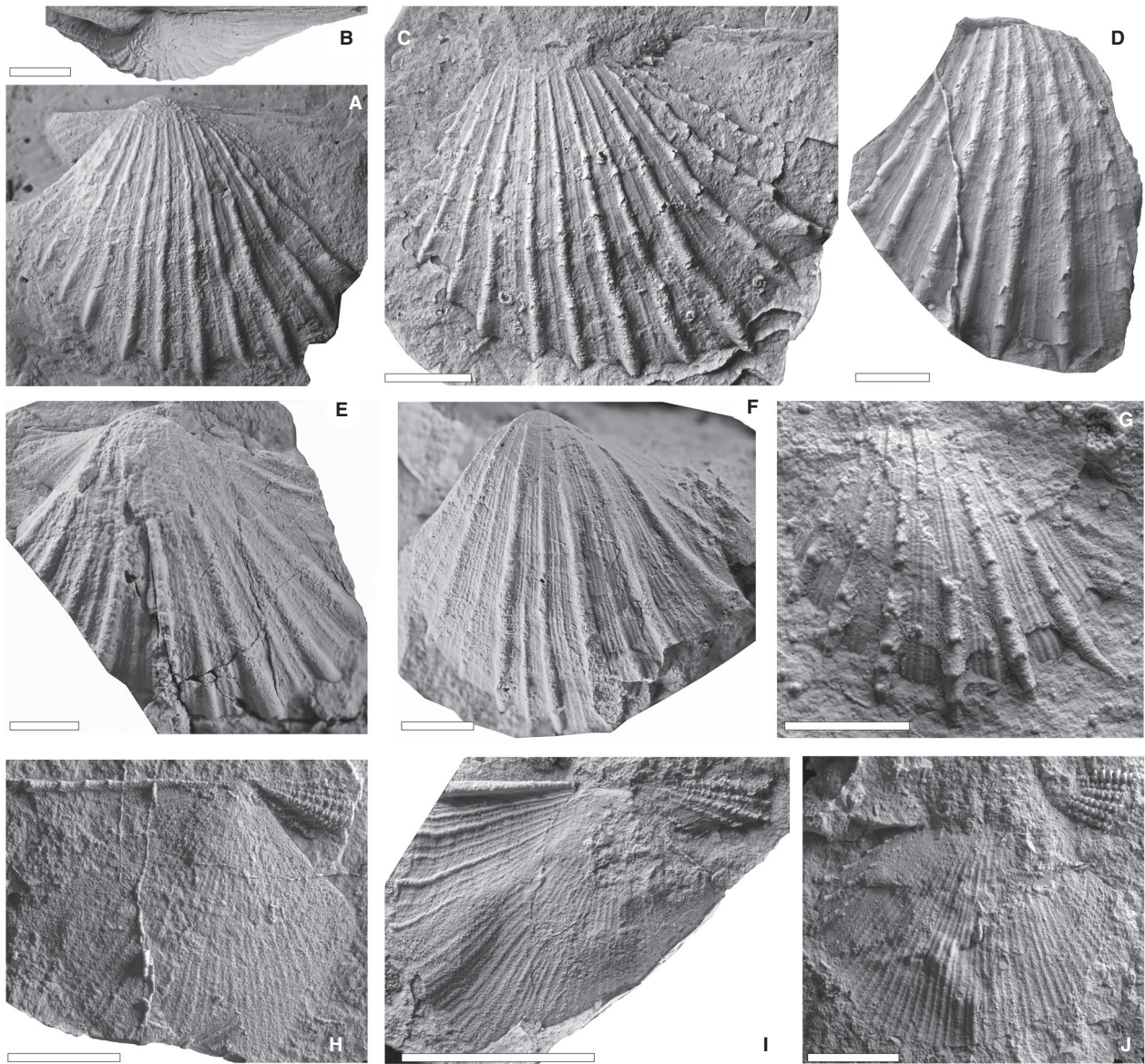


FIG. 15. *Eumorphotis praecurrens* (Merla, 1930), Bellerophon Fm, NH A at Balest (BA). A–C, MLCS154, BA189.25, LV: A, steinkern, lateral view; B, steinkern, dorsal view; C, plaster cast of external mould. D, MLCS139, BA189.10a, LV, plaster cast of external mould. E, MLCS139, BA189.10b, LV, steinkern. F, MLCS132, BA189.03, LV, composite mould. G, MLCS150, BA189.21, LV, plaster cast of external mould with spines. H, MLCS99, BA150.02. RV, plaster cast of external mould. I, MLCS1716, BA189.44, RV, plaster cast of external mould. J, MLCS103, BA150.06, RV, plaster cast of external mould. Scale bars represent 5 mm.

from BA713; 2 LVs from BA731; 17 LVs and 1 RV from PR61; 1 LV from RPGVBB; 8 LVs from SE56; 1 LV from SE142; 3 LVs from JM28; 39 LVs and 2 RVs from JM188; 1 LV from TR.

Description. Shell medium-sized (max. H = 45 mm), infracrescent to slightly retrocrescent. LV hinge line slightly shorter than shell length; posterior disc flank considerably longer than anterior one. Ventral margin long and well rounded. Umbonal angle c. 80°. Beak slightly opisthogyrate, from small and acuminate in early growth stages to broad and obtuse in mature specimens, at about the anterior one-third of valve length. Hinge margin

thickened and scaly. Anterior auricle small, subtriangular, with faint radial riblets and strong growth lines, sharply separated from disc by steep anterior disc flank.

Posterior auricle broad, wing-like expanded, not distinctly delimited from disc, acuminate and with shallow auricular sinus. Posterior auricle with up to seven radial ribs bearing short hyote scales.

Disc with 9–16 broad, but low, first-order radial plicae, intercalated with considerably smaller and narrower second-order ribs and slightly thinner third-order riblets, forming bundles on slopes of primary plicae. Second and third order ribs not always

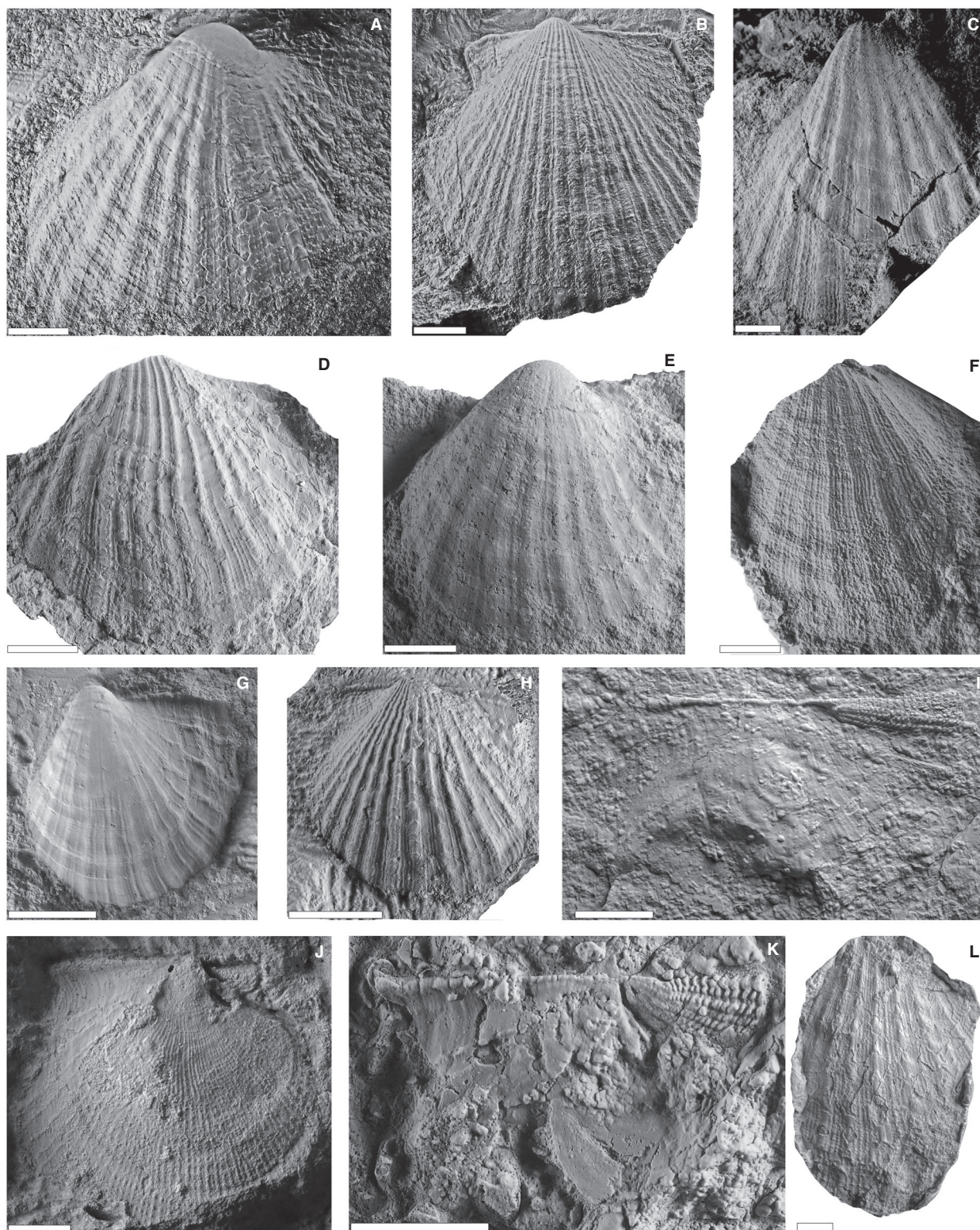


FIG. 16. *Eumorphotis striatocostata* (Stache, 1878), Bellerophon Fm, NH B at Balest (BA), Jmucia da Insom (JM) and Preroman (PR). All specimens except E preserved as shells replaced by calcite. A, MLCS754, BA463b.01, LV. B, MLCS1713, BA463.89, LV. C, MLCS1712, BA463.88, LV. D, MLCS1718, PR61a.277, incomplete LV. E, MLCS1715, BA463.91.01, LV, steinkern. F, MLCS1722, JM28.01, incomplete LV. G, MLCS755, BA463b.02, LV of juvenile specimen. H, MLCS534, BA463.39, LV of juvenile specimen. I, MLCS837, JM188a.01c.02, RV. J, MLCS561, BA463.66, RV. K, MLCS1717, JM197.05, RV. L, MLCS1938, PR61a.289.01, LV. Scale bars represent 5 mm.

clearly distinguishable. First-order plicae sometimes with nodes and small scales. Disc and primary ribs with faint crenulate and dorsally arched growth lines.

RV flat, thinner than LV and with flattened umbo. Posterior auricle expanded, almost undifferentiated from disc and with auricular sinus on posterior margin. Hinge margin thickened with slight scales, larger on posterior part. Anterior auricle with 4–5 radial scaly riblets. Disc ornamentation weak with low and scaly radial plicae.

Remarks. Stache (1878) remarked on the great similarity of *Avicula* (= *Eumorphotis striatocostata*) to *A.* (= *Eumorphotis cingulata*), both species coming from Monte Croce di Comelico/Kreuzberg. The holotype of *E. cingulata* is lacking the anterior auricle and the ornamentation consists in narrowly packed, variously protruding and irregularly arranged radial ribs, which are the distinctive features of this species. None of specimens here described belongs to this species. Tommasi (1896) and Gortani (1906) assigned more than a hundred specimens from Carnia to '*Avicula striato-costata*' Stache, but for the irregular ornamentation they should be attributed to *E. cingulata*.

The holotype of *Hinnites crinifer* Stache, 1878 is a badly preserved LV with multiple growth interruptions. The disc ornamentation consists of broad and flat first-order ribs intercalated with finer riblets, which can be grouped into bundles. This ornamentation pattern is typical for *E. striatocostata* and therefore *H. crinifer* is considered a synonym of former species. *Eumorphotis striatocostata* seems to be related to some Early Triassic *Eumorphotis* species. *Pseudomonotis* (= *Eumorphotis bocharica* Bittner, 1898, erected based on a badly preserved specimen from the ?Early Triassic of Tajikistan and *Eumorphotis* sp. aff. *bokharica* Nakazawa, 1981, from the Early Triassic of Kashmir, have a nearly identical shell shape to *E. striatocostata*, but *E. bocharica* and *E. sp. aff. bokharica* seem to possess only one second-order riblet intercalated with the broad and flattened first-order ribs. This ornamentation type, although rare, falls within the variability of *E. striatocostata* therefore the two species could be considered as synonymous. *Eumorphotis duronicus* (Wittenburg, 1908) from the lower Werfen Fm has a very similar ornamentation to *E. striatocostata*. However, the incompleteness and absence of the auricles of *E. duronicus* do not permit a definitive diagnosis. The ornamentation pattern of *E. amplicostata* Ciriacks, 1963 from the Lower Triassic Dinwoody Fm of USA (Ciriacks 1963; Hofmann *et al.* 2013b) is nearly identical to *E. striatocostata*. But in *E. striatocostata* the posterior auricle of the LV has small spines on the ribs and only a shallow auricular sinus, whereas the posterior auricle of *E. amplicostata* is small, has a deep auricular sinus and is lacking spines.

Palaeoecology. Stationary (epibyssate), epifaunal suspension feeder.

Superfamily AVICULOPECTINOIDEA Meek & Hayden, 1865

Family ASOELLIDAE Begg & Campbell, 1985

Genus GARDENAPECTEN nov.

LSID. <https://zoobank.org/nomenclaturalacts/F6412949-5F31-4279-80D6-1F0193470587>

Derivation of name. The new genus is named after Gardena Valley, where the majority of specimens were found.

Type species. '*Pecten trinkeri* (Stache, 1878).

Diagnosis. Shell pectiniform with anterior auricle of LV slightly larger than posterior one and radially folded, with rounded anterior margin and shallow to absent auricular sinus; posterior auricle of LV acuminate with deep auricular sinus; disc with three orders of radial plicae intercalated in different ranks; beak slightly projecting over hinge line; anterior auricle of RV, narrow, triangular, separated from disc by deep byssal notch and bipartite by radial furrow; left auricle separated from disc by radial swell.

Remarks. Stache (1878) described five species of '*Pecten (Aviculopecten)*' from the Bellerophon Fm: *P. (A.) guembeli*, *P. (A.) trinkeri*, *P. (A.) pardulus*, *P. (A.) comelicanus* and *P. (A.) cf. coxanus* Meek & Worthen, 1860. The comparison of Stache's holotypes with the new collected specimens led us to consider all of the afore cited species as congeneric and belonging to the here proposed new genus *Gardenapecten*. The differences between the species described by Stache (1878) can be explained by poor preservation, growth anomalies, high intraspecific variability and different shape of growth stages.

Gardenapecten gen. nov. has similarities (e.g. distinct auricles and plicated ornamentation) but also significant differences to the following genera: *Aviculopecten* differs in having subequal radial plicae on the disc and an anterior auricle that is not radially bipartite; *Guizhoupecten* Chen, 1962 has a lower number of radial plicae on disc and an anterior auricle much smaller than the posterior one; *Deltopecten* Etheridge in Jack & Etheridge, 1892, differs in having simple radial plications and an anterior auricle of RV much larger than posterior one; *Streblochondria* Newell, 1938 has a smaller right anterior auricle on the RV and an inequilateral shell.

The ornamentation of *Limipecten* Girty, 1904, consists of riblets, large low plications and pointed intercostal scales, which are absent in the here proposed new genus. *Heteropecten* and *Etheripecten* have well-defined auricles on LVs but in both genera the radial undulations on the left anterior auricle and the bipartition of the right anterior auricle are missing. *Fransonia* Newell & Boyd, 1995, has a bipartite anterior auricle on the RV, similar to the proposed new genus, but the radial sculpture of the LV consists of ribs and not plicae. The RV is smooth and the hinge has a distinctive dentition, which is lacking in the specimens from the Bellerophon Fm. *Eumorphotis* has the left posterior auricle much larger than the anterior one. The auricles of *Leptochondria* Bittner, 1891, are subequal, slightly separated from the disc and the anterior auricle is not radially bipartite. *Gardenapecten* gen. nov. has an external alivincular ligament and can therefore be assigned to the family Asoellidae.

Gardenapecten trinkeri (Stache, 1878) comb. nov.

Figure 17

v*1878 *Pecten (Aviculopecten) trinkeri* Stache, p. 105, pl. 1, fig. 6.

- v1878 *Pecten pardulus* Stache, p. 104, pl. 1, fig. 7.
v1878 *Pecten (Aviculopecten) Gümbeli* Stache, p.107–108, pl. 1, fig. 5.
1906 *Pseudomonotis forojuliensis* Gortani, p. 104, pl. 5, figs 1, 2, 10.9.
1906 *Pseudomonotis irregularis* Gortani, p. 105, pl. 5, fig. 7.
1927 *Pecten gümbeli* Stache; Ogilvie Gordon, p. 11, pl. 1, fig. 2a–c.
1927 *Pecten trinkereri* Stache; Ogilvie Gordon, p. 12, pl. 1, fig. 3a, b.
1930 *Eumorphotis josephi* Leonardi, pl. 1, figs 2, 3.
v1930 *Chlamys pardula* Stache; Merla, p. 110, pl. 9, fig. 5.
v1930 *Pecten gümbeli* Stache; Merla, p. 111, pl. 9, fig. 7.

Material. 1116 specimens. 26 LVs and 15 RVs from BA231; 15 LVs and 1 RV from BA599; 36 LVs from BA634; 29 LVs and 6 RVs from BA713; 16 LVs and 1 RV from BU36; 8 LVs from BU112; 62 LVs from CUGVBB; 176 LVs from RPGVBB; 1 RV from PR11; 1 LV from PR3,117; 12 LVs from PR136; 189 LVs and 14 RVs from PR139; 11 LVs and 5 RVs from PR145; 18 LVs and 4 RVs from SE56; 125 LVs and 18 RVs from SE140; 67 LVs from SE142; 45 LVs and 1 RV from SE145; 19 LVs from SE164; 56 LVs from SE168; 5 LVs and 2 RVs from TR; 7 LVs from JM144; 3 LVs from JM188; 95 LVs and 27 RVs from JM195.

Description. LV pectiniform, thin-shelled, small (max. H = 20 mm), weakly inflated, subequilateral and infracrescent. H/L = 0.90–1.17. Until height of 13 mm shell slightly higher than long, then height and length nearly equal. Anterior and posterior disc flanks long and straight, with anterior slightly shorter than posterior. Ventral margin well-rounded and gradually connected to anterior and posterior margins. Hinge margin straight and shorter than shell length. Beak low and pointed, situated at centre of hinge margin. Umbonal angle 98°–110°. Ligament external alivincular, resilient small and elongated; defined bourrelets lacking. Anterior auricular angle 38°–45°, posterior auricular angle 30°–41°. Anterior auricle subrectangular and larger than posterior one, with rounded anterior margin and shallow auricular sinus; radially undulating, with ventral fold followed by dorsal radial sulcus towards hinge margin; ornamented with slight radial ribs and strong growth lines. Posterior auricle acuminate, with deep auricular sinus, decorated with fine radial ribs and growth lines; and separated from disc by shallow radial furrow.

Disc with three orders of radial plicae, from 25 in juveniles to 64 in adults. Primary plicae rounded and slightly widening ventrally; secondary and tertiary plicae irregularly inserted by intercalation; lateral plicae slightly concave. Disc surface with slightly raised growth lines which form, with radial plicae, a reticulate pattern.

RV flattened and thinner than LV. Dorsal margin shorter than shell length. Umbo almost flattened. Posterior auricle acuminate with deep auricular sinus. Anterior auricle subtriangular, bipartite by radial furrow and separated from disc by deep and narrow byssal notch. Auricle ornament of faint growth lines only. Disc ornament of shallow radial plicae.

Remarks. Stache's (1878) '*Pecten (Aviculopecten)*' species were exclusively based on LVs lacking both auricles, except for *P. (A.)*

trinkereri, which is here designated as the *Gardenapekten* type species.

Pecten (A.) trinkereri and *P. (A.) pardulus* are both juvenile specimens of the same species. *Pecten (A.) gümbeli* has a shell slightly longer than high due to deformation, but it is here considered as conspecific with *P. (A.) trinkereri*. *Pecten (A.) trinkereri* can instead be distinguished from *P. (A.) comelicanus* and the conspecific *P. (A.) cf. coxanus* Meek & Worthen by its narrower shell shape and smaller umbonal angle.

Gortani (1906) described several pectinid species from the Bellerophon Fm of Carnia, which he assigned to *Pecten* sp., *Aviculopecten comelicanus* Stache, *A. cf. gümbeli* Stache, *Pseudomonotis irregularis* Gortani, *A. trinkereri* Stache and *Pseudomonotis forojuliensis* Gortani. All of these specimens, which came from a single limestone slab, are conspecific and belong to *Gardenapekten* gen. nov.

Ogilvie Gordon (1927) described *P. comelicanus* and *P. gümbeli* from the Bellerophon Fm of Val Gardena and identified the smaller specimens as *P. gümbeli*, a species here considered a synonym of *Gardenapekten trinkereri*. *Chlamys pardula* Merla (1930) and *Eumorphotis josephi* Leonardi, 1930, with a bipartite right anterior auricle, are also here considered as synonymous with *G. trinkereri*.

Palaeoecology. Stationary (epibyssate), epifaunal suspension feeder.

Gardenapekten comelicanus (Stache, 1878) comb. nov.

Figure 18

- v*1878 *Pecten (Aviculopecten) comelicanus* Stache, p. 106, pl. 1, fig. 4.
v1878 *Pecten (Aviculopecten) cf. coxanus* Meek & Worthen; Stache, p. 105, pl. 1, fig. 3.
1927 *Pecten comelicanus* Stache; Ogilvie Gordon, p. 11, pl. 1, fig. 1.

Material. 171 specimens. 27 LVs from BA461; 2 LVs and 1 RV from BA463; 9 LVs and 1 RV from BA731; 5 LVs from PR61; 29 LVs and 2 RVs from PR152; 64 LVs from PR246; 19 LVs from SE164; 12 LVs from JM28.

Description. LV pectiniform, thin-shelled, small (max. H = 20 mm), weakly inflated, subequilateral and infracrescent. Mature shells with height equal to or slightly exceeding length. Anterior disc flank straight, extending ventrally to about one-third of shell height and posterior disc flank straight to slightly convex, extending ventrally to about half shell height. Ventral margin broadly rounded, continuously passing to anterior and posterior margins.

Hinge margin straight and shorter than shell length (hinge L/L c. 1.3). Beak acuminate, low, situated at centre of hinge line and only slightly projecting. Umbonal angle 106°–122°. H/L ratio 0.93–1.08. Posterior auricular angle 22°–30°. Anterior auricle narrow, subrectangular and slightly larger than posterior one, with rounded anterior margin and shallow auricular sinus. Anterior auricle radially folded with swollen

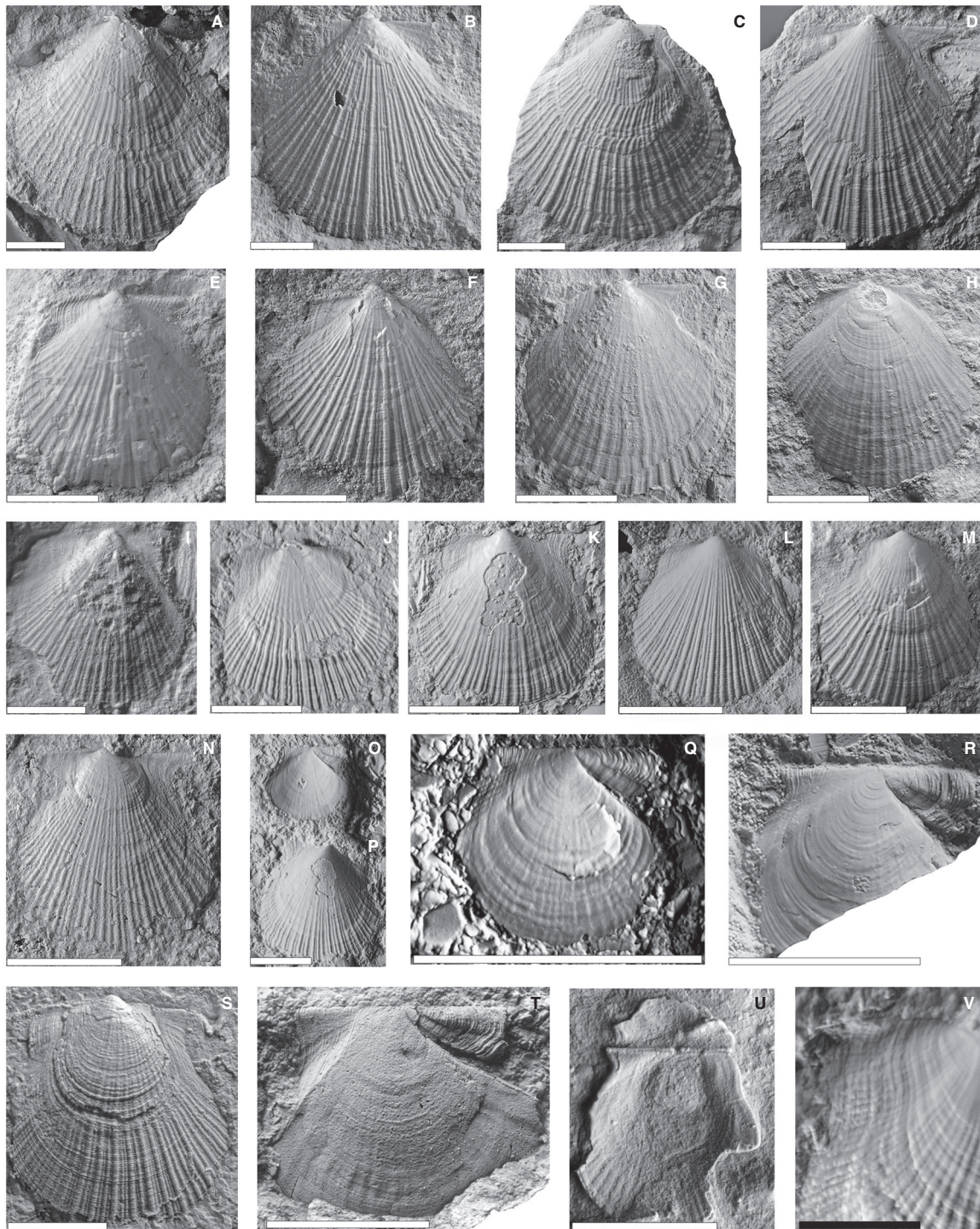


FIG. 17. *Gardenapeecten trinkeri* (Stache, 1878) comb. nov., Bellerophon Fm, GVBB at Culatsch (CU) and Balest (BA). All specimens preserved as shell replaced by calcite: A, MLCS975, CUGVBB.02, LV. B, MLCS1666, CUBHGV.76, LV. C, MLCS1696, CUGVBB.96, LV. D, MLCS1674, CUGVBB.84, LV. E, MLCS1685, CUGVBB.91, LV. F, MLCS1673, CUGVBB.83, LV. G, MLCS1695, CUGVBB.95, LV. H, MLCS1686, CUGVBB.92, LV. I, GBA1878/001/0006, holotype, LV. J, MLCS1689, BA231.158, LV. K, MLCS1585, BA231.145, LV. L, MLCS1579, BA231.144, LV. M, MLCS1580, BA461.138.02, LV. N, MLCS1682, CUBHGV.89. O, MLCS1586, BA231.146, RV. P, MLCS1585, 231.145, LV, internal view. Q, MLCS1588, BA231.148, RV. R, MLCS1595, BA231.155, RV. S, MLCS192, BA231.20, LV, plaster cast of external mould. T, MLCS187, BA231.15a.01, RV, plaster cast of external mould. U, MLCS1939, PR141.01, articulated shells with LV and broken RV. V, MLCS1689, BA231.158, detail of anterior auricle of J. Scale bars represent: 5 mm (A–U); 1 mm (V).

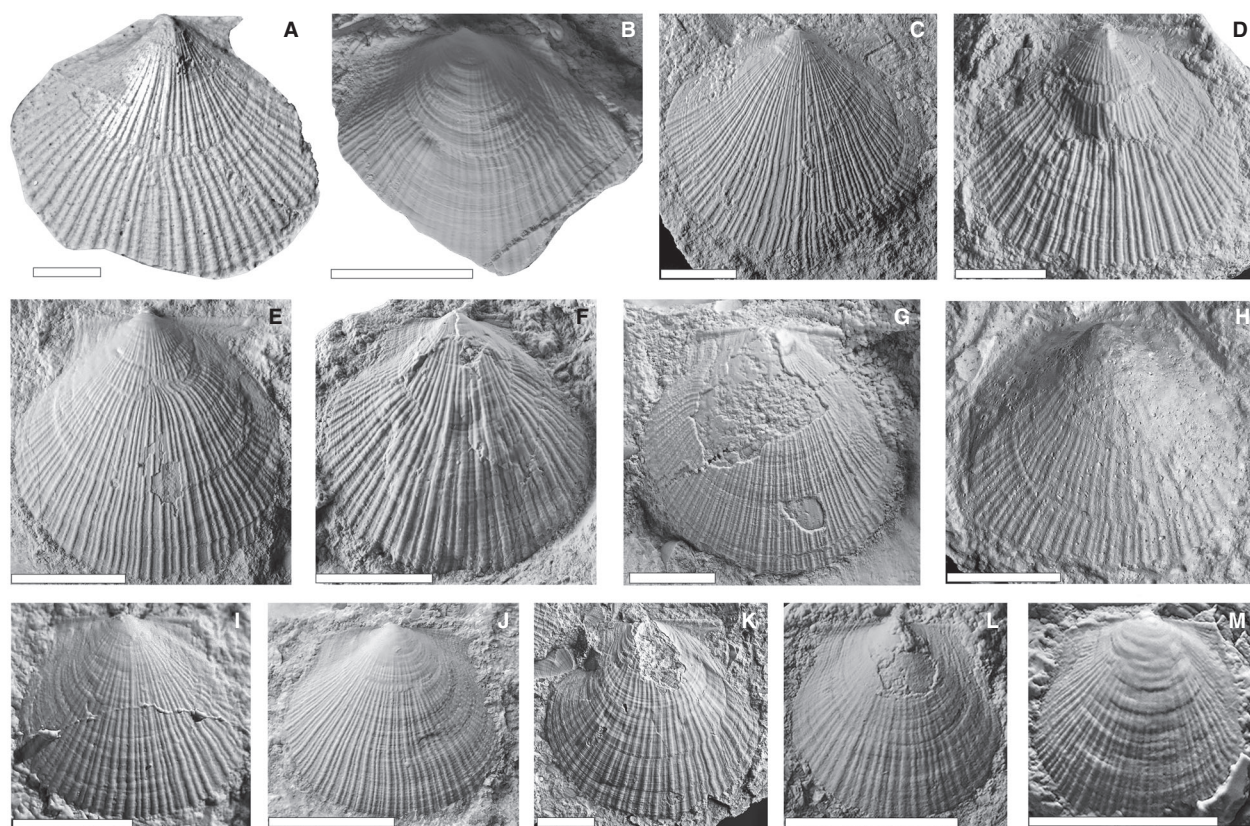


FIG. 18. *Gardenapecten comelicanus* (Stache, 1878) comb. nov., Bellerophon Fm, NH B at Balest (BA) and Jmueia da Insom (JM). A, GBA1878/001/0007, LV, gypsum cast of holotype from Val di Rin, Auronzo di Cadore. B, MLCS1677, BA461.151, LV. C, MLCS1599, BA461.144, LV. D, MLCS1690, BA461.154, LV. E, MLCS1602, BA461.147, LV. F, MLCS1600, BA461.145, LV, plaster cast. G, MLCS1693, JM28.02, LV. H, GBA1878/001/0005, '*Pecten (Aviculopecten)*' cf. *coxanus* Meek & Worthen from San Giacomo/St Jacob, LV, gypsum cast. I, MLCS1581, BA461.139, LV, plaster cast. J, MLCS1601, BA461.146 LV. K, MLCS1363, PR152.11.01, LV. L, MLCS1583.01, BA461.141, LV. M, MLCS1598, BA461.143, LV. Scale bars represent 5 mm.

ventral part and sulcus near hinge margin. Anterior auricle ornamented with fine radial ribs and growth lines. Posterior auricle narrow, acuminate, with deep auricular sinus and ornamented with fine radial ribs and strong growth lines. Disc with variable number of radial plications of three orders, ranging from 43 in the holotype to 86 in specimen MLCS1693, JM28.02 (Fig. 18G). Primary plicae rounded and slightly widening ventrally, secondary and tertiary plicae irregularly inserted by intercalation. Lateral plicae bending slightly outwards.

Remarks. *Pecten comelicanus* Stache is assigned to the new genus *Gardenapecten* for the radially folded anterior auricle. It can be distinguished from *G. trinkeri* by the larger umbilical angle, the smaller auricular angles and a more rounded outline. *Pecten (A.)* cf. *coxanus* Meek & Worthen (Fig. 18H) is conspecific with *G. comelicanus* because it has a large umbonal angle.

Palaeoecology. Stationary (epibyssate), epifaunal suspension feeder.

Superfamily LIMOIDEA Rafinesque, 1815

Family LIMIDAE Rafinesque, 1815

Genus PALAEOlima Hind, 1903

Type species. *Pecten simplex* Phillips, 1836, p. 212; by subsequent designation (Cox 1952, p. 48).

Remarks. The genus *Palaeolima* is characterized principally by a small obliquely ovate shell with obtuse auricles; the surface is smooth or with radial ribs, grouped in pairs or bunches in some species (Cox & Hertlein in Cox *et al.* 1969). Our specimens have all of these typical characters.

Palaeolima badiotica sp. nov.

Figure 19

1906 *Lima footei* Waagen; Gortani, p. 107, pl. 5, fig. 5.

LSID. <https://zoobank.org/nomenclaturalacts/1B8A4BB4-1A55-419C-AAB6-71DD57CA08C2>

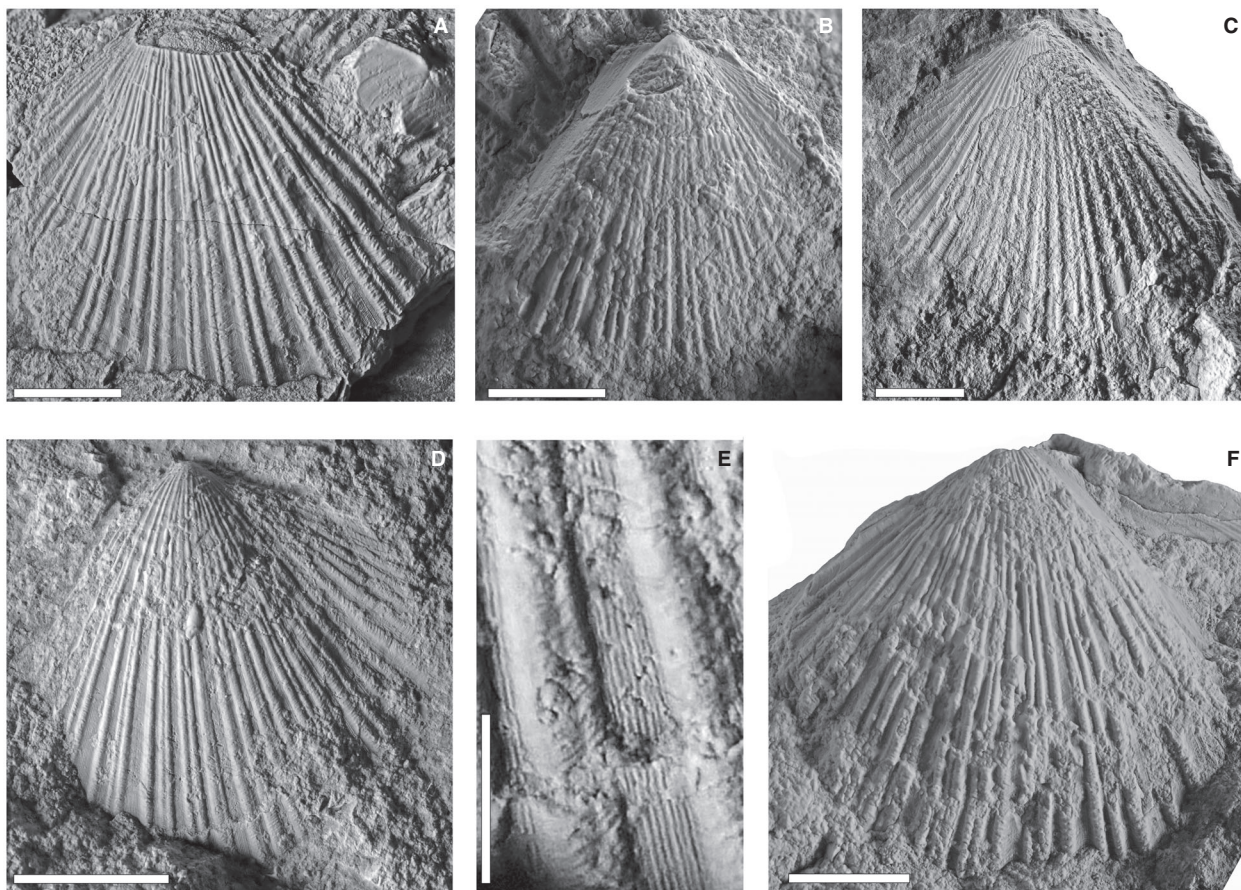


FIG. 19. *Palaeolima badiotica* sp. nov., Bellerophon Fm, NH B at Preroman (PR) and Balest (BA). All specimens preserved as shells replaced by calcite. A, MLCS1069, PR61a.38, LV. B, MLCS1048, PR61a.17, holotype, RV. C, MLCS1286, PR61a.256a, LV, steinkern. D, MLCS308, BA460.04, RV. E, detail of D, riblets between ribs. F, MLCS1894, PR61a.287, LV. Scale bars represent: 5 mm (A–D, F); 1 mm (E).

Derivation of name. From Badia Valley, the locality where the holotype was found.

Holotype. MLCS1048, PR61a.17, RV preserved as shell replaced by calcite (Fig. 19B).

Other material. 12 specimens. 2 LVs from BA460; 1 LV from BA461; 4 LVs and 4 RVs from PR61; 1 RV from JM28.

Type locality & stratum. Preroman near San Martino/St Martin in Thurn (Badia Valley), bed 61a. Upper Permian, Bellerophon Fm, Changhsingian.

Diagnosis. *Palaeolima* with very small anterior auricle. Posterior auricle long, narrow, slightly separated from disc and with broadly rounded anterior margin; posterior auricle and disc with up to 34 radial plicae, grouped in bundles each with 2–3 plicae; broad interspaces with weak radial riblets.

Description. Medium-sized, equivalve, broad, obliquely suboval, slightly prorescent shell with height and length almost equal. Anterior disc flank obliquely truncated, forming a steep step.

Shell surface inclined from anterior disc flank towards posterior auricle. Posterior auricle obtuse triangular, almost flat, much larger than anterior auricle, only weakly separated from disc by slight radial furrow and with broadly rounded posterior margin. Anterior auricle small and obtuse-triangular, almost indistinct from anterior disc flank. Beak small, acuminate, placed a little anteriorly from midpoint of hinge and protruding slightly above it. Umbonal angle *c.* 85°.

Up to 34 irregularly arranged strong plicae covering disc and anterior auricle. Plicae with triangular section on umbo, becoming more rounded and flattened ventrally. Plicae splitting in equal pairs or into primary and much smaller secondary plicae; bundles of 3 plicae also present. Plicae more crowded on posterior part of disc and posterior auricle, where also interspaces are narrower than on anterior part. Wide interspaces between plicae with up to 12 very faint radial riblets. Strong growth lines on plicae. Posterior auricle with 7–8 plicae, gradually decreasing in size towards posterior margin.

Remarks. The limiids from the Dolomites are characterized by a broadly rounded posterior auricular margin and fine riblets between plicae, which distinguish them from the majority of

Palaeolima species. *Palaeolima furcopicata* (Grabau, 1931) from the upper Permian of Mongolia has similar riblets between the primary plicae. However, *P. furcopicata* has a more perpendicular shell and both stronger and fewer plicae, which split only in pairs of equal strength. The specimen of *P. chekiangensis* (Ku & Chen in Li *et al.*, 1963) from Changhsingian of China figured by Gu *et al.* (1976, pl. 17, fig. 23) has a similar shell shape with the shallow posterior furrow, as noted for the specimens from the Bellerophon Fm. *Palaeolima chekiangensis* bears c. 35 plicae grouped in bundles on the disc and posterior auricle, but the interspaces between the plicae are lacking the fine riblets, which distinguish it from the Dolomites specimens. *Palaeolima fasciculicostata* Liu in Gu *et al.*, 1976 (p. 236, pl. 17, figs 22, 24, 25; Zhang *et al.* 1977, p. 519, pl., 198, fig. 18) from the Changhsingian of China has a similar shell shape with splitting plicae on disc, but the posterior furrow is absent, the number of plicae on disc and auricles is lower (only 26) and the striations in the plicae interspaces are fewer. The new species here proposed is intermediate between *P. chekiangensis* and *P. fasciculicostata*.

Palaeoecology. Stationary (byssate), low-level epifaunal suspension feeder.

Infraclass HETEROCONCHIA Hertwig, 1895
Order TRIGONIIDAE Dall, 1889
Superfamily TRIGONIOIDEA Lamarck, 1819
Family LADINOMYIDAE nov.

LSID. <https://zoobank.org/nomenclaturalacts/A16391BA-EC59-4614-B158-3D38286CD023>

Derivation of name. Combination of ‘Ladino’, the language spoken by the Ladin people of the Dolomites, and the family suffix ‘myidae’.

Type genus. *Ladinomya* gen. nov.

Diagnosis. Trigonioidean bivalves with reduced hinge teeth (two lateral teeth in LV and two main teeth of RV missing), consisting of one blunt tooth in LV and corresponding socket in RV; escutcheon narrow and without lunule; short ligament on nymphs; posterior adductor bordered anteriorly by slight myophoric buttress.

Remarks. The dentition of the Trigonioidea consists mostly of three teeth on LV and two teeth on RV with corresponding sockets in the opposite valve. The here-proposed new family is placed in the Trigonioidea despite the reduced dentition, because the diagnosis of the superfamily given by Cox *et al.* (1969) mentioned that ‘some of the teeth may be obsolete’.

The here-proposed new family is similar to Scaphellinidae Newell & Ciriacks, 1962. Both families share similar shell shapes, an escutcheon, a buttress in front of the posterior adductor and are lacking the lunule and posterior carina, typical of the other families of the Trigonioidea. However, although the Scaphellinidae maintains the trigonacean dentition, the Ladinomyidae fam. nov. reduces it radically.

Genus LADINOMYA nov.

LSID. <https://zoobank.org/nomenclaturalacts/22F474EF-F447-432E-BF35-DE88AB8E9D0A>

Type species. *Ladinomya fosteri* sp. nov.

Derivation of name. Combination of ‘Ladino’ and the genus name *Mya*.

Diagnosis. As for type and only species.

Remarks. In *Ladinomya* the posterior myophoric buttress is very weak and the pallial line is posteriorly truncated, as it occurs in *Schizodus*. The absence of a pallial sinus suggests that both genera were shallow burrowers.

Ladinomya fosteri sp. nov.

Figure 20

LSID. <https://zoobank.org/nomenclaturalacts/51171550-EFEA-4EAD-B005-736FE63BAA6D>

Derivation of name. Named after William Foster in recognition of his research on bivalve systematics and the end-Permian mass extinction.

Holotype. MLCS942, PRII.23b, steinkern of RV (Fig. 20L, M).

Paratypes. MLCS1958, PRII.95, an LV; MLCS1959, PRII.96, an RV.

Other material. 711 specimens. 4 LVs from Ff1; 76 LVs and 68 RVs from BA14; 2 LVs and 3 RVs from BA97; 2 LVs and 2 RVs from BA189; 68 LVs and 95 RVs from PRII; 38 LVs and 44 RVs from PR136; 116 LVs and 157 RVs from PR139; 17 LVs and 19 RVs from PR145.

Type locality & stratum. Preroman II section (PRII, 46°40′31.49″N, 11°54′18.34″E), on the road from Preroman to the locality Costa, near San Martin de Tor in Badia Valley, bed PRII.21 (Lo5). Upper Permian, Bellerophon Fm, Changhsingian.

Diagnosis. Shell trigonally ovate; hinge with central blunt tooth on LV and corresponding funnel-shaped socket on RV; escutcheon narrow, bordered by sulci; lunule absent; ligament short, located on nymphs; posterior adductor anteriorly delimited by slight myophoric buttress (Fig. 20N).

Description. Shell medium-sized (max. L = 25 mm), equivalve, strongly inequilateral, from posteriorly more elongated in juveniles to trigonally ovate in adults. Anterior margin narrowly rounded. Anterior part of dorsal margin short, oblique, straight or slightly concave. Ventral margin broad and convex. Dorsal margin long, oblique and straight or slightly concave. Posterior margin short and obliquely truncated. Umbo wide and well

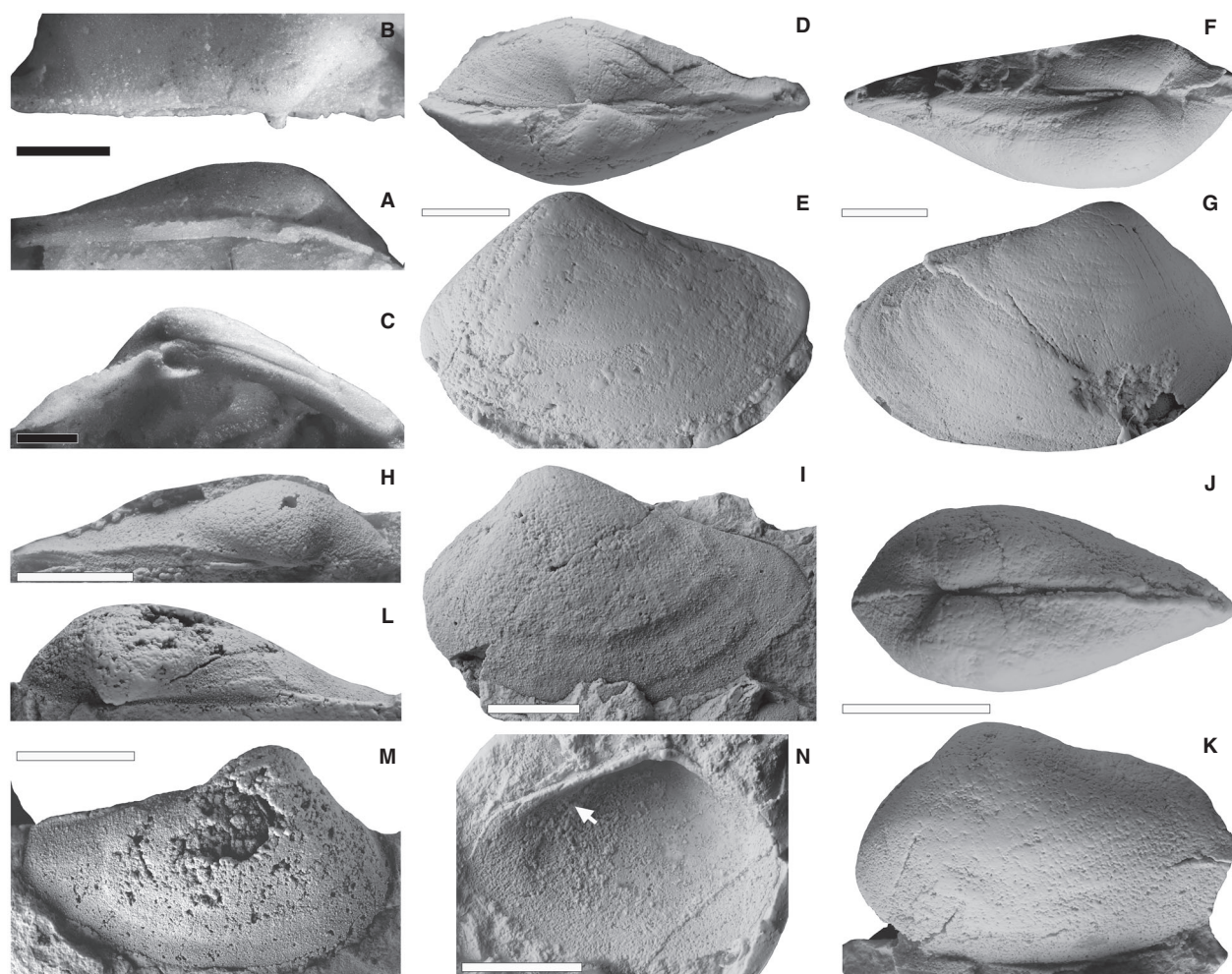


FIG. 20. *Ladinomya fosteri* gen. et sp. nov., Bellerophon Fm at Preroman II (PRII). All specimens, except A–B, have been whitened with magnesium oxide. All specimens, except L, M and I are plaster casts. A–B, MLCS1958, PRII.95, LV, paratype: A, lateral; B, dorsal view of hinge region with hinge tooth. C, MLCS1959, PRII.96, paratype, RV, internal lateral view, hinge region with subumbonal socket. D–E, MLCS940, PRII.21.01.06a, external mould of articulated specimens: D, dorsal view with tooth on LV hinge; E, lateral view of LV. F–G, MLCS940, PRII.21.01.05a, articulated specimen: F, dorsal view of external mould, G, lateral view of RV. H, MLCS948, PRII.29.01b, LV, dorsal view of external mould of hinge region with nymph and escutcheon. I, MLCS1004, PRII.86, LV, steinkern with radial striations, probably muscle scars. J–K, MLCS1000, PRII.82ab, juvenile articulated specimen: J, dorsal view; K, lateral view of LV. L–M, MLCS942, PRII.23b, holotype, RV, steinkern: L, dorsal; M, lateral view with muscle scars and pallial line. N, MLCS1966, PRII.103, LV, internal view with hinge tooth and posterior myophoric buttress (white arrow). Scale bars represent: 1 mm (A–C); 5 mm (D–N).

inflated, from orthogyrate to slightly prosogyrate. Beaks small, very close but not touching, located anteriorly at about one-third of shell length. Escutcheon narrow, posteriorly flattened and bordered by ridges, ventrally delimited by slight sulci. Ligament external and attached to short bladeliike nymphs. Lunule absent. Shell surface with faint growth lines. Below and slightly in front of the beak of RV the hinge margin forms a funnel-shaped socket. Chisel-shaped hinge tooth below LV beak, fitting into corresponding socket of RV.

Adductor muscle scars inconspicuous and nearly isomyarian. Subelliptical anterior adductor scar near anterior margin. Subrounded posterior adductor scar, slightly ventral of dorsal margin and anteriorly bounded by slight myophoric buttress.

Pedal retractor muscle scar small, narrow and elongated; slightly dorsal to posterior adductor. Pallial line entire and posteriorly truncated.

Palaeoecology. Facultatively mobile, infaunal suspension feeder.

Family SCHIZODIDAE Newell & Boyd, 1975
Subfamily SCHIZODINAE Newell & Boyd, 1975
Genus SCHIZODUS Verneuil & Murchison, 1844

Type species. *Axinus obscurus* J. Sowerby, 1823 (p. 12, pl. 314 upper fig.); by subsequent designation (Verneuil 1845, p. 308).

Remarks. *Schizodus* differs from other Schizodidae such as *Eoschizodus* by its different hinge structure (Cox 1951). The mainly Permian genus *Schizodus* differs from the mainly Triassic genus *Neoschizodus* Giebel, 1855, by the occurrence in *Neoschizodus* of a peculiar strong myophoric buttress (Newell & Boyd 1975).

Schizodus obscurus (J. Sowerby, 1823)

Figure 21

- *1823 *Axinus obscurus* J. Sowerby, p. 12, pl. 314 (upper three figures).
- v1878 ?*Schizodus* cf. *truncatus* King; Stache, pp. 117–118, pl. 1, fig. 25.
- 1906 *Schizodus dubiiformis* Waagen; Gortani, pp. 115–126, pl. 4, fig. 19.
- 1927 *Edmondia* cf. *rudis* M'Coy; Ogilvie Gordon, p. 13, pl. 1 fig. 6.
- 1967 *Schizodus obscurus* (J. Sowerby); Logan, pp. 47–48, pl. 8, figs 2–4 [cum syn.]

Material. 152 specimens. 4 LVs and 2 RVs from BA460; 13 LVs and 16 RVs from BA461; 31 LVs and 46 RVs from BA463; 1 LV from BU112; 1 RV from BA599; 2 RVs from BA634; 16 LVs and 11 RVs from PR61; 1 LV from RPGVBB; 4 LVs and 4 RVs from JM28.

Description. Medium-sized and subtrigonal shell with small, slightly opisthogyrate umbo. Beak small and slightly protruding above hinge line. Broadly rounded anterodorsal margin passing gradually to broadly arched ventral margin. Faint and slightly concave posterior carina on posterior umbonal margin bordering ventrally narrow subtriangular posterodorsal area. Dorsal margin oblique, slightly convex and connecting to short and truncated posterior margin with a c. 150° angle. Shell surface with faint growth lines.

Chisel-shaped RV pivotal tooth (3a) inclined in anterior direction with subtriangular apex. Posteriorly, acute ridge dorsally delimiting the socket (or hiatus *sensu* Newell & Boyd 1975) and terminating without forming any tooth. LV pivotal tooth (4a) slightly inclined in posterior direction with chisel-like apex. Small lamellar second cardinal tooth, attached to hinge margin, placed anteriorly to socket. Posteriorly, pivotal tooth delimited by short, oblique and narrow groove. Both valves with small nymph posterior of beak. Small anterior and posterior muscle retractor scars placed dorsally of large adductor scars (Fig. 21E). On internal shell surface, posterior umbonal area with short irregular radial grooves. Pallial line entire. Ventral to pallial line, surface with very faint radial striations (Fig. 21M).

Remarks. The specimens from the Bellerophon Fm have a great intraspecies-level variability concerning the elongation of shell outline and the inclination and length of the posterior margin. These specimens are similar to both *Schizodus obscurus* and *Schizodus schlotheimi* (Geinitz, 1841), with also intermediate morphotypes. *Schizodus schlotheimi* has a 3b tooth on the RVs, which differentiates it from *S. obscurus*. According to

Pattison (1970) the presence of the 3b tooth on the RVs is related to the ontogenetic stage and seems to occur only in juvenile specimens and be absent in adults. Therefore, adopting the classification proposed by Gruenewaldt (1851), Pattison (1970) and Newell & Boyd (1975), *S. schlotheimi* is here considered as a junior synonym of *S. obscurus*.

Palaeoecology. Facultatively mobile, infaunal suspension feeder.

Order LUCINIDA J. Gray, 1854

Superfamily LUCINACEA Fleming, 1828

Family LUCINIDAE Fleming, 1828

Subfamily MYRTEINAE? Chavan *in* Cox *et al.*, 1969

Remarks. The suprageneric classification of Lucinidae has been revised by recent genetic analyses (Williams *et al.* 2004; Taylor & Glover 2006; Taylor *et al.* 2011). The specimens from the Bellerophon Fm have an elongate, edentulous and subelliptical shell that is very similar to the Recent genera *Taylorina* Cosel & Bouchet, 2008, *Elliptiolucina* Cosel & Bouchet, 2008 and *Elongatolucina* Gill & Little, 2012. Taylor *et al.* (2011) identified seven lucinid subfamilies and tentatively placed the previously mentioned genera in the subfamily Myrteinae. Chavan (*in* Cox *et al.* 1969) erected this subfamily for thin, more or less quadrangular or transverse, moderately compressed shells with concentric sculpture and a medium-sized anterior scar. The Dolomites specimens differ from *Elliptiolucina* and *Elongatolucina* mainly by the deeply impressed lunule and the considerably smaller dimensions (*Elliptiolucina* and *Elongatolucina* can reach 135 mm and 80 mm, respectively; Cosel & Bouchet 2008; Gill & Little 2012). The lunule of *Taylorina* is longer and it has a shallow posterodorsal radial depression (Cosel & Bouchet 2008). Except for the similarities in shell shape with *Taylorina*, *Elliptiolucina* and *Elongatolucina* and their edentulous hinge, the specimens studied here are tentatively included in the Myrteinae. *Gigantocyclus* Termier & Termier *in* Termier *et al.*, 1977, from the middle Permian of Tunisia, which is edentulous, similar to the specimens from the Bellerophon Fm, has instead a subcircular outline, a larger shell and is lacking a lunule. Other known Permian lucinids, mainly described by Waagen (1881) and Reed (1932, 1944) from the Productus limestone of Kashmir/Pakistan (*Lucina*, *Sphaeriola*, *Loripes*, *Palaeolucina*) also have subrounded shell shapes and one or two cardinal teeth. Considering the differences between our specimens, the already known Permian lucinid genera and the extant edentulous transversely ovate lucinid genera, the new genus *Lovarulucina* is here proposed.

Genus LOVARALUCINA nov.

LSID. <https://zoobank.org/nomenclaturalacts/D2203EF4-6B39-4775-A86F-AD6CA942709E>

Derivation of name. From Lovara, a farm located near the outcrop of Preroman in Badia Valley, where most of the specimens were found.

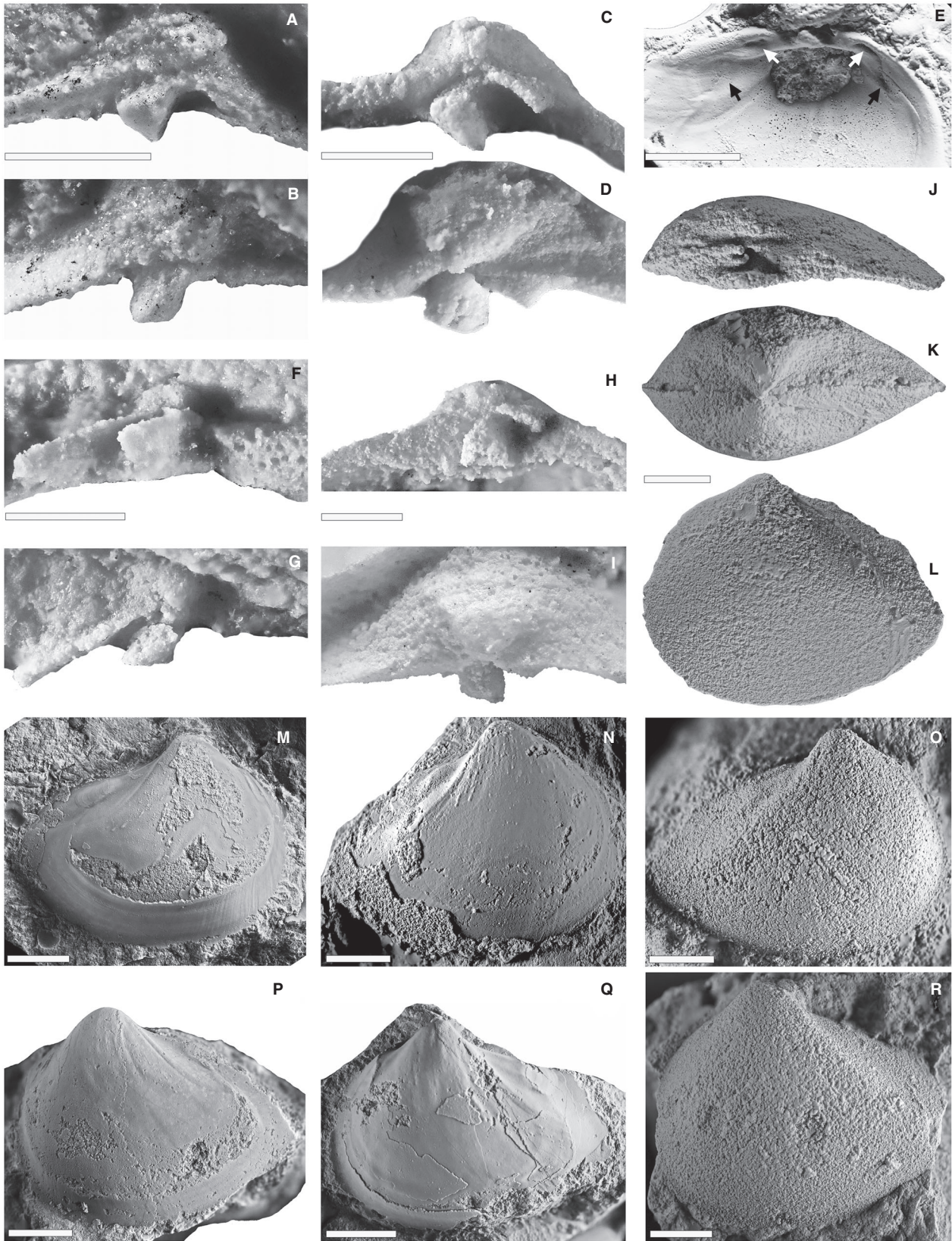


FIG. 21. *Schizodus obscurus* (Sowerby, 1823), Bellerophon Fm, NH B at Balest (BA). E, J–R, specimens are whitened with magnesium oxide. J, M, N, P, Q are steinkerns. A–B, MLCS1805, BA463.95.01, RV, plaster cast of hinge, in: A, lateral; B, dorsal view. C–D, MLCS1801, BA463.85.02, LV, plaster cast of hinge, in: C, lateral; D, dorsal view. E, MLCS1832, BA461.137.01, LV, plaster cast, internal view with muscle retractor scars (white arrows) above larger adductor scars (black arrows). F–G, MLCS1809, BA463.98.01, RV, plaster cast of hinge, in: F, lateral; G, dorsal view. H–I, MLCS1801, BA463.85, LV, plaster cast of hinge, in: H, lateral; I, dorsal view. J–L, MLCS1807, BA463.96, articulated specimens: J, dorsal view with hinge; K, dorsal view of plaster cast of external mould; L, LV, lateral view of external mould. M, MLCS1821, BA461.126.01a, RV. N, MLCS1824, BA461.129, RV. O, MLCS1809, BA463.98.01, RV, external mould. P, MLCS1819, BA461.124, LV. Q, MLCS1822, BA461.127, LV. R, MLCS1833, BA460.91, LV, external mould. Scale bars represent 2 mm (A–D, F–I); 5 mm (E, J–R).

Type species. *Lovaralucina covidi* sp. nov.

Diagnosis. Transversely ovate, narrow and edentulous shell with short and deeply sunken asymmetric lunule. Anterior adductor muscle scar large and lunuliform with a posteroventral tip dorsal and divergent from the pallial line. Posterior adductor scar large; pallial line slightly curved and entire.

Lovaralucina covidi sp. nov.

Figure 22

LSID. <https://zoobank.org/nomenclaturalacts/A67172A4-C43F-4ACC-A9DE-0254AFEDBFF3>

Derivation of name. This species was described during the COVID-19 pandemic.

Holotype. MLCS1849, BA461.168, LV with replaced test (Fig. 22A).

Paratypes. MLCS1853, BA461.172, steinkern of RV; MLCS1839, PR61b.11.01, steinkern of LV.

Other material. 44 specimens. 3 LVs and 5 RVs from BA460; 14 LVs and 5 RVs from BA461; 1 RV from BA463; 12 LVs and 2 RVs from PR61; 1 LV and 1 RV from JM28.

Type locality & stratum. Balest, a mountain near Ortisei/St Ulrich (Gardena Valley), bed BA461, NH B. Upper Permian, Bellerophon Fm, Changhsingian.

Diagnosis. Subelliptical, elongate, narrow, flattened *Lovaralucina* with asymmetric and deep lunule, edentulous hinge and narrow ligament groove.

Description. Shell equivalve, inequilateral, medium-sized (max L = 17.4 mm), elongate, transversely ovate and narrow. Umbo prominent with anterior umbonal margin slightly detached from anterior part of dorsal margin (Fig. 22F). Small, prosogyrate beak in centre of dorsal margin. Anterior part of dorsal margin connected to broadly rounded anterior margin by rounded corner.

Ventral margin slightly rounded. Dorsal margin obliquely truncated. Posterior margin rounded. Shell surface with dense concentric lamellae and occasional growth breaks. Hinge

edentulous. LV with small but deep and asymmetrical lunule slightly protruding beyond commissural plane. Lunule with faint concentric folds and limited by sharp margins (Fig. 22P). Ligament opisthodontic, ligament groove deep, elongated and narrow.

Anterior adductor muscle scar lunuliform with posteroventral tip dorsal and divergent from pallial line (Fig. 22E). Posterior adductor scar rounded and larger than anterior one. On internal shell surface two radial ridges delimit posterior and anterior triangular areas bearing adductor muscle scars (Fig. 22D). Internal shell surface with faint radial striations (Fig. 22I).

Palaeoecology. Facultatively mobile, infaunal, chemosymbiotic.

Superorder PALAEOHETERODONTA Newell, 1965

Order MODIOMORPHIDA Newell, 1969

Family KALENTERIDAE Marwick, 1953

Subfamily KALENTERINAE Marwick, 1953

Genus STUTCHBURIA Etheridge, 1900

Remarks. Transversally elongated shells occasionally with obscure cardinal teeth have been referred to *Stutchburia* or *Netschajewia* Licharew, 1925. These genera have been distinguished by the occurrence (*Netschajewia*) or absence (*Stutchburia*) of the posterior lateral tooth (Newell 1957; Chavan in Cox *et al.* 1969). However, the presence of this tooth has been regarded as a variable character and, therefore, *Netschajewia* is considered a junior synonym of *Stutchburia* (Dickins 1963; Logan 1964).

Stutchburia costata (Morris, 1845)

Figure 23A–F

1845 *Orthonota? costata* Morris, p. 273, pl. 11, figs 1, 2.

1878 *?Pleurophorus* sp.; Stache, p. 122, pl. 2, fig. 9a, b.

Material. 16 specimens. 2 RVs from BA460; 7 LVs and 6 RVs from PR61; 1 RV from JM28.

Description. Shell elongated, subelliptical (L/H = 2.5–3.3), slightly expanding posteriorly, equivalve and strongly inequilateral. Umbo small, low, prosogyrate and subterminal. Valve moderately inflated without umbonal ridge. Shallow radial sulcus from beak to anterior part of ventral margin. Posterior edge of anterior adductor scar with myophoric buttress. Escutcheon shallow and narrow extending nearly over whole dorsal region

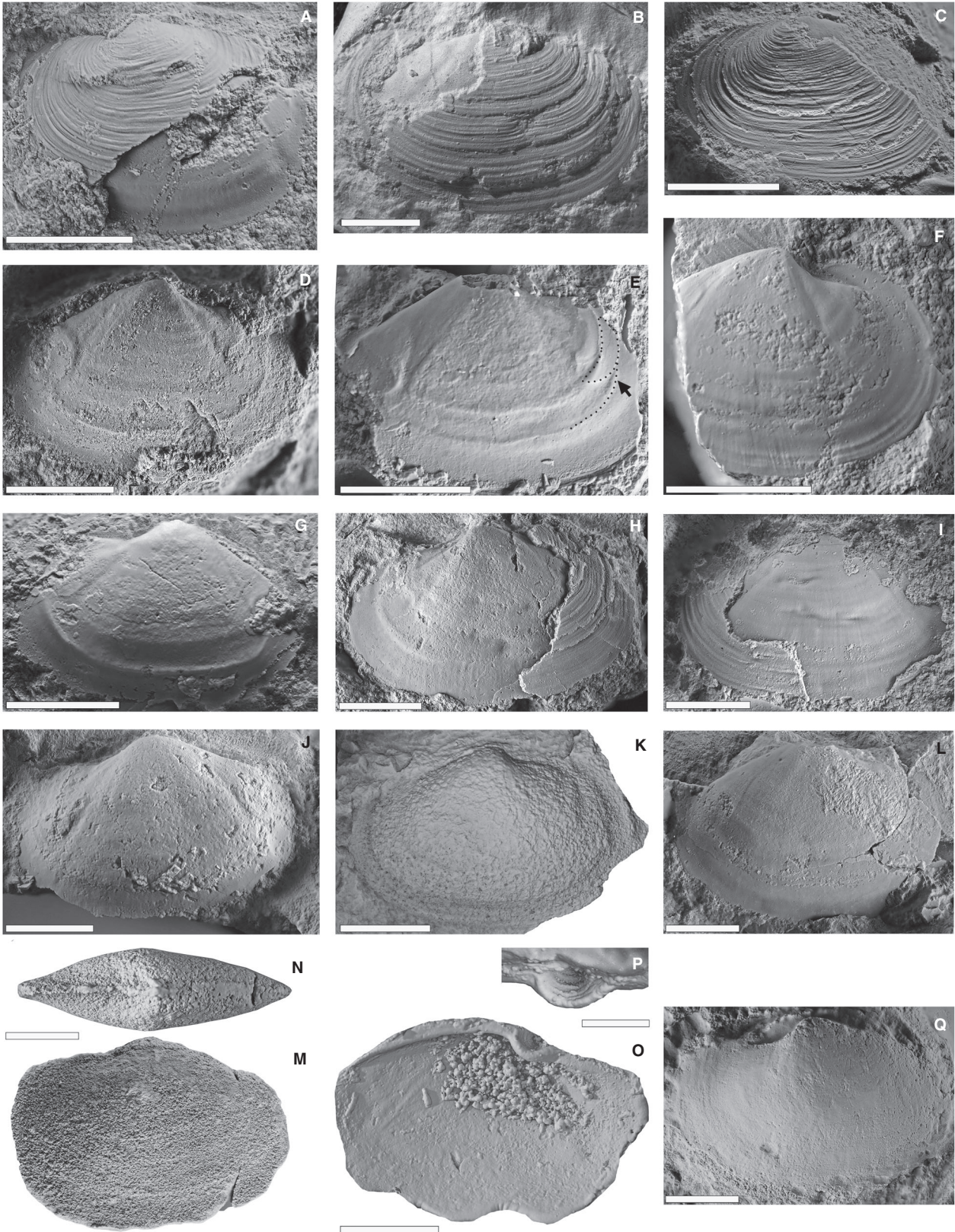


FIG. 22. *Lovaralucina covidi* gen. et sp. nov., Bellerophon Fm, NH B at Balest (BA) and Preroman (PR). A–C, H–I, specimens preserved partially as shells replaced by calcite. D–G, J, L, steinkerns. A, MLCS1849, BA461.168, holotype, LV. B, MLCS1840, BA461.102, LV. C, MLCS1845, BA461.164, LV. D, MLCS1846, BA461.165, RV. E, MLCS1853, BA461.172, paratype, RV, black arrow indicates palial line diverging outwards from anterior adductor. F, MLCS1841, BA461.103, RV. G, MLCS1842, BA461.104, LV. H, MLCS1844, BA461.163, LV. I, MLCS1847, BA461.166, LV. J, MLCS1851, BA461.170, LV. K, MLCS1105, PR61a.74.01, RV, composite mould. L, MLCS1843, BA461.162, RV. M–N, MLCS1854, PR61a.282, articulated specimen, composite mould: M, LV, lateral view; N, dorsal view. O–P, MLCS1839, PR61b.11.01, paratype, plaster cast of steinkern: O, LV, internal view; P, dorsal view, detail of lunule. Q, MLCS1855, PR61a.283, LV, composite mould. Scale bars represent: 5 mm (A–O, Q); 2 mm (P).

and bordered by carinate edge, ventrally delimiting shallow sulcus. Lunule not observed. Ornamented with low concentric imbricated lamellae and weak, narrowly spaced posterior radial riblets, ranging from 8 in juveniles to 14 in adults.

Remarks. The specimens from the Bellerophon Fm have strong similarities to *Stutchburia costata* from the Permian of Australia and New Zealand with a narrow and elongated shell, a deep escutcheon and a variable number of radial ribs, which range from 6 to 15 (Waterhouse 1980). The juvenile incomplete specimen of *Pleurophorus* sp. (L = 7 mm) described by Stache (1878, pl. 2, fig. 9a, b) has not been found in the collection of the Geologische Bundesanstalt Wien, but it is probably conspecific with the specimens described here. A radial ornamentation characterizes *Stutchburia hoskingae* Dickins, 1963 from the Permian of Australia, which also has a slender escutcheon and a rudimentary posterior lateral tooth on the LV. The shell is, however, shorter and is posteriorly more expanded than the specimens from the Bellerophon Fm. The Dolomites specimens are also similar to '*Cleidophorus striatulus* Waagen, 1881 from the Upper Productus Limestone of Salt Range, Kashmir, a species probably belonging to *S. costata*. They share faint radial striations on the posterodorsal part of the shell, but the specimens from the Dolomites have a more protruding beak and a smaller and more rounded anterior margin. *Stutchburia costata* is present in the upper Permian of Australia, New Zealand, Russia (Muromtseva & Guskov 1984) and probably of China (Gu *et al.* 1976).

Palaeoecology. A facultatively mobile (byssate), infaunal suspension feeder.

Stutchburia tschernyschewi (Licharew, 1933)

Figure 23G–T

- v1878 *?Clidophorus* sp.; Stache, pp. 118–119, pl. 1, fig. 17, pl. 2, figs 7, 8.
 1894 *Modiolopsis teplofi* Netschajew, p. 233, pl. 8, figs 5–6, 10–13.
 1903 *Modiolopsis teplofi* Diener, p. 172, pl. 8, fig. 6.
 v1930 *Modiolopsis* sp. aff. *antiqua* Barrande; Merla, pp. 116–117, pl. 11, fig. 20.
 *1933 *Netschajewia tschernyschewi* Licharew, p. 39, pl. 69.
 1935 *Stutchburia tschernyschewi*; Maslennikov, pp. 76–78, pl. 2, fig. 18a, b.
 1981 *Stutchburia tschernyschewi*; Muromtseva, p. 42, pl. 10, fig. 9.
 1984 *Stutchburia tschernyschewi*; Muromtseva & Guskov, p. 86, pl. 36, figs 19, 20, 22; pl. 52, figs 22, 23.

Material. 94 specimens. 4 LVs and 9 RVs from BA97; 4 LVs and 3 RVs from BA189; 8 LVs and 8 RVs from BA460; 4 LVs and 6 RVs from BA461; 3 LVs and 5 RVs from BA463; 11 LVs and 18 RVs from PR61; 7 LVs and 4 RVs from JM28.

Description. Shell subtrapezoidal, elongated (L/H = 2.5), equivalve, transversely inflated and posteriorly expanded. Beak small, strongly prosogyrate and subterminal. Umbonal ridge well developed, straight to slightly concave. Dorsal margin from straight to slightly convex, forming a rounded corner with an oblique dorsal part of the posterior margin. Ventral margin oblique, straight or slightly convex. Anterior margin narrowly rounded. Sometimes-shallow radial sulcus extending from beak to ventral margin, forming a shallow sinuation. Posterior edge of anterior adductor scar with oblique myophoric buttress. Occasional rudimentary posterior lateral tooth on the LV (Fig. 23Q). Escutcheon narrow and bordered by a sharp keel, ventrally delimited by sulcus (Fig. 23K). Lunule small and deep. Ornament consisting of concentric folds and weak growth lines. Posterior part of shell with occasional weak radial striations.

Remarks. Chernyshev (1929) noted that the specimens previously determined by Netschajew (1894) as *Modiolopsis teplofi* from the Permian deposits of Kazan (Russia) were different from the type material of Verneuil's species from the Carboniferous of Donezk (Ukraine). Later, Licharew (1933) proposed for the Netschajew (1894) specimens the new species *Netschajewia tschernyschewi*. The specimens from the Bellerophon Fm agree with *Netschajewia* (= *Stutchburia*) *tschernyschewi* and not with *Modiolopsis teplofi* (= *Stutchburia teplofi*) because in this species the beak is placed more anteriorly, the posterior margin is rounded, the umbonal ridge is convex and the shell is anteriorly narrower. Stache (1878) assigned two very small incomplete specimens to *?Clidophorus* sp., recognizing their affinities with '*Mytilus pallasii* Verneuil, 1845, which is the type species of *Netschajewia*. Merla (1930) described two crushed valves in butterfly position from Val da Rin (Auronzo) as *Modiolopsis* cf. *antiqua* Barrande, 1881. These specimens of Stache and Merla are conspecific with the new material from the Bellerophon Fm discussed here.

Palaeoecology. Facultatively mobile (byssate), infaunal suspension feeder.

Stutchburia sp.

Figure 24K–N

Material. 7 specimens. 3 LVs and 3 RVs from BA461; 1 LV from PR61.

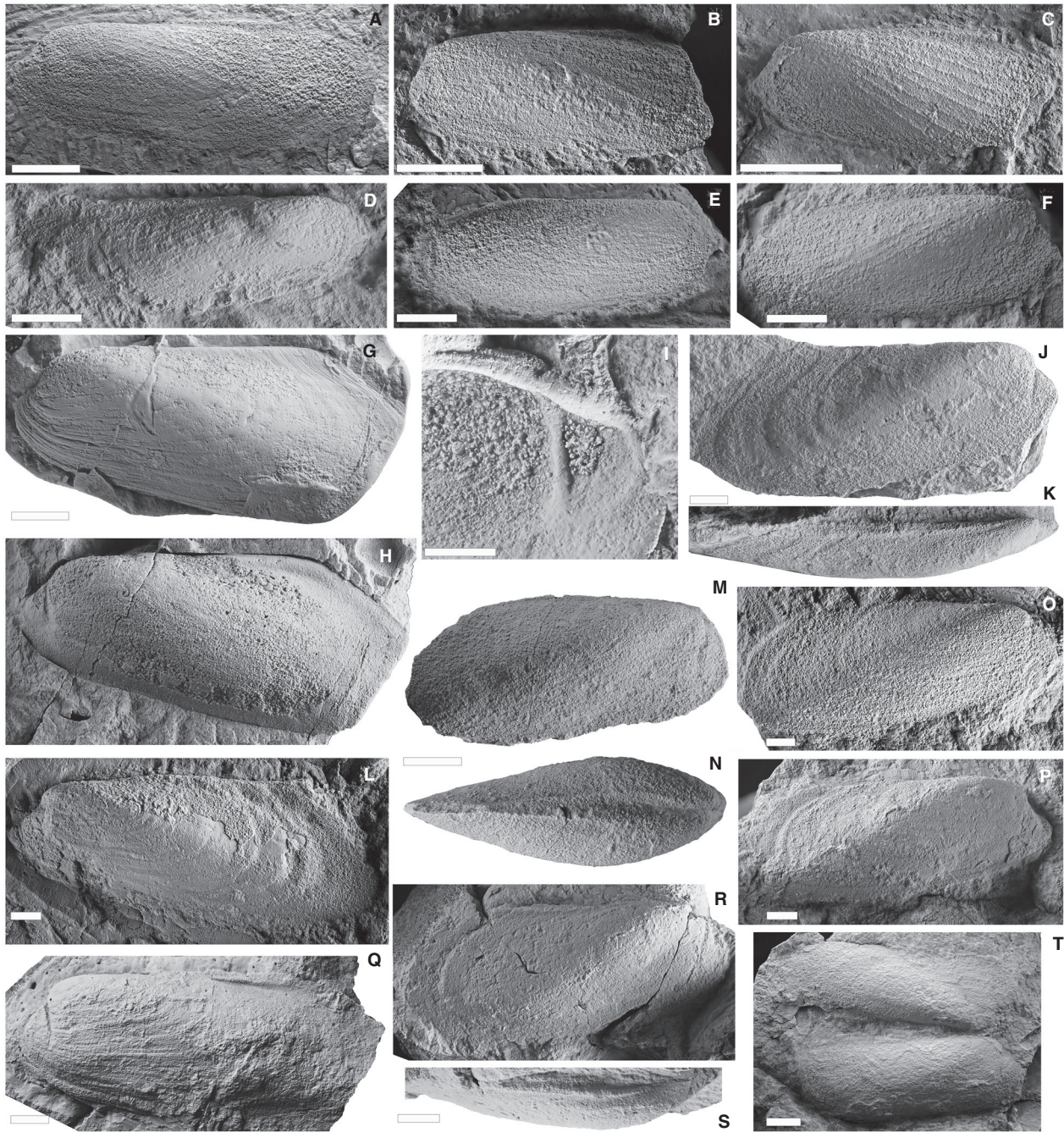


FIG. 23. A–F, *Stutchburia costata* (Morris, 1845), Bellerophon Fm, NH B at Preroman (PR); all specimens are composite moulds. A, MLCS1220, PR61a.190, LV. B, MLCS1084, PR61a.53, LV. C, MLCS1260, PR61a.230, LV. D, MLCS1856, PR61a.284, RV. E, MLCS1857, PR61a.285, RV. F, MLCS1858, PR61a.286, RV. G–T, *Stutchburia tschernyschewi* (Licharew, 1933) from the Bellerophon Fm of Preroman (PR) and Balest (BA). G–I, MLCS1859, PR61b.13a: G, plaster cast of external mould of LV; H, steinkern; I, internal view of hinge region. J–K, MLCS1134, PR61a.103, composite mould: J, RV; K, dorsal view. L, MLCS1860, BA460.93, LV, external mould. M–N, MLCS1861, BA460.94ab, articulated specimen, composite mould: M, RV; N, dorsal view. O, MLCS313, BA460.09, RV, composite mould. P, MLCS314, BA460.10, RV, external mould. Q, MLCS145, BA189.16, LV, steinkern. R–S, MLCS1198, PR61a.168, RV, composite mould, in: R, lateral; S, dorsal view. T, MLCS1200, PR61a.170, composite mould of two valves in butterfly position. Scale bars represent 5 mm.

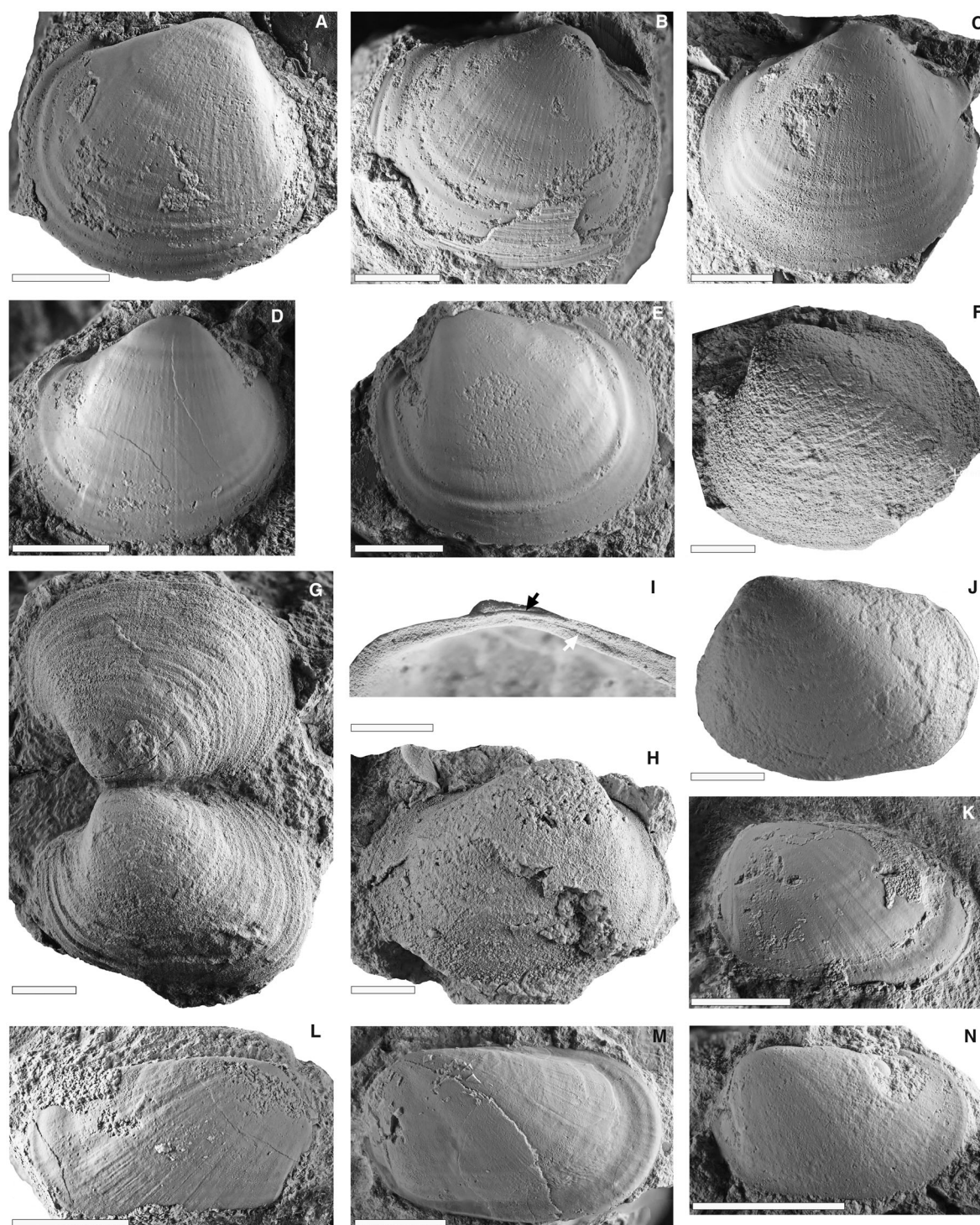


FIG. 24. A–I, *Edmondia hautmanni* sp. nov., Bellerophon Fm, NH B at Balest (BA) and Preroman (PR). All specimens are steinkerns except F, G and J. A, MLCS395, BA461.01, RV. B, MLCS398, BA461.04, holotype, RV with traces of shell replaced by calcite. C, MLCS1834, BA461.157, RV. D, MLCS1832, BA461.137.02, RV. E, MLCS397, BA461.03, LV. F, MLCS1038, PR61a.07b.01, RV, composite mould. G, MLCS1276, PR61a.246ab, external mould of articulated valves in butterfly position. H–I, MLCS1143, PR61a.112: H, RV; I, plaster cast, internal view, black arrow indicates the subumbonal sulcus, the white arrow indicates the sulcus on the hinge plate. J, *Edmondia* cf. *radiata* Hall (Stache 1878), GBA1878/001/0030, LV, external mould. K–N, *Stutchburia* sp., Bellerophon Fm, NH B at Balest (BA). All specimens preserved as steinkerns. K, MLCS1835, BA461.158, LV. L, MLCS1836, BA461.159, RV. M, MLCS1837, BA461.160, LV. N, MLCS1838, BA461.161, LV. Scale bars represent 5 mm.

Description. Shell small (max. L = 14 mm), elongated and subelliptical (L/H c. 1.7). Umbo small and not protruding beyond hinge line. Beak prosogyrate, subterminal, placed posterior to anterodorsal margin. Posterodorsal margin slightly convex and subparallel or slightly inclined towards ventral margin. Posterior margin rounded, ventral margin a little convex. Shell well-inflated without umbonal ridge. Slight, narrow radial sulcus extending from beak to ventral margin, bordering posteriorly well-inflated dorsal area (Fig. 24M). External shell surface with faint growth lines. Internally, anterior adductor scar delimited by low and elongated myophoric buttress. Internal shell surface with dense, faint radial striations and slight concentric folds. Posterior adductor scar shallow, large and rounded near rounded posterodorsal corner. Escutcheon very narrow, delimited by slight carina, extending from beak to about the midpoint of the dorsal margin. Pallial line entire. Lunule not observed.

Remarks. Netschajew (1894) described similar small shells from the upper Permian of Russia as *Modiolopsis* (= *Stutchburia*) *globosus*. These Russian specimens agree with those from the Dolomites in the subterminal beak. However, they have larger beaks, a more convex dorsal margin and are expanded posteriorly. The specimens studied here agree partially also with a juvenile specimen of *S. costata* from the Permian of Australia described by Wass & Gould (1969, pl. 14, fig. 4). The dimensions of this specimen are comparable with the Dolomites specimens, the shell shape is nearly identical and both have fine radial striations on the steinkern. Nevertheless, the Australian specimen is less inflated and the beak is terminal, whereas in the Dolomites specimens the beak is placed slightly posterior of the anterior margin. Stache (1878, pl. 1, fig. 28) described *Edmondia* cf. *radiata* Hall, 1858, from the Bellerophon Fm of Braies/Prags. This specimen (Fig. 24J) is similar to the specimens discussed here in shell shape and radial striation on internal shell surface, but it has a slight umbonal ridge and therefore it could belong to another species. The specimens discussed here are preserved as steinkerns or composite moulds and the hinge morphology is therefore not able to be observed and, hence, they are left in open nomenclature.

Palaeoecology. Facultatively mobile (byssate), infaunal suspension feeder.

Order HIATELLIDA Carter *et al.*, 2011
 Superfamily EDMONDIOIDEA W. King, 1850
 Family EDMONDIIDAE W. King, 1850
 Genus EDMONDIA De Koninck, 1841

Type species. *Isocardia unioniformis* Phillips, 1836.

Remarks. The specimens studied here have a narrow subumbonal sulcus subparallel to the dorsal margin and a furrowed hinge plate. Valves have subrectangular outlines and large prosogyrate umbos. This shell shape is shared by *Edmondia* and *Scaldia* Ryckholt, 1851: the first genus is edentulous while the second is dentate. In our specimens the cardinal teeth are lacking therefore they are attributed to *Edmondia*.

Edmondia hautmanni sp. nov.

Figure 24A–I

- v1878 *Edmondia* cf. *rudis* M'Coy; Stache, pp. 123–124, pl. 1, fig. 21.
 1927 *Edmondia* cf. *radiata* Hall; Ogilvie Gordon, p. 13, pl. 1, fig. 7.

LSID. <https://zoobank.org/nomenclaturalacts/3CFDFC57-71AB-4423-8EB3-9D144447F72D>

Derivation of name. After Michael Hautmann in recognition of his research on bivalve systematics and evolutionary palaeoecology.

Holotype. MLCS398, BA461.04, steinkern of RV with fragments of replaced shell (Fig. 24B).

Other material. 90 specimens. 2 LVs and 2 RVs from BA460; 8 LVs and 15 RVs from BA461; 1 LV from BA463; 20 LVs and 26 RVs from PR61; 1 RV from RPGVBB; 4 LVs and 11 RVs from JM28.

Type locality & stratum. Balest, a mountain near Ortsei-St Ulrich (Gardena Valley), bed BA461. Upper Permian, Bellerophon Fm, Changhsingian.

Diagnosis. *Edmondia* with shallow and irregular concentric folds on outer surface; faint radial striations on internal surface.

Description. Shell medium sized (max. L = 21.7 mm), from subquadrate in juveniles to subrectangular in adults. Umbo large, prosogyrate, located at about two-fifths of valve length from anterior margin. Anterior and posterior margins slightly convex, anterior margin shorter than posterior one. Dorsal margin slightly convex, ventral margin from well-rounded in juveniles to slightly convex in adults. Anterodorsal and posterodorsal corners narrowly rounded; anteroventral and posteroventral corners broadly rounded. Shell inflation decreasing during ontogeny. External shell surface covered, in juvenile growth stages, by feebly concentric riblets. Adult growth stages with low irregular concentric folds, intercalate by narrowly spaced growth lines. Shell interior with faint radial striations. Narrow subumbonal furrow sub-parallel to dorsal margin. Hinge plate edentulous with a slight longitudinal median furrow (Fig. 24I).

Remarks. Only a small number of species of *Edmondia* have low concentric ornamentation on the outer shell surface and internal radial shallow striations, which represent the most important taxonomical character of this new species. *Edmondia senilis* (Phillips, 1836) and *Edmondia rudis* M'Coy, 1853, from the Carboniferous of England and *Edmondia rugata* De Koninck, 1885, from the Carboniferous of Belgium have a shell shape similar to the specimens from the Bellerophon Fm, but they are larger and lack the internal radial striations. *Edmondia gibbosa* (M'Coy, 1844) from the Carboniferous of Ireland and USA has a shell shape and size comparable to the specimens studied here, but they are more inflated and have a stronger concentric

ornamentation; they are also generally lacking the internal radial striations. Fine radial striations and low concentric folds on the internal moulds are also present in *Edmondia aspenwallensis* Meek, 1871, from the Carboniferous of USA, *Edmondia lowickensis* Hind, 1899, and *Edmondia goldfussi* Hind, 1899, from the Carboniferous of England, but their shells are larger and less inflated than those of *E. hautmanni*.

Palaeoecology. Facultatively mobile, infaunal suspension feeder.

Superfamily PLEUROMYOIDEA Zittel, 1895
Family VACUNELLIDAE Astafieva-Urbajtis, 1973
Genus VACUNELLA Waterhouse, 1965

Type species. *Allorisma curvatum* Morris, 1845.

Remarks. Stache (1878) described a poorly preserved specimen from the Bellerophon Fm as *Leptodomus (Sanguinolites)* sp., which has the same characters of the specimens discussed here. However, in *Sanguinolites* M'Coy, 1844 the posterior dorsal flank has three radiating ribs (Morris *et al.* 1991), which are absent in the Dolomites specimens. A shell shape similar to our specimens is also present in *Dyasmya* Morris *et al.*, 1991, *Praeundulomya* Dickins, 1957, *Wilingia* Wilson, 1959, *Australomya* Runnegar, 1969, *Chaenomya* Meek in Meek & Hayden, 1865, and *Vacunella*. However, for the long and narrow subtrapezoidal shell outline, the deep pallial sinus and the slight posterior shell gape the specimens from the Bellerophon Fm are attributed to *Vacunella*.

Vacunella elongata (Ciriacks, 1963)

Figure 25

- v1878 *Leptodomus (Sanguinolites)* sp.; Stache, pp. 119–120, pl. 2, fig. 1.
*1963 *Sanguinolites? elongatus* Ciriacks, pp. 72–73, pl. 14, figs 6–10.
1963 *Sanguinolites* sp.; Ciriacks, p. 73, pl. 14, figs 12–13.
1968 *Sanguinolites? elongatus*; Yochelson & Sickle, pp. 621, 627.

Material. 37 specimens. 1 LV and 1 RV from BA97; 10 LVs and 13 RVs from BA231; 1 LV and 1 RV from BA460; 1 LV from BA461; 2 RVs from BA664; 3 LVs and 4 RVs from PR61.

Description. Shell medium sized (max. L = 45 mm), subtrapezoidal, very elongated (L/H up to 2.4), equivalve and strongly inequilateral. Maximum convexity near mid-length. Umbo broad, flattened and orthogyrate; beak anterior at about one-fourth of shell length and protruding above hinge line. Umbonal ridge broad and strongly inflated, bordered posteriorly by narrow sulcus, delimiting backwards a flattened surface (Fig. 25A, C, H). Occasionally, umbonal ridge with one or two flat and broad radial folds, absent on steinkerns (Fig. 25A, F, O). Escutcheon narrow with short nymph. Lunule very slender. Shell slightly gaping posteriorly. Posterior adductor scar rounded, near

central part of dorsal margin and dorsal of pallial sinus (Fig. 25B, J). Pallial sinus deep and narrowly rounded, surrounding anteriorly the impression of hypertrophied siphon retractor muscle (Fig. 25B), (Runnegar 1974). Internal surface of beak with pedal elevator muscle scar. Anterior adductor muscle scar slight and slender near anterior margin. Ornament of faint concentric folds and thin vertical rows of small pustules (Fig. 25M).

Remarks. The specimens from the Bellerophon Fm are nearly identical to *Sanguinolites? elongatus* Ciriacks, 1963, from the lower Permian Grandeur Member of Utah, USA, and to *Sanguinolites?* sp. from the upper Permian Franson Member and Ervay Member of Utah, USA (Davydov *et al.* 2018). Both US species are here considered to be conspecific with the specimens from the Bellerophon Fm, and all are assigned to *Vacunella*. The Dolomites and US specimens are characterized by a wide intraspecific variability with regard to the presence or absence of a raised umbonal ridge, the radial folds on the umbonal ridge and the shape of the antero-dorsal margin. The shape of the posterior part of the shell of *V. elongata* resembles that of *Vacunella curvata* (Morris, 1845) but it is much longer. The specimens from the Bellerophon Fm differ from *V. etheridgei* (De Koninck, 1876) because they have a longer shell, a deeper pallial sinus and no umbonal sulcus. They also differ from *Vacunella? waterhousei* (Dun, 1932) by a longer shell outline, not posteriorly tapering and a less rounded ventral margin. The Dolomites individuals are instead quite similar to *Vacunella dawsoneensis* Runnegar, 1967. Both have an elongated shell shape, strong, rounded posterodorsal adductor scar and orthogyrate umbo. However, *V. dawsoneensis* has a shallow pallial sinus. In comparison to *Vacunella camachoi* Rocha-Campos & de Carvalho, 1975, of the Sakmarian of Argentina, the specimens from the Bellerophon Fm have a more elongated shell shape and orthogyrate umbos, which are placed at a greater distance from the anterior margin. *Vacunella lunulata* (Keyserling, 1846) from the upper Permian of Russia has a similar outline, but it has a broader posterior margin and the umbonal ridge is missing. *Vacunella rostrata* Nakazawa & Newell, 1968, is posteriorly tapering, while *Vacunella praecurvata* Astafieva-Urbajtis, 1990, is much shorter than the specimens from the Bellerophon Fm.

Palaeoecology. Facultatively mobile, deep infaunal suspension feeder.

Infraclass HETEROCONCHIA Hertwig, 1895
Superorder PALAEOHETERODONTA Newell, 1965
Order UNIONOIDA Stoliczka, 1871
Family ANTHRACOSIIDAE Amalizky, 1892
Genus UNIONITES Wissmann, 1841

Type species. *Unionites muensteri* Wissmann, 1841.

Remarks. Stache (1878) described the new species *Pleurophorus jacobii* from an incomplete but large composite mould and ? *Anthracosia ladina* from two small and overlapping valves not belonging to the same individual. Both holotypes are here considered to be different ontogenetic stages of the same species and, therefore, congeneric.

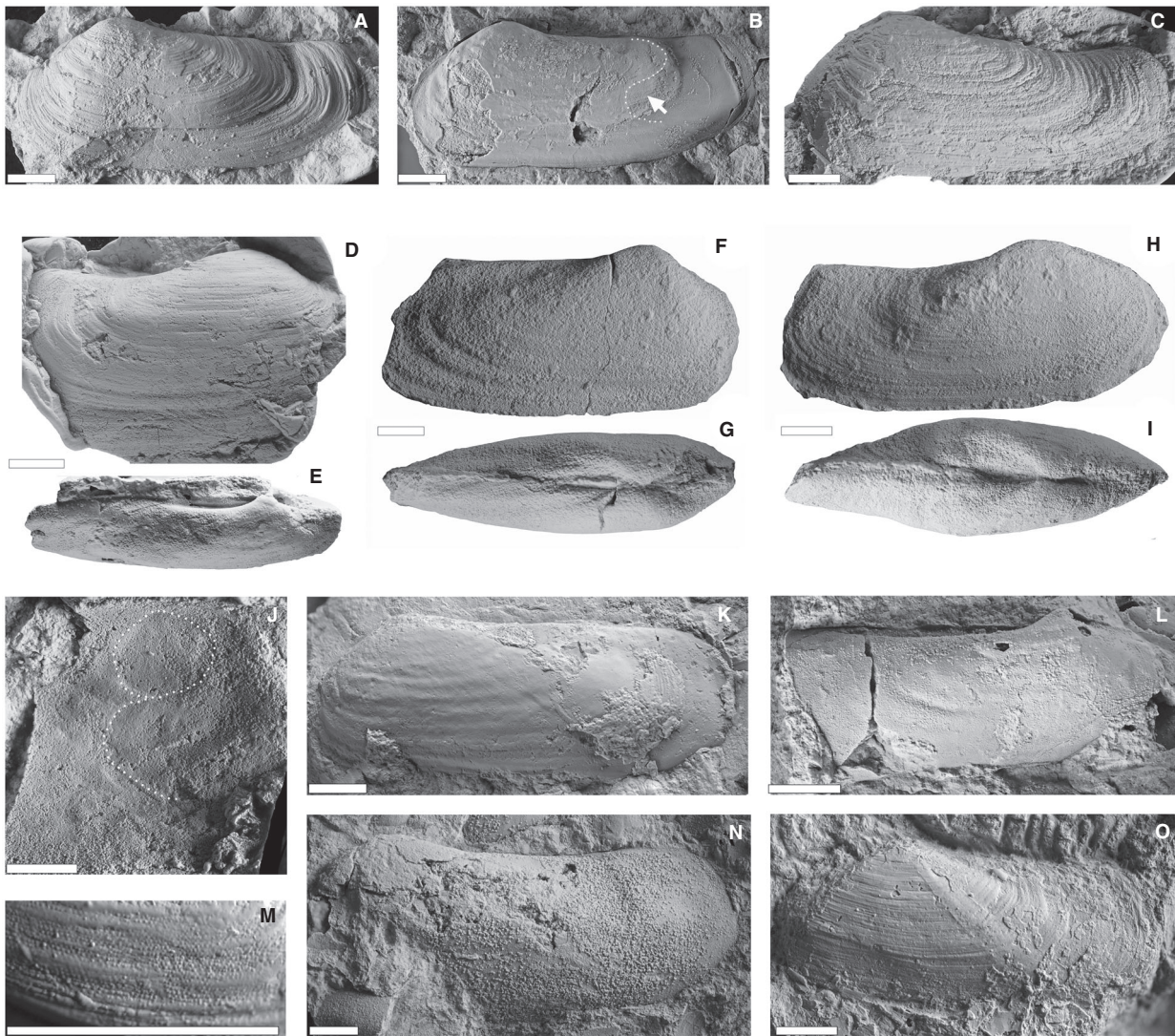


FIG. 25. *Vacunella elongata* (Ciriacks, 1963), Bellerophon Fm at Balest (BA) and Preroman (PR). A–B, MLCS1733, BA231.161, LV: A, plaster cast of external mould with radial rib on broad umbonal ridge; B, steinkern, dotted line highlights the deep pallial sinus, white arrow: impression of hypertrophied siphon retractor muscle. C, MLCS1738, BA231.166a, LV, plaster cast of external mould. D–E, MLCS1740, BA231.168a, RV: D, plaster cast of partially preserved external mould; E, dorsal view of steinkern. F–G, MLCS1135, PR61a.104ab, RV: F, lateral view of articulated specimen preserved as composite mould, with two slight radial ribs on umbonal ridge; G, dorsal view. H–I, MLCS1216, PR61a.186ab, RV: H, lateral view of articulated specimen preserved as composite mould; I, dorsal view. J, MLCS1732, BA231.160, LV, plaster cast of fragment of steinkern with adductor scar and deep pallial sinus, highlighted by dotted line. K, MLCS1746, BA461.157a, LV, steinkern with traces of shell replaced by calcite. L, MLCS1731, BA231.159a, RV, steinkern. M, detail of A with radial rows of pustules. N, LV, MLCS1736, BA231.164, steinkern. O, MLCS1739, BA231.167, LV, shell replaced by calcite with two radial folds on umbonal ridge. Scale bars represent 5 mm.

The new collected specimens from the Bellerophon Fm have some similarities to *Permophorus*. They share an elongated shell shape, prosogyrate beak and hinge morphology with a left posterolateral secondary ridge, which has no corresponding socket in the RV (Logan 1967). The Dolomites specimens do not show true subumbonal cardinal teeth, their posterior lateral tooth does not reach the beak and the anterior myophoric buttress is inclined anteriorly. On

the plaster casts of well-preserved adult RVs, the anterior hinge margin is projected slightly beyond the commissure plane, fitting into a recess of the opposite valve. This is a taxonomical character of some Anthracosiidae, such as *Unionites*, *Carbonicola* M'Coy, 1855, and *Anthracosia* King, 1856 (Skawina & Dzik 2011).

According to Skawina & Dzik (2011), a distinctive feature distinguishing *Unionites* from other Anthracosiidae genera is

the peculiar shape of the probable anterior pedal retractor scar. *Carbonicola* has a single rounded scar or a series of separate small scars in continuity with the adductor scar. *Unionites* has instead a single elongated, probable anterior pedal retractor scar, which also occurs in the Dolomites specimens. These specimens share with the holotype of *Unionites* the following characters: in adult specimens the anterior hinge margin of the RV fits into a recess of the LV; the nymphs extend nearly half the length of the posterior hinge margin; the anterior adductor muscle scar is deeply impressed and bounded by a myophoric buttress; the probable anterior pedal retractor is fused to a single scar; a deeply impressed lunule, and a long and narrow escutcheon in adult individuals and a posterolateral secondary ridge on the LV, which is there delimiting ventrally a shallow socket and has no corresponding socket on the RV (Bittner 1895; Cox *et al.* 1969; Geyer *et al.* 2005; Skawina & Dzik 2011).

Unionites jacobi (Stache, 1878)

Figures 26, 27

- *v1878 *Pleurophorus jacobi* Stache, p. 121, pl. 1, fig. 30.
- v1878 ?*Anthracosia ladina* Stache, p. 120, pl. 1, fig. 23a, b.
- v1878 ?*Allorisma* sp.; Stache, pp. 125–126, pl. 1, fig. 29.
- v1878 ?*Allorisma tirolense* Stache, p. 125, pl. 1, fig. 28.
- v1878 ?*Arca* sp.; Stache, p. 118 pl. 2, fig. 2.
- v1878 ?*Nucula* sp.; Stache, p. 117, pl. 2, fig. 3.
- v1878 ?*Nucula* sp.; Stache, p. 115, pl. 2, fig. 4.
- 1903 *Pleurophorus jacobi* Stache; Kittl, p. 692, pl. 22, figs 13, 14.
- v1930 *Pleurophorus Jacobi* Stache; Merla, pp. 117–118, pl. 11, fig. 34.
- v1930 *Allorisma ?variabilis* M'Coy; Merla, p. 128, pl. 11, fig. 31.
- v1930 *Allorisma dubium* Waagen; Merla, p. 128, pl. 11, fig. 15.
- v1930 *Sanguinolites* aff. *hybridus* De Koninck; Merla, p. 127, pl. 11, figs 28, 32.
- v1930 *Leda* sp.; Merla, p. 88, pl. 11, fig. 35.

Material. 1713 specimens. 119 LVs and 125 RVs from BA14; 8 LVs and 7 RVs from BA97; 1 LV and 4 RVs from BA150; 5 LVs and 3 RVs from BA189; 198 LVs and 208 RVs from BA231; 2 RVs from BA460; 67 LVs and 78 RVs from BA599; 53 LVs and 49 RVs from BA634; 23 LVs and 22 RVs from BA664; 13 LVs and 12 RVs from BA713; 13 LVs and 17 RVs from BA731; 7 LVs and 10 RVs from BU112; 9 LVs and 17 RVs from CUGVBB; 2 LVs and 3 RVs from PR61; 10 LVs and 6 RVs from PR11; 8 LVs and 7 RVs from PR3,117; 1 LV and 4 RVs from PR136; 9 LVs and 8 RVs from PR139; 8 LVs and 7 RVs from PR145; 31 LVs and 11 RVs from PR152; 2 LVs and 2 RVs from PR246; 25 LVs and 28 RVs from RPGVBB; 86 LVs and 88 RVs from SE56; 6 LVs and 3 RVs from SE140; 5 LVs and 8 RVs from SE142; 9 LVs and 2 RVs from SE145; 3 LVs and 3 RVs from SE168; 43 LVs and 39 RVs from TR; 46 LVs and 45 RVs from JM188; 13 LVs and 7 RVs from JM195; 36 LVs and 29 RVs from JM198.

Description. Shell medium sized (max. L = 46 mm), elongated subovate to subtriangular (L/H = 2.25). Beak small, depressed and strongly prosogyrate, not protruding above dorsal margin; at about one-fifth of shell length from anterior margin. Dorsal margin slightly convex to straight, joining dorsal part of posterior margin at a 50° angle. Posterior margin slightly convex and obliquely truncated with narrowly rounded posterior extremity. Ventral margin straight to slightly convex. Umbonal ridge delimiting subtriangular posterodorsal area. Escutcheon long, narrow, bounded by sharp ridge and with narrow nymph. Lunule elongated, shallow in juveniles, deep in adults, bordered by sharp ridge. Anterior hinge margin of adult RV projecting slightly beyond commissural plane and fitting into recess in opposite valve (Fig. 27A, B). Anterior adductor scar large, subtriangular, deeply impressed and with dorsally placed smaller and comma-shaped scar, presumably representing the anterior pedal retractor scar. Both scars separated by small buttress and posteriorly bounded by myophoric buttress.

Posterior adductor scar subrounded, shallower and slightly larger than anterior adductor. Hinge plate of large RVs with slight subumbonal tubercle (Fig. 27E, I) and posterior shallow recess (Fig. 27A). LV with complementary hinge structures (Fig. 27C). RV hinge plate with posterior lateral tooth vanishing before reaching posterior margin (Fig. 27L); LV with corresponding socket. Internal surface of LV with very elongated and narrow secondary ridge almost parallel to dorsal margin.

RV without corresponding socket or occasionally with very short and narrow ridge below posterior part of dorsal margin (Fig. 26E). Up to four internal weak posterior radial ridges vanishing before reaching posterior margin. Outer shell surface with faint commarginal growth lines. Pallial line entire and deeply impressed.

Remarks. *Unionites jacobi* from the Bellerophon Fm shares with *U. muensteri* from the Carnian of the Dolomites, *Unionites longus* (Schauroth, 1857) from the Ladinian of Germany and *Unionites subrectus* (Bittner, 1901b) from the Middle Triassic of Hungary a well-developed posterior keel and an elongated shell with the length decidedly exceeding the height. *Unionites jacobi* most closely resembles *Unionites subrectus*, because they share a narrow and long escutcheon delimited by sharp ridges, a deep lunule and a strong myophoric buttress posterior of the anterior adductor. *Unionites jacobi* differs from the Hungarian species in the shell shape: *U. subrectus* has a posteriorly slightly tapering shell and a broadly rounded posterior margin with its dorsal part only slightly inclined. The specimens from the Dolomites share with *U. muensteri* (Bittner 1895, pl. 1, fig. 24; Fang & Morris 1997, pl. 2, fig. 7) and *U. aff. subrectus* of Foster *et al.* (2017a) a posterior lateral oblique ridge in the LV, which delimits ventrally a shallow socket and an anterior adductor, bounded posteriorly by a myophoric buttress. *Unionites kobyumensis* Biakov & Kutugin, 2021, from the Changhsingian of northeast Russia seems to belong to another group of *Unionites* characterized by a more centrally placed umbo, typical also of *Unionites? fassaensis* (Wissmann, 1841) and *Unionites? canalensis* (Catullo, 1846).

Palaeoecology. Facultatively mobile, infaunal suspension feeder.

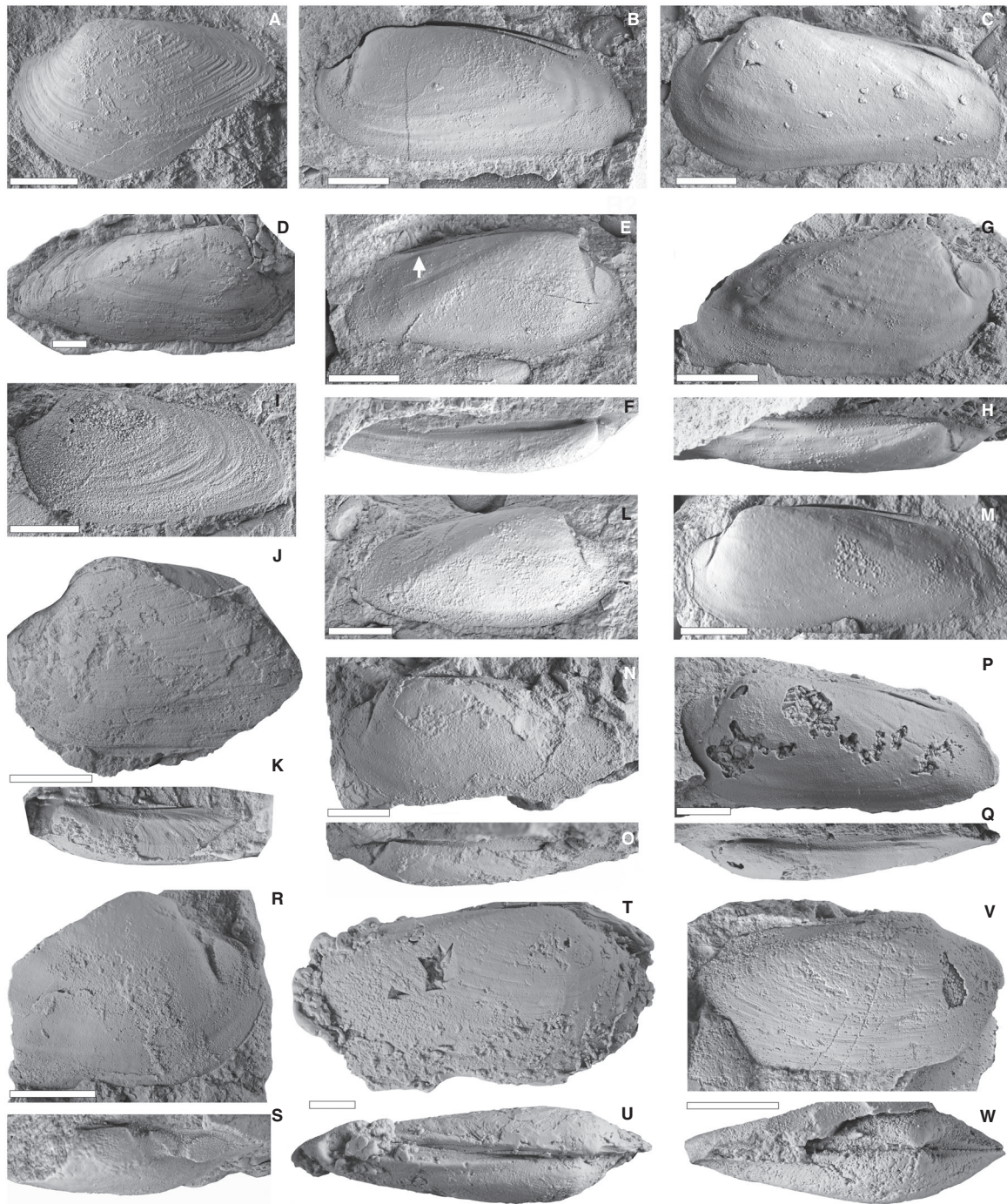


FIG. 26. *Unionites jacobii* (Stache, 1878), Bellerophon Fm at Balest (BA), Plan (PL) and Preroman (PR). B–C, E–I, L–S are steinkerns. A, MLCS1886, BA231.189, partially preserved LV with shell replaced by calcite. B, MLCS177, BA231.05.01, LV. C, MLCS173, BA231.01.01, LV. D, MLCS1887ab, BA231.190, RV, plaster cast of external mould. E–F, MLCS174, BA231.02.02, RV, in: E, lateral view, arrow indicates the short posterodorsal ridge; F, dorsal view. G–H, MLCS1748, BA231.175, RV, in: G, lateral; H, dorsal view. I, MLCS1888, BA231.191, LV with shell replaced by calcite. J–K, MLCS1889, BA231.192, partially preserved LV, plaster cast of external mould, in: J, lateral; K, dorsal view with nymph. L, MLCS183, BA231.11b.03, RV. M, MLCS175, BA231.03.02, LV. N–O, MLCS1755, BA231.182, LV, in: N, lateral; O, dorsal view. P–Q, MLCS1756, BA231.183, LV, in: P, lateral; Q, dorsal view. R–S, MLCS224, BA231.52, RV, in: R, lateral; S, dorsal view, note the fused muscle pits of the probable anterior pedal retractor musculature. T–U, MLCS1762, PLdebris13a, RV, plaster cast of external mould of an articulated specimen, in: T, lateral; U, dorsal view. V–W, MLCS179, BA231.07, RV, plaster cast of external mould of an articulated specimen, in: V, lateral; W, dorsal view. Scale bars represent 5 mm.

RESULTS

Biostratigraphy

In the Bellerophon Fm, index fossils with high chronostratigraphic value are rare: conodonts are sparse (Perri & Farabegoli 2003) while very few ammonoid specimens have been found (Diener 1897; Posenato & Prinoth 1999). Of the nautiloids only *Tirolonautilus* can be considered as a Changhsingian index fossil for shallow marine settings of the tropical Tethys (Posenato 2010).

Eumorphotis species have been proposed as Lower Triassic subzonal markers after the disappearance of *Claraia*. The *Eumorphotis* subzones (*E. multiformis*, *E. hinmitidea*, *E. kittli*, *E. telleri*) range from upper Induan to Olenekian (e.g. Broglio Loriga *et al.* 1983, 1990; Posenato 2008a, 2019). Here we show that this genus has a wider stratigraphic distribution, being already present in the Changhsingian Bellerophon Fm, and thus it can be used as a biozone marker for the Permian. We also propose to divide the *Eumorphotis* Zone into an upper Permian Lower *Eumorphotis* Zone and a Lower Triassic Upper *Eumorphotis* Zone (Fig. 28). Each Permian *Eumorphotis* species has a peculiar stratigraphic range that enables it to be used as a local subzone marker. For this reason, *Eumorphotis praecurrens* is here proposed as the subzone marker for the sequence Lo3, *Eumorphotis striatocostata* for the sequences Lo4 and Lo5, and *Eumorphotis lorigae* for the uppermost Lo5 and In1. *Eumorphotis lorigae* occurs also in the basal beds of the latest Permian beds of Gerennavår Limestone of Hungary (Posenato *et al.* 2005) and could therefore be considered as a subzone marker in a wider European context.

Biodiversity and palaeoecology

The investigated bivalve fauna from the upper Permian Bellerophon Fm contains 19 genera (3 new), 26 species (10 new) (Table 1) and is found throughout the whole Bellerophon Fm (Fig. 29).

Biofacies

Biofacies are species assemblages identified using cluster analysis on the basis of similarities in taxonomical composition, with similar relative abundances that occur in each sample (Ludvigsen *et al.* 1986). These statistical units are generally restricted to the same stratigraphical unit, thus they can reflect similar ecological conditions and be useful in palaeoenvironmental reconstruction (Figs 30, 31).

Biofacies A occurs exclusively in the marly dolostones, which alternate with gypsum beds, from the Fiammazza Facies of the lower part of sequence Lo3 (Rio Barbide Mb), for example, in bed Ff1. This biofacies is dominated by *Bakevella* (*B. binneyi*) (species richness = 3; dominance = 0.9), which inhabited stressed environments of coastal sabkhas and restricted lagoons (Bosellini & Hardie 1973). The lagoons were delimited to the east by the so-called Comelico High, responsible for the more restricted environment in the western basin, compared with the more open marine eastern part of the Bellerophon Fm (Noè 1987). High temperatures and salinity were the most important limiting factors and only very few eurytopic bivalves could thrive. *Bakevella* (*B. binneyi*) was also abundant in the Zechstein basin (*Bakevella* sea), where it is characteristic of a hypersaline landlocked basin community together with *Schizodus obscurus* (Ramsbottom 1978).

Biofacies B and C occur in the same stratigraphic interval (upper part of Lo4 sequence, NH B). They have a very similar taxonomical composition and a slight difference in abundance of some species. The higher richness and abundance in biofacies B probably reflects a more open marine environment in the Preroman section located slightly more distally than the Balest section.

For these reasons, these two biofacies are discussed together. They are contained in the dark limestone beds BA460 and PR61 (Biofacies B, N = 241) and in the slightly arenaceous and slightly dolomitized limestone beds BA461, BA463 and JM28 (Biofacies C, N = 408). Species richness and dominance of these two biofacies are the highest and the lowest, respectively, for the whole of the Bellerophon Fm. Species richness of biofacies B ranges from 13 to 19 (mean = 16) and the dominance ranges from 0.09 to 0.08 (mean = 0.085). Species richness of biofacies C ranges from 8 to 13 (mean = 11) and the dominance ranges from 0.21 to 0.31 (mean = 0.26). The upper beds of the Lo4 sequence also contain, besides the rich bivalve fauna, green calcareous algae, small *Comelicania* shells and a rich nautiloid fauna (NH B). This assemblage suggests fully marine conditions. However, the foraminifers are dominated by eurytopic taxa (Posenato & Prinoth 2004), which suggests a marine setting affected by some environmental stress (e.g. salinity fluctuations, high temperature, and terrigenous input). Stressed marine conditions are also confirmed by the abundant occurrence of the euryhaline *Bakevella ceratophaga*, *Schizodus obscurus* and bellerophontid gastropods (Logan 1967; Kammer & Lake 2001).

Biofacies D occurs in the dark limestone beds PR152, PR246 and SE164 of the middle higher part of the regressive phase of sequence Lo5 (Ostracod assemblage of Broglio Loriga *et al.* 1988). It is characterized by a very low species richness ranging from 1 to 2. The

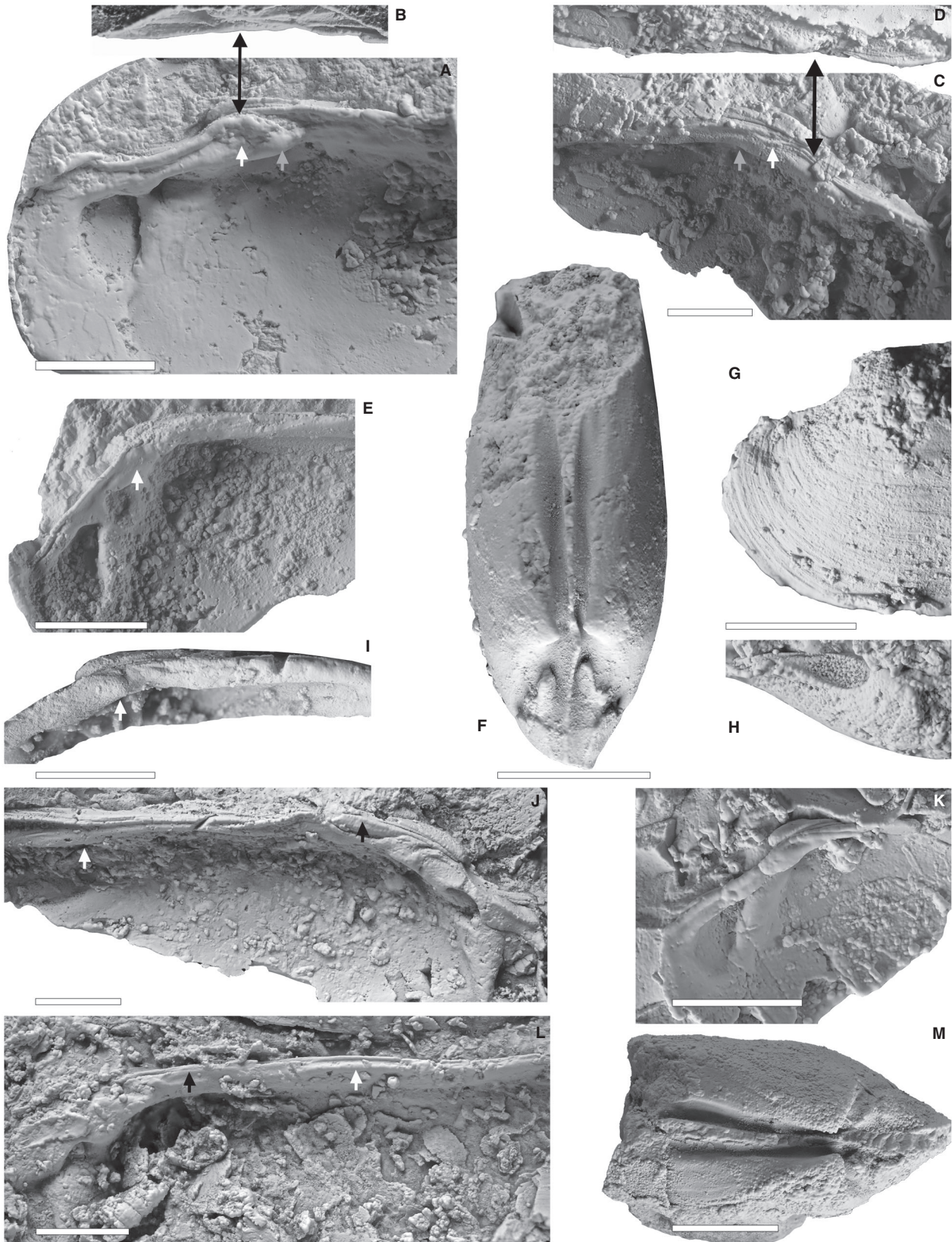


FIG. 27. *Unionites jacobi* (Stache, 1878), Bellerophon Fm at Balest (BA), Plan (PL) and Preroman (PR). A–B, MLCS1890, PL.16, RV: A, plaster cast, internal anterior view; B, dorsal view, black arrow indicates the right anterior hinge margin projecting slightly beyond the plane of commissure, white arrow indicates subumbonal recess for slight oblique ridge of LV, grey arrow indicates the subumbonal tubercle. C–D, MLCS1764, PL.14, LV: C, plaster cast, internal anterior view; D, dorsal view, black arrow indicates the subumbonal recess of the LV for the projecting anterior hinge margin of the RV, the white arrow indicates a slight subumbonal ridge fitting in the recess of the RV, the grey arrow indicates a recess for the subumbonal tubercle of the RV. E, MLCS1765, PL.15, posterior part of RV, plaster cast, internal view, arrow indicates subumbonal tubercle. F, MLCS1360, PR152.08.01ab, steinkern of articulated specimen with right anterior hinge margin slightly projecting beyond the plane of commissure. G–H, MLCS1893, PLdebris.19, plaster cast, external mould of anterior region of LV, in: G, lateral; H, dorsal view, deeply impressed lunula. I, MLCS1892, PLdebris.18, plaster cast of hinge of RV, white arrow indicates the subumbonal tubercle. J, MLCS1501, PLdebris 02.01a, plaster cast of hinge of LV, black arrow indicates nymph, white arrow indicates a secondary ridge. K, MLCS1891, PLdebris.17, plaster cast of internal posterior part of LV. L, MLCS1896, PLdebris16, plaster cast of hinge of RV; black arrow indicates nymph, white arrow indicates a posterior lateral tooth. M, MLCS1761, BA231.188ab, anterior part of steinkern of articulated specimen. Scale bars represent 5 mm.

Formation	Third-order depositional sequences	Zone	Subzone
Bellerophon Formation	In1	Lower <i>Eumorphotis</i> Zone	<i>E. lorigae</i>
	Lo5		<i>E. striatocostata</i>
	Lo4		
	Lo3		<i>E. praecurrens</i>

FIG. 28. Proposed new Lower *Eumorphotis* Zone and subzones from the Bellerophon Fm.

dominance is moderate–high, ranging from 0.5 to 1 (mean = 0.81). This biofacies is dominated by *Gardenapecten comelicanus* and *Unionites jacobi*. The absence of marine taxa adapted to constant normal marine conditions (e.g. brachiopods, fusulinids) and the occurrence of rare eurytopic foraminifers (e.g. *Glomospira*) suggest a stressed environment controlled by high salinity and temperature and very shallow marine conditions (Farabegoli *et al.* 2007).

Biofacies E occurs in the dark limestones, marls and marly limestones of BU36, JM144, RPGVBB, SE140, SE168, PR11, PR139, PR136, PR145, BA731, PR3,117, JM198, BA713, TR, JM195, SE142, SE145, CUGVBB, BA634, BU112, BA231, SE56, BA599, JM188 from sequence Lo5 and BA231 of Lo4. Species richness is low–moderate, ranging from 1 to 7 (mean = 4) and dominance is highly variable, ranging from 0.32 to 1 (mean = 0.53). This biofacies comprises most beds of the sequence Lo5, corresponding to the ‘Algae Assemblage’ of Broglio Loriga *et al.* (1988) or the Casera Razzo Member of Farabegoli *et al.* (2007). It is dominated by *Gardenapecten trinkeri* and *Unionites jacobi*. *Volsellina carinata* and *Bakevellia (B.) preromangica* are also abundant. *Ladinomya fosteri*, *Towapteria peracuta*

and *Eumorphotis striatocostata* are common in only a few beds.

Unionites jacobi is very similar to *Unionites muensteri* from the lower Carnian (Upper Triassic) Heiligkreuz Fm of the Dolomites. There *U. muensteri* is interpreted, on the basis of C and O isotope data, as a normal marine taxon, but the monotypic occurrence together with a few species of ostracods indicates that it occurred in stressed oxygen-depleted environments (Keim *et al.* 2006). *Unionites donacinus* and *U. brevis* from the lower Keuper (Ladinian) of Southwest Germany is characteristic of brackish environments (Geyer *et al.* 2005). The limiting factors for bivalves of biofacies E were probably salinity, temperature and oxygen. In the lower part of depositional sequence Lo4, *U. jacobi* sometimes co-occurs with the lingulid *Trentingula prinothi* Posenato, 2016, suggesting brackish water influx. In the Gardena Valley Bivalve Bed (GVBB), *U. jacobi* occurs together with *Schizodus obscurus*, which indicates a slightly hypersaline environment in the middle part of depositional sequence Lo5.

We also interpret *Gardenapecten* as a euryhaline pectinoid similar to *Dunbarella* (Johnson 1962; Murphy 1967). It dominates the stressed environments of biofacies E but is also present in the more open marine environment of biofacies C. Noteworthy is the absence of *Gardenapecten* in biofacies B, where it was not able to compete with stenohaline bivalves. *Volsellina carinata* was also euryhaline, like many modern mytiloids. The presence of *Eumorphotis* in all biofacies of the Bellerophon Fm reflects the eurytopic nature of this bivalve, which occurs from the hypersaline lagoon environments of biofacies A to the nearly open marine environment of biofacies B. For its ‘paper pecten’ morphology with ‘broad hinge line, numerous radial ribs, well developed ear in RV’ (Allison *et al.* 1995), *Eumorphotis* can be considered as tolerant of highly stressed oxygen-depleted environments (Posenato 2008b).

Biofacies F occurs in marls and dolostones of beds BA14, BA97, BA150, BA189 and BA664 from the sequence Lo3 and bed BA664 of Lo4. Species richness is

TABLE 1. List of bivalve genera and species from the Bellerophon Fm of the Dolomites classified and described in this paper.

Genus	Species
<i>Acharax</i> Dall, 1908	<i>Acharax frenademezi</i> sp. nov.
<i>Promytilus</i> Newell, 1942	<i>Promytilus merlai</i> sp. nov.
<i>Volsellina</i> Newell, 1942	<i>Volsellina carinata</i> sp. nov.
<i>Grammatodon</i> Branson, 1942	<i>Grammatodon</i> (<i>Cosmetodon</i>) <i>obsoletiformis</i> (Hayasaka, 1925)
<i>Bakevella</i> King, 1848	<i>Bakevella</i> (<i>Bakevella</i>) <i>binneyi</i> (Brown, 1841) <i>Bakevella</i> (<i>Bakevella</i>) <i>ceratophaga</i> (Schlotheim, 1816) <i>Bakevella</i> (<i>Bakevella</i>) <i>preromangica</i> sp. nov.
<i>Tambanella</i> Nakazawa & Newell, 1968	<i>Tambanella?</i> <i>stetteneckensis</i> sp. nov.
<i>Towapteria</i> Nakazawa & Newell, 1968	<i>Towapteria peracuta</i> (Stache, 1878)
<i>Pernopecten</i> Winchell, 1865	<i>Pernopecten tirolensis</i> (Stache, 1878)
<i>Etheripecten</i> Waterhouse, 1963	<i>Etheripecten stuflesseri</i> sp. nov.
<i>Eumorphotis</i> Bittner, 1901a	<i>Eumorphotis lorigae</i> Posenato <i>et al.</i> 2005 <i>Eumorphotis praecurrens</i> (Merla 1930) <i>Eumorphotis lorigae</i> Posenato <i>et al.</i> 2005
<i>Gardenapecten</i> gen. nov.	<i>Gardenapecten comelicanus</i> (Stache, 1878) <i>Gardenapecten trinkeri</i> (Stache, 1878)
<i>Palaeolima</i> Hind, 1903	<i>Palaeolima badiotica</i> sp. nov.
<i>Ladinomya</i> gen. nov.	<i>Ladinomya fosteri</i> sp. nov.
<i>Schizodus</i> Verneuil & Murchison, 1844	<i>Schizodus obscurus</i> (Sowerby, 1823)
<i>Lovarulucina</i> gen. nov.	<i>Lovarulucina covidi</i> sp. nov.
<i>Stutchburia</i> Etheridge, 1900	<i>Stutchburia tschernyschewi</i> (Licharew, 1933) <i>Stutchburia costata</i> (Morris, 1845) <i>Stutchburia</i> sp.
<i>Edmondia</i> De Koninck, 1841	<i>Edmondia hautmanni</i> sp. nov.
<i>Vacunella</i> Waterhouse, 1965	<i>Vacunella elongata</i> (Ciriacks, 1963)
<i>Unionites</i> Wissmann, 1841	<i>Unionites jacobi</i> (Stache, 1878)

low, ranging from 2 to 6 (mean = 4) and dominance D is variable, ranging from 0.22 to 0.84 (mean = 0.48).

The presence of nautiloids and *Stutchburia tschernyschewi* (euryhaline to stenohaline; Logan 1967) suggests more stable marine conditions for biofacies F compared with biofacies E, in particular for bed BA189, which represents the maximum flooding surface (NH A) of sequence Lo3.

Ecofacies

Ecofacies are functional and trophic assemblages identified using cluster analysis based on similarities in relative abundance. These evolutionary ecological units can provide useful information on the environmental evolution of the late Permian succession close to the end Permian extinction (Fig. 32).

Ecofacies A, restricted to bed BA664, is dominated by mobile, infaunal, suspension feeders and by facultatively mobile, deep infaunal, suspension feeders.

Ecofacies B, restricted to bed Ff1, is dominated by facultatively mobile, infaunal, suspension feeders. Stationary, semi-infaunal, suspension feeders are very rare.

Ecofacies C occurs in beds BA460, PR61, BA461 and JM28 from the maximum flooding surface (NH B) of sequence Lo4 and consists of all of the life habits and trophic guilds listed in Figure 31, only the facultatively mobile, deep infaunal, suspension feeders are rare. This could be due to increasing amounts of toxic H₂S with depth (Aberhan 1994). In this context, the presence of chemosymbiotic *Lovarulucina* and *Acharax* in ecofacies C can be interpreted as a response to high organic matter input. In modern oceans, some Solemyidae and Lucinidae live in shallow marine areas colonized by seagrass, where the abundant supply of decaying organic material promotes the generation of sulphide (Dubilier *et al.* 2008).

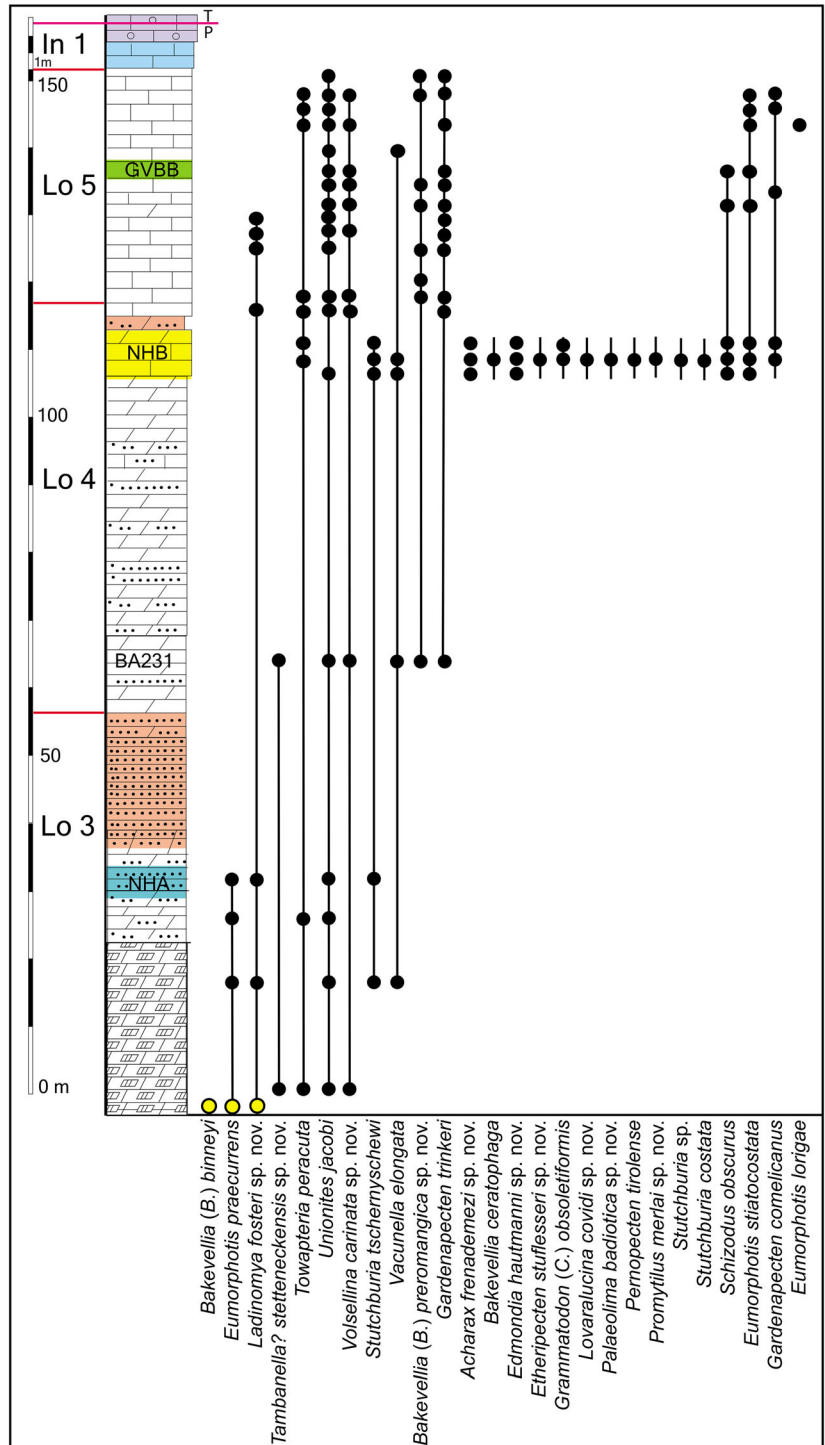
Ecofacies D occurs in most beds of the Bellerophon Fm and is dominated by stationary, epifaunal, suspension feeders and by facultatively mobile, infaunal, suspension feeders. Stationary, semi-infaunal, suspension feeders are also frequent but the facultatively mobile, deep infaunal, suspension feeders are rare.

Ecofacies A and B and D occurred in stressed environments: salinity, temperature (cf. Knoll *et al.* 2007) or oxygen-controlled environments of restricted lagoons (Bosellini & Hardie 1973) and more or less restricted inner shelf areas (Noè 1987), and have a relatively narrow range of life habits with high dominance and low diversity. In contrast, the deposition of the maximum flooding surface of sequence Lo4 (NH B), with its favourable environmental conditions, enables the settlement of a broad spectrum of modes of life of ecofacies C, with low dominance and high diversity. Fully and well-oxygenated marine conditions are recorded by the brachiopod and fusulinid-dominated benthic assemblage of the Bulla Mb, where the bivalves become a negligibly small component.

Extinction and survival pattern

Of the 19 bivalve genera identified in the Bellerophon Fm, 9 genera (c. 47%) disappear during the end-Permian

FIG. 29. Composite range chart of bivalves of the Bellerophon Fm. See Figure 2 for the stratigraphic log key. Yellow circles indicate that species are present starting from bed Ff1 of the middle part of Fiammazza Facies. Abbreviations: GVBB, Gardena Valley Bivalve Bed; NH A, Nautiloid Horizon A; NH B, Nautiloid Horizon B; P, Permian; T, Triassic.



mass extinction (Fig. 33). This value is decidedly lower than the ‘global extinction rate’ of bivalves at the genus level of *c.* 64% reported by Tu *et al.* (2016). *Unionites*, *Eumorphotis*, *Towapteria* and *Bakevellia* are abundant in the Bellerophon Fm. These genera survived the extinction event and became, together with *Claraia* and *Promyalina*,

the most abundant and widespread bivalves in Lower Triassic marine successions globally (Broglia Loriga *et al.* 1990; Schubert & Bottjer 1995; Kashiyama & Oji 2004; Fraiser & Bottjer 2007; Posenato 2009; Hautmann *et al.* 2013, 2015; Hofmann *et al.* 2014; Pietsch *et al.* 2014, 2016; Hofmann *et al.* 2015; Foster *et al.* 2015,

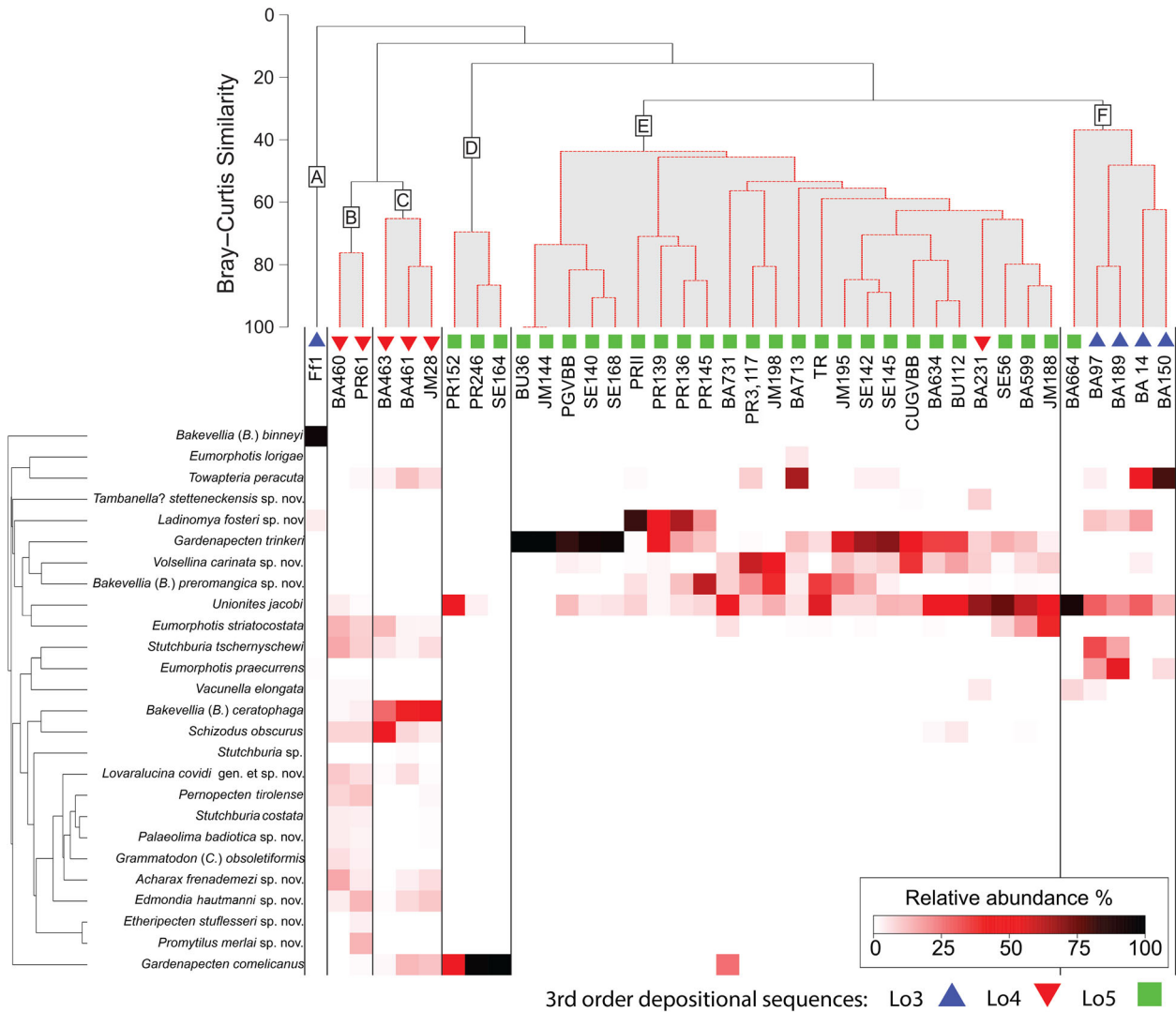


FIG. 30. Q-Mode (samples) cluster analysis, using the unweighted paired group algorithm and Bray–Curtis index of similarity and the SIMPROF test (Clarke & Warwick 2001). The samples are clustered into six groups (A–F) based on taxonomic composition; these are interpreted as different biofacies associations.

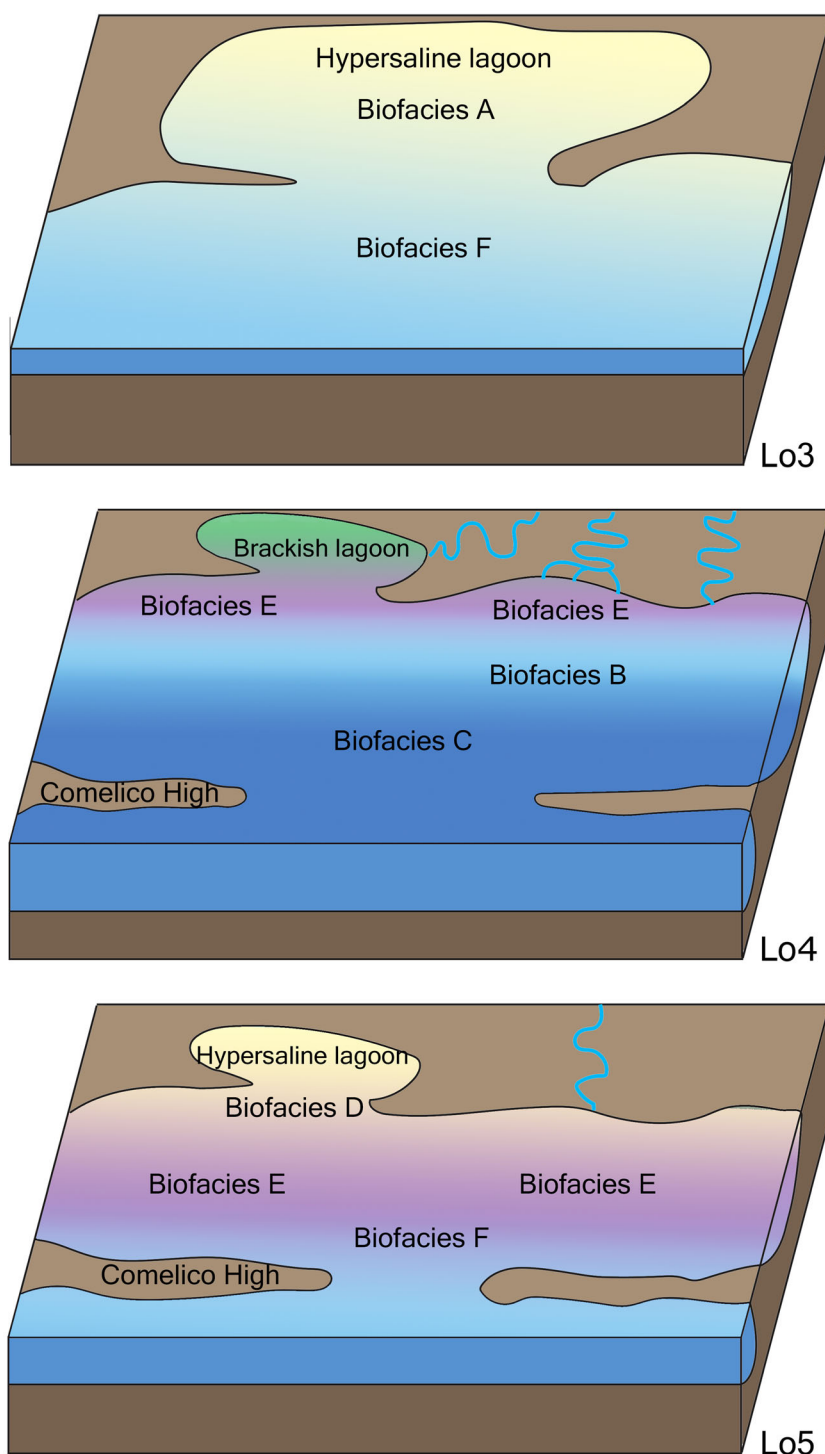
2017a, 2017b, 2018). Other genera are only occasionally cited in the Lower Triassic: *Stutchburia* occurs in the Siusi Member of the Werfen Fm from the Dolomites (Hofmann *et al.* 2014) and dubiously in the Feixianguan Fm of China (Gou & Lin 1996). *Promytilus* is recorded in the Spathian of Russia (Dagis *et al.* 1989), while *Pernopecten* occurs in the Spathian Virgin Limestone of the USA (Hofmann *et al.* 2013a). *Etheripecten* disappears at the base of the *Hindeodus parvus* zone in Kashmir (Nakazawa 1981) and, therefore, is considered a ‘dead clade walking’ (Jablonski 2001, 2002). Other genera can be considered as ‘Lazarus taxa’ given that they have not yet been recorded from the Early Triassic. *Palaeolima* is recorded in the Ladinian of USA (Waller & Stanley 2005)

while *Grammatodon* (*Cosmetodon*) occurs in the Norian–Rhaetian of Iran (Hautmann 2001). *Acharax* is cited in the Cretaceous of Japan (Kiel *et al.* 2008), although some fossil traces suggest its occurrence already in the Rhaetian of Germany (Seilacher 1990).

None of the Bellerophon Fm bivalve species is present in the Werfen Fm, but *Bakevellia ceratophaga* occurs in the earliest Triassic of South China (Hautmann *et al.* 2015; Foster *et al.* 2019) and *Eumorphotis striatocostata* is strictly related to *E. sp. aff. bocharica* of the earliest Triassic of Kashmir (Nakazawa 1981).

The new Triassic species rapidly evolved from Permian ancestors, which were, therefore, affected by a high species turnover. In the Bellerophon Fm, infaunal bivalves

FIG. 31. Palaeoenvironmental setting of the biofacies of the Bellerophon Fm during the deposition of the third-order depositional sequences Lo3, Lo4 and Lo5. Lo3 reconstruction refers to the deposition of sabkha cycles of Fiammazza facies or Rio Barbide Mb. Lo4 reconstruction refers to the deposition of Nautiloid Horizon B. Lo5 reconstruction refers to the deposition of the upper regressive part of the Ostracod unit.



(5 genera) experienced nearly the same extinction as the epifaunal bivalves (4 genera). This is in full agreement with the global extinction pattern, in which epifaunal bivalves experienced the same loss as the infaunal bivalves (Tu *et al.* 2016).

Biofacies E of the Bellerophon Fm consists of 11 genera, and the bivalve faunas of the Werfen Fm of Dolomites consist of 12 genera (Hofmann *et al.* 2014) (Fig. 34). Considering that five genera of the Werfen Fm (*Bakevella*, *Eumorphotis*, *Stutchburia*, *Towapteria* and

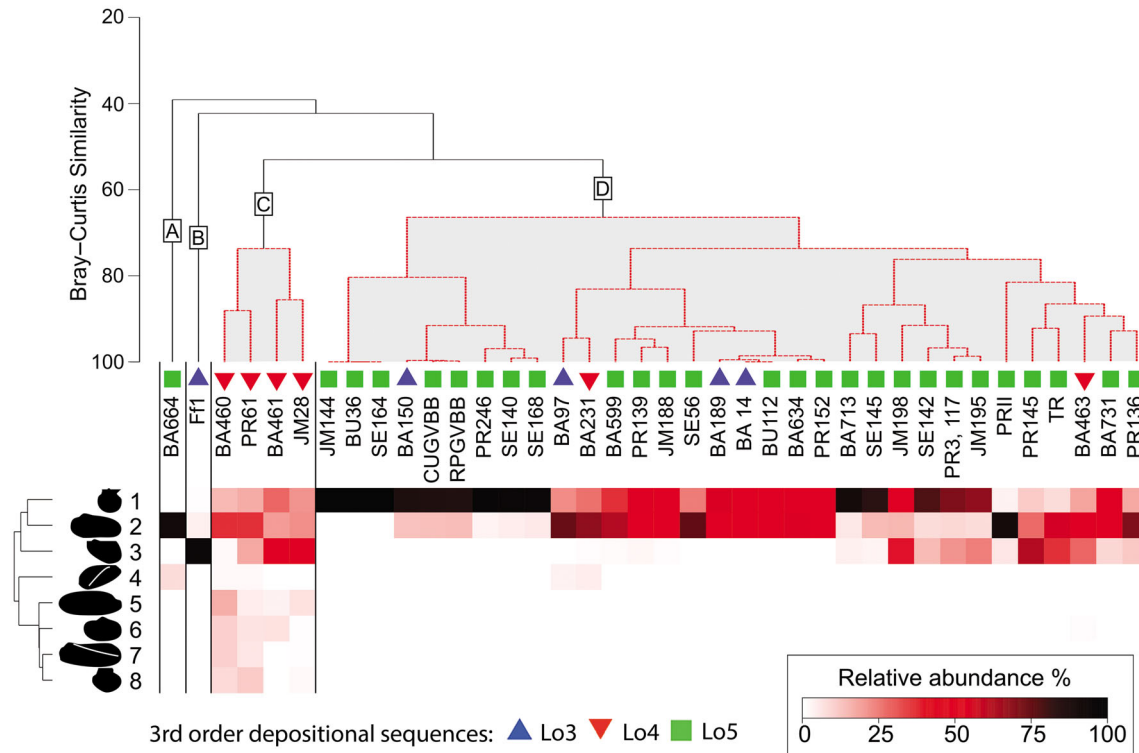


FIG. 32. Q-Mode (samples) cluster analysis, using the unweighted paired group algorithm and Bray–Curtis index of similarity and the SIMPROF test, identified four groups (A–D) of samples that are statistically distinct. The groups are interpreted as different benthic ecofacies associations, which have the following modes of life: 1, stationary, epifaunal suspension feeder; 2, facultatively mobile, infaunal suspension feeder; 3, stationary, semi-infaunal suspension feeder; 4, facultatively mobile, deep infaunal suspension feeder; 5, facultatively mobile, infaunal deposit feeder – chemosymbiotic; 6, facultatively mobile, infaunal chemosymbiotic; 7, stationary, low-level epifaunal suspension feeder; 8, facultatively mobile, epifaunal suspension feeder.

Bivalve genera from the Bellerophon Formation	Genera that survived locally (Werfen Formation)	Genera that survived globally (Early Triassic)	Lazarus genera reappearing after the Early Triassic
<i>Acharax</i>			
<i>Grammatodon</i>			
<i>Palaeolima</i>			
<i>Pernopecten</i>			
<i>Promytilus</i>			
<i>Bakevellia</i>			
<i>Eumorphotis</i>			
<i>Stutchburia</i>			
<i>Towapteria</i>			
<i>Unionites</i>			
<i>Edmondia</i> †			
<i>Etheripecten</i> †			
<i>Gardenapecten</i> gen. nov. †			
<i>Lovalucina</i> gen. nov. †			
<i>Schizodus</i> †			
<i>Tambanella</i> ? †			
<i>Vacunella</i> †			
<i>Volsellina</i> †			

FIG. 33. Ranges of bivalve genera reported from the Bellerophon Fm. †Went extinct.

Bellerophon Fm Biofacies E	Ecology	Werfen Fm
	1	<i>Avichlamys</i>
	8	<i>Scythentolium</i>
<i>Tambanella</i>	1	<i>Claraia</i>
<i>Volsellina</i>	1	<i>Costatoria</i>
<i>Eumorphotis</i>	1	<i>Eumorphotis</i>
<i>Gardenapekten</i>	1	<i>Leptochondria</i>
<i>Towapteria</i>	1	<i>Towapteria</i>
<i>Bakevellia</i>	3	<i>Bakevellia</i>
	3	<i>Pteria</i>
<i>Stutchburia</i>	2	<i>Stutchburia</i>
<i>Schizodus</i>	2	<i>Neoschizodus</i>
<i>Unionites</i>	2	<i>Unionites</i>
<i>Ladinomya</i>	2	
<i>Vacunella</i>		

Epifaunal

Semi-infaunal

Infaunal

Common genera

Substituted genera

FIG. 34. Comparison between the bivalve genera of biofacies E from the Bellerophon Fm and bivalve genera from the Werfen Fm (Posenato 2008b; Hofmann *et al.* 2014). Note the similar ecological categories. Modes of life (see Fig. 32): 1, stationary, epifaunal suspension feeder; 2, facultatively mobile, infaunal suspension feeder; 3, stationary, semi-infaunal suspension feeder; 8, facultatively mobile, epifaunal suspension feeder.

Unionites) were already present in biofacies E of the Bellerophon Fm and that *Leptochondria* replaced *Gardenapekten*, and *Neoschizodus* replaced *Schizodus*, it can be seen that the genus-level compositions of biofacies E and the Werfen Fm are very similar. Low similarities exist instead between the bivalve genera of the Werfen Fm and biofacies B and C of the Bellerophon Fm.

According to Clapham & Bottjer (2007) the late Permian offshore communities were very similar to early Permian onshore communities, in that both appear to have contained a heterogeneous mosaic of mixed mollusc–brachiopod assemblages, in contrast to the rather homogeneous extreme brachiopod dominance in early and middle Permian offshore settings. The onset of anoxic–euxinic deep waters on shelves around the Guadalupian–Lopingian boundary enabled the bivalves to spread in these environments and to compete with brachiopods, increasing their abundance during the Lopingian. Complete bivalve dominance is instead recorded in the nearshore environments from the early Permian (Clapham & Bottjer 2007). Here, we show that the more stress-adapted onshore bivalve communities from the Changhsingian Bellerophon Fm were perhaps very

TABLE 2. Criteria that facilitated the survival of genera from the Bellerophon Fm during the end-Permian extinction.

Genus	Broad geographical range	>2 biofacies	High population density	>2 species	Eurytopic
<i>Acharax</i> *	1				
<i>Grammatodon</i> *	1				0.5
<i>Palaeolima</i> *	1				
<i>Pernopecten</i> *	1				
<i>Promytilus</i> *	1				
<i>Bakevellia</i> *	1	1	1	1	1
<i>Eumorphotis</i> *		1	1	1	1
<i>Stutchburia</i> *	1	1	1	1	0.5
<i>Towapteria</i> *	1	1	1	1	1
<i>Unionites</i> *		1	1		1
<i>Edmondia</i> †	1				
<i>Etheripecten</i> †	1				
<i>Gardenapekten</i> gen. nov.†		1	1		1
<i>Ladinomya</i> gen. nov.†		1	1		1
<i>Lovaralucina</i> gen. nov.†					
<i>Schizodus</i> †	1	1	1		1
<i>Tambanella</i> ?†	1				
<i>Vacunella</i> †	1				
<i>Volsellina</i> †	1		1		1

*Survived end-Permian extinction.

†Went extinct. 0.5 in the final column indicates eurytopic to stenotopic genus.

similar to Early Triassic offshore communities, like the one of the Werfen Fm, which were nearly exclusively dominated by molluscs. This is also confirmed by the fact that almost all of the genera of the Werfen Fm (except for *Avichlamys* and *Scythentolium*) were already present in the Permian and 83% of the bivalve fauna of the Werfen Fm consists of Permian holdovers at the genus level.

The genera of the Bellerophon Fm, which are found also in the Werfen Fm (Table 2) are eurytopic generalists with a high population density, diffused in >2 biofacies and with a high number of within-genus species (Foster *et al.* 2022). *Acharax* probably survived because it was adapted to high H₂S levels. Extinct genera were instead often adapted to normal marine stenotopic conditions, very rare and restricted to only one or two biofacies (*Etheripecten*, *Tambanella*, *Vacunella*) and adapted to a specific habitat such as the deep burrower *Vacunella* and the chemosymbiotic *Lovaralucina*. Other extinct genera are documented only from the Bellerophon Fm, even though they had a high population density (*Ladinomya* and *Gardenapekten*).

The worldwide distribution of a genus seems to be the most important factor for surviving the end-Permian

mass extinction (McKinney 1997), which enabled *Grammatodon*, *Palaeolima*, *Pernopecten* and *Promytilus* to survive, even if they were adapted prevalently to normal marine conditions. This agrees with extinction selectivity studies that suggest that a broad distribution is a good predictor of survival during a mass extinction (Finnegan *et al.* 2015; Foster *et al.* 2020). More difficult to explain is the extinction of eurytopic genera from the Bellerophon Fm, such as *Gardenapecten*, *Schizodus* and *Volsellina*. Probably the limited distribution and competition with *Leptochondria* (which had a worldwide distribution already during the Changhsingian) were important factors, which made *Gardenapecten* vulnerable to extinction. *Schizodus* was replaced by the very similar *Neoschizodus* after the end-Permian extinction, but *Volsellina*, like all mytilidae, was absent from the Werfen Fm. The disappearance of these highly resistant genera is evidence of the extreme conditions during the end-Permian extinction.

CONCLUSION

Extensive outcrops of the Bellerophon Fm in the Gardena and Badia Valleys (western Dolomites, Italy) have enabled the collection of c. 6500 bivalve specimens. The systematic analysis of this collection has allowed us to determine and describe 26 species (10 new), 19 genera (3 new: *Gardenapecten*, *Ladinomya*, *Lovarylucina*) and one new family (Ladinomyidae). The precise stratigraphic setting of the collected material has facilitated the recognition of six bivalve biofacies and four ecofacies, which record the environmental evolution of the Bellerophon Fm, which ranges from marginal and restricted marine environments to shallow-water and nearly fully marine settings.

The abundance of *Eumorphotis* and *Unionites* in the upper Permian of the Dolomites is noteworthy. During the Early Triassic, these bivalves proliferated and have been referred to as ‘disaster taxa’, owing to their opportunistic ecology. The high survival at genus level of the Changhsingian bivalves from the Dolomites (63%) and the occurrence of genera that dominated the Early Triassic post-extinction benthic assemblages, can be related to the marginal and shallow marine conditions of the Bellerophon Fm. The oxygen depletion, high temperature and salinity recorded in the Bellerophon Fm indicate that bivalves were adapted to these stressors prior to the end-Permian mass extinction. This is also indicated by the high similarity of biofacies E of Bellerophon Fm with the fauna of the Werfen Fm at genus level, which occurred in a salinity-, temperature- and oxygen-stressed setting. Once the extinction terminated,

the survival genera expanded in the offshore environments because their competitors, mainly the brachiopods, were extinct.

Acknowledgements. We thank Irene Zorn from the Geologische Bundesanstalt in Vienna, Maria Gabriella Fornasiero and Letizia Del Favero of the Dipartimento di Geologia, Paleontologia e Geofisica Museum of the University of Padova, Carlo Sarti from the Museum Giovanni Capellini of the University of Bologna, and Alexander Nützel and Winfried Werner from the Bayerische Staatssammlung für Paläontologie und Geologie of Munich for access to their collections. We are also grateful to Andreas Kroh from the Natural History Museum Vienna (NHMW) for providing the pictures of *Towapteria waehneri*. We are particularly grateful to William Foster from the University of Hamburg who provided suggestions and comments on an early version of the article and for his courtesy in correcting, together with Monica Alejandra Gómez Correa, the English text. We thank Evelyn Kustatscher from the Museum of Nature South Tyrol for her valuable comments on the article. This article benefited from careful reviews by Michael Amler, Michael Hautmann, Sally Thomas and Winfried Werner. This research was financed by the Research Fund of the South Tyrolean Provincial Museums, for work for the Museum Ladin Ćiastel de Tor. The research of RP was also supported by funding provided by project ‘Biota resilience to global change: biomineralization of planktic and benthic calcifiers in the past, present and future’ supported by MURST (PRIN 2017RX9XXXY) and Ferrara University (FAR 2018 and 2019). The fossils from Termeno were collected as part of a research project of the Euregio Science Fund (call 2014, IPN16: The end-Permian mass extinction in the Southern and Eastern Alps: extinction rates vs taphonomic biases in different depositional environments) of the Tyrol–South Tyrol–Trentino Euroregion. The authors thank the Department of Innovation, Research, University and Museums of the Autonomous Province of Bozen/Bolzano for covering the open access publication costs.

Author contributions. HP coordinated the project, logged the sections, collected and determined the bivalves, prepared the plates with bivalves and analysed the palaeoecological data. HP and RP discussed the data and wrote the manuscript.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/48088B07-9B35-4DF2-8704-64DA71CDF7D7>

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n8pk0p2zz>

Editor. Michael Hautmann

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