

A contribution to the study of the genus *Cadomella* Ehlert and Ehlert, 1887 (Brachiopoda, Jurassic)

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ABSTRACT:

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On the basis of a biometric analysis of German and English representatives of the peculiar Early Jurassic rhynchonellate brachiopod *Cadomella*, two species, the early Toarcian *C. moorei* (Davidson in Davidson and Morris, 1847) and the late Pliensbachian *C. quenstedti* Rau, 1905, are considered as synonyms. Moreover, a certain number of misinterpretations concerning the genus is corrected. Its authorship belongs to Daniel and Pauline Ehlert (15th of June, 1887) and not to Ernest Munier-Chalmas (not earlier than the 30th of June, 1887), even if the latter orally presented the new genus along with its name at the meeting on the 23rd of February, 1887. The distribution of the monotypic genus *Cadomella* includes the upper Pliensbachian of Germany and the lower Toarcian of England, France, and North Africa. The Cadomellidae are undoubted rhynchonellates, but their further affinities are still enigmatic: there exist several similarities with some thecideides (concavo-convex shell, dorsal valve features), but important differences (impunctate vs. endopunctate microstructure) occur as well.

Key words: Rhynchonellata; Systematics; Biometry; Lias.

INTRODUCTION

Cadomella Ehlert and Ehlert, 1887 is a peculiar Jurassic brachiopod, externally homoeomorphic with some Palaeozoic strophomenates. The shell microstructure of *Cadomella moorei* (Davidson in Davidson and Morris, 1847) has been shown to be fibrous and not laminar, and therefore this brachiopod is a rhynchonellate and not a strophomenate (Brunton and MacKinnon 1972); however, this discovery was published in a paper otherwise devoted to *Koninckodonta davidsonii* (Deslongchamps, 1853) misidentified therein as a representative of *Cadomella*. The resulting confusion persisted until the beginning of the present century and *Cadomella* was still classified as a strophomenide by Alméras *et al.* (2007).

The present short note is devoted in the first place to analysis of the relationships of the representa-

tives of *Cadomella* found in England and France (*C. moorei*) and in Germany (often distinguished as *C. quenstedti* Rau, 1905), as well as to illustration of the microstructure of the shell. In addition, a few nomenclatural questions are clarified and a critical assessment of published data on the distribution of the genus is given.

MATERIAL AND METHODS

The present study is largely based on reinvestigation of the collection made by Karl Rau and preserved at the University of Tübingen (see Werneburg 2023). Most of this collection (including all the illustrated specimens) comes from the 'Leptaenenbett' belonging to the 'Lias delta oben' of Wilflingen (Landkreis Rottweil, Baden-Württemberg; Text-fig. 1; see Rau 1905, pp. 84–91). Additionally, a few specimens are



reported to have come from Erzingen, Hechingen, and Reutlingen, but these were not found in the collection. The Lias $\delta 2$ in the stratigraphy established by Quenstedt (1858) corresponds to the beds immediately below and above the Pliensbachian–Toarcian boundary, the uppermost part of the *Pleuroceras spinatum* Zone and the lower part of the *Dactylioceras tenuicostatum* Zone (Schelgelmilch 1992, p. 24). In more detail, the ‘Leptaenenbett’ is situated under the bed with *Ammonites costatus* von Schlotheim, 1820 [Engel 1883, p. 103; = *Pleuroceras spinatum* (Bruguière, 1789), see Bardin *et al.* 2013], now called the ‘*spinatum*-Kalk’ (Schlatter 1985). As a consequence, even if there may be some doubt on the exact age of the uppermost limestone bed of the Lias δ (Maisch 2007), the ‘Leptaenenbett’ undoubtedly belongs to the *Pleuroceras spinatum* Zone (see also Vörös 2002, p. 347), and is thus of Domerian age.

Unfortunately, out of 60 articulated shells and about 30 dorsal and 30 ventral valves reported by Rau (1905, p. 9), only 22 specimens could be found at the University of Tübingen. Even despite that, Rau’s collection is the largest sample of *Cadomella* the present authors were able to locate after searching in major Western European natural history museums. In particular, the authors were unable to find any specimen coming from France (collections in Paris – both MNHN and Sorbonne, Lyon, and Caen searched) and only a single shell was located at the Natural History Museum [formerly British Museum (Natural History)] in London. The specimens from south-western Germany are larger-sized than English or French ones (data after published sources, see below), and allow appreciation of the variability of external and internal characters. The shells illustrated by Rau (1905) were re-studied under a binocular microscope, but due to concerns for the preservation of the original specimens they could not be borrowed. These shells are illustrated here, using the original photographs taken by Rau (1905), the use of which was kindly authorised by the Palaeontological Collection of the University of Tübingen.

A single non-illustrated specimen from Rau’s collection (a fragmentary dorsal valve) was selected for study of the shell microstructure. It was embedded in epoxy resin and cut to obtain two surfaces: sub-radial and transverse one, the latter being close to and parallel to the anterior margin of the valve. The cut surfaces were polished and then etched with a 10% acetic acid solution for about 60 seconds. The specimen was then coated with platinum and investigated and photographed under a scanning electron microscope. The examined dorsal valve is heavily

weathered, which resulted in the complete removal of the primary shell layer. The secondary shell layer in places shows alteration due to re-crystallization and rare inclusions of pyrite crystals.

Institutional abbreviations

FLS – Université Claude Bernard Lyon 1, Lyon, France;

GPIT – Paläontologische Sammlungen, Universität Tübingen, Tübingen, Baden-Württemberg, Germany;

SMNS – Staatliches Museum für Naturkunde Stuttgart, Baden-Württemberg, Germany.

SYSTEMATICS

Phylum Brachiopoda Duméril, 1805

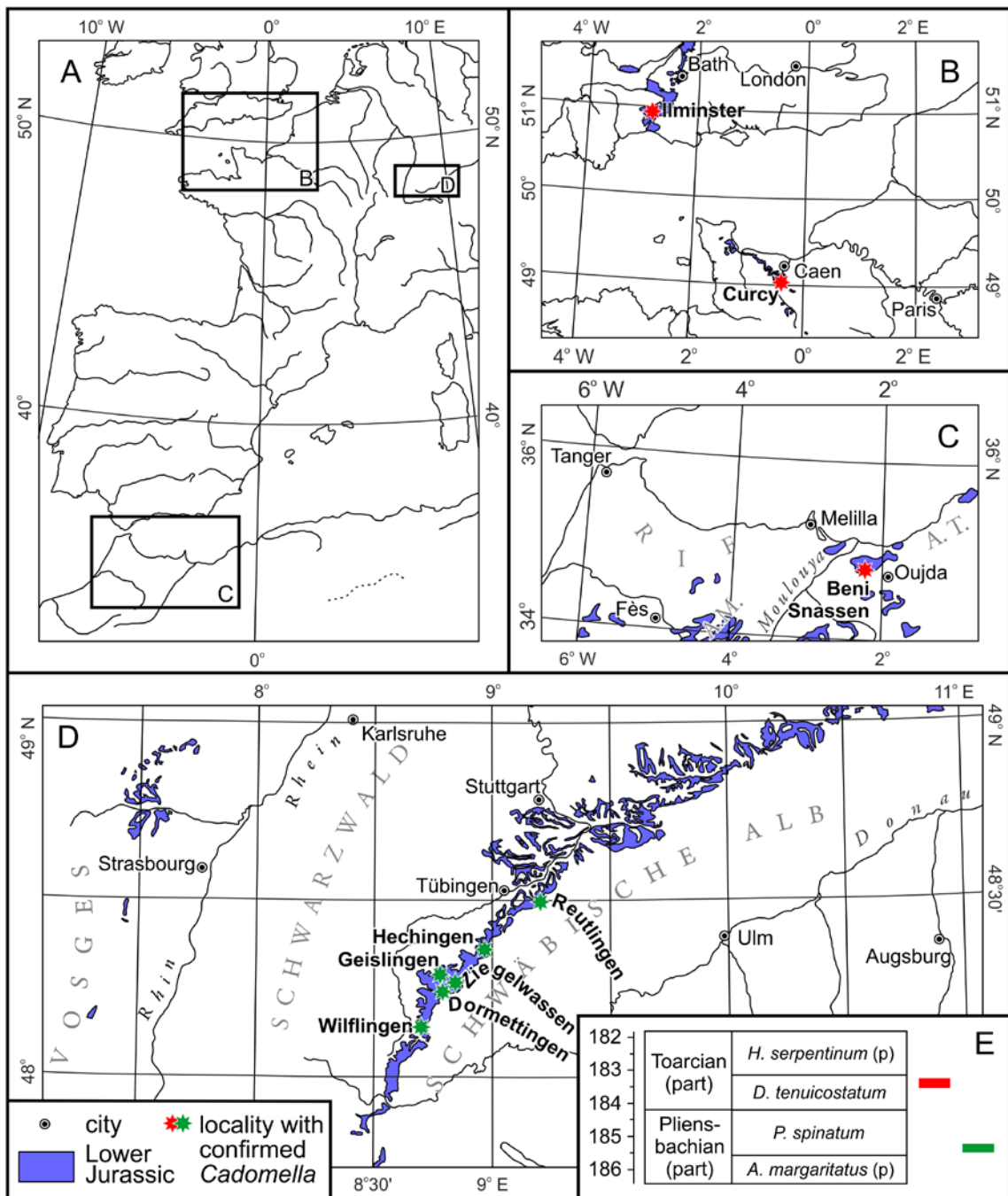
Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer and Popov, 1996

Class Rhynchonellata Williams, Carlson, Brunton, Holmer and Popov, 1996

Order unknown

Family Cadomellidae Munier-Chalmas, 1887

REMARKS: The Cadomellidae belong to the class Rhynchonellata on account of their fibrous shell microstructure (see Williams *et al.* 1996, p. 1193). At the current stage of research, the question of their position within that class has not been satisfactorily resolved. According to MacKinnon (2006), lack of a spiral brachidium precludes koninckinidine (athyridide) affinities. This need not be true, insofar as secondary morphological simplification can easily be conceived; a similar case was documented with micromorphic terebratulides secondarily lacking the loop otherwise diagnostic for that order (suborder Gwynioidina Halamski and Bitner in Halamski *et al.* 2015). At this point it is worth pointing out a number of similarities between *Cadomella* and some representatives of the order Thecideida Elliott, 1958: a concavo-convex shell (in some Thecospiroidea, see Baker 2006; a character otherwise very rare among the rhynchonellates); a bilobed cardinal process; the dorsal median septum anteriorly divided; brachial ridges turning inwards (in *Stentorina* Baker and Wilson, 1999), not unlike the crura in *Cadomella*. However, there are also important differences, above all the shell microstructure (impunctate in *Cadomella*, endopunctate in the thecideides). *Cadomella* might either be related to the thecideides, or represent an independently arisen lineage: the above-mentioned similarities would thus have appeared as convergences.



Text-fig. 1. Geographic and geologic context of the studied brachiopods. A – Map of Western Europe with insets showing the extent of the more detailed maps. B–D – Maps of areas with confirmed localities (green asterisks: Pliensbachian; red ones: Toarcian) of *Cadomella moorei*, showing the extent of the Lower Jurassic at outcrop. E – Stratigraphic scheme of the upper part of the Pliensbachian and the lower part of the Toarcian (simplified after Hesselbo *et al.* 2020), showing absolute ages in millions of years, ammonite zones, and the approximate positions of the ‘*Leptaena* bed’ in England and France (red line) and in Germany (green line). Maps redrawn after Cukierska (1987), Bodelle *et al.* (1980), Landesamt für Geologie, Rohstoffe und Bergbau Baden-Württemberg (1998), Asch (2005), and British Geological Survey (ed., 2007).

The Cadomellinae was first proposed by Munier-Chalmas (1887, p. XL) in the following words: “il doit constituer pour lui un petit groupe sous le nom de

Cadomellinae” (it [*scil.* the genus *Cadomella*] should constitute a small group, named *Cadomellinae*, for itself). No diagnosis was given, but according to the

present rules of zoological nomenclature, before 1931 an ‘indication’ consisting in basing the (sub)family name on a genus [see below], was sufficient for validly introducing the name (ICZN, Art. 12.2.4). Other requirements of the Code (Art. 11) are also met, so in the opinion of the present authors this constitutes the valid publication of the subfamily name, even if no family to which this subfamily should belong was given (not a condition in the Code). Schuchert (1893, p. 153) classified the “Cadomellinae Munier-Chalmas, 1887” as a subfamily of the Strophomenidae King, 1846 and, subsequently, the subfamily was reclassified within the presumably strophomenacean family Thecideidae Gray, 1840 by Schuchert and LeVene (1929, p. 17). Such a classification was followed also by Roger (1952, p. 71). The superfamily Cadomelloidea and the family Cadomellidae were erected by Muir-Wood (1955, p. 90) who indicated the authorship as “Cadomellinae ? of Schuchert 1893, not of Munier-Chalmas 1887”, but the reasons for this opinion on authorship were not given. Muir-Wood classified the superfamily in the suborder Chonetoida (see also Muir-Wood 1962, p. 30). The family “Cadomellidae Muir-Wood 1955” was included in the “Groupe des Strophomena” (a subdivision of the subclass Articulata corresponding more or less to the order Strophomenida *s.l.*) by Roger (1960, p. 1474). The Cadomellinae Munier-Chalmas, 1887 were classified tentatively as a subfamily in the purportedly terebratulide family Thecideidae Gray, 1840 by Licharew *et al.* (1960, p. 305). The superfamily “Cadomelloidea Schuchert, 1893” was classified as rhynchonellates *incerti ordinis* by MacKinnon (2006, p. 2251) and as strophomenides by Alméras *et al.* (2007, p. 34).

Genus *Cadomella* Ehlert and Ehlert, 1887

TYPE SPECIES: *Leptaena moorei* Davidson in Davidson and Morris, 1847; ‘*Leptaena* bed’, *Dactylioceras tenuicostatum* Zone (see Arkell 1933, p. 170; Ager 1967, p. 139), lower Toarcian, Lias; Ilminster, Somerset, England.

REMARKS: Most of the time the authorship of the genus was attributed to Munier-Chalmas (1887). A few authors (Muir-Wood and Williams 1965, p. H438; Cowen and Rudwick 1966; Grant 1972, p. 232; Sulser 2004, p. 428; Alméras *et al.* 2007, p. 34; Emig 2013, p. 308), however, credit “Ehlert, 1887” (sometimes as “Ehlert in Fischer”). Rollier (1916, p. 44) used a spelling that might be confusing to some extent: “*Cadomella* (Munier-Chalmas), Ehlert in Fischer, 1887”.

The question of the authorship of the genus *Cadomella* is somewhat complicated. It requires establishing priority between two publications printed in the same year, a paper by Ernest Munier-Chalmas and a book chapter by Daniel and Pauline Ehlert (D.-P. stands for Daniel and Pauline, see Emig 2013). The paper by Munier-Chalmas was printed in the ninth issue of the *Comptes-rendus sommaires de la Société géologique de France*, among the summaries of matters treated at the meeting held on the 23rd of February, 1887. However, it should be stressed that presenting a matter on a meeting does not constitute a publication and does not count towards priority issues. The date of printing of the report is the determining factor. Monthly publication dates were printed on the covers of *Comptes-rendus sommaires* issues, and the covers were removed when the volumes were bound (standard practice in the 19th century). No unbound issue containing the report of the meeting held on the 23rd of February, 1887 could be found, but it was possible to find one for the issue with the report of the meeting of the 7th of February: that issue was published in June 1887 (so, for nomenclatural reasons, as no further precision is given, on the last day of the month, the 30th of June, 1887). It follows that, in all probability, the issue containing the report of the meeting held two weeks later, could be printed on the same date at the earliest.

On the other hand, the last part [Fascicule XI, pp. 1009–1369] of the *Manuel de conchyliologie* by Paul Fischer, containing the chapter by Daniel and Pauline Ehlert, was printed on the 15th of June, 1887 (the information on the publication date of the fascicles is given in the *Manuel* itself, just after the title page). As a consequence, the publication by Ehlert and Ehlert (1887) is the earliest one to validly introduce the genus name discussed here.

Two more issues require discussion. First, it is worth emphasising that the authorship of both the publication and the taxa introduced in it belongs to both Ehlerts, as indicated by the abbreviation of their names D.-P. (P. is not an abbreviation of the middle name of Daniel Victor Ehlert). The correct way of citing according to the modern standards is therefore “Ehlert and Ehlert, 1887” (as noticed in relation to other papers authored by the Ehlert couple by Carter *et al.* 1994, p. 355 and Blodgett *et al.* 1999, p. 1082) and not “Ehlert, 1887”.

Secondly, authorship of the genus *Cadomella* in the book chapter written by Ehlert and Ehlert is attributed to Munier-Chalmas. In accordance with modern rules of zoological nomenclature, “if it is clear from the contents that some person other than an author of

the work is alone responsible both for the name or act and for satisfying the criteria of availability other than actual publication, then that other person is the author of the name or act" (ICZN, Art. 50.1.1). However, this criterion is not met, because it cannot be demonstrated that Munier-Chalmas is the sole author (the drawing is credited to Munier-Chalmas, but not the text, meaning that the latter may be partially or entirely by Ehlert and Ehlert). In such a case, Ehlert and Ehlert alone must be recognized as the authors of the genus name. One could comment here that the rules of botanical nomenclature would have allowed for justice to be given to Munier-Chalmas, who is conceptually the author of the name (it would be "Munier-Chalmas ex Ehlert et Ehlert"), but obviously zoological nomenclature is governed by separate rules.

SPECIES ASSIGNED: The only species belonging to *Cadomella* is the type species, understood here widely, that is, including the German forms sometimes segregated as *C. quenstedti* (see below).

SPECIES REJECTED: The reasons for excluding *Leptaena pearcei* Davidson, 1851 and *L. granulosa* Davidson, 1851 from the genus *Cadomella* are summarised by Rollier (1916, p. 45). In turn, *Thecidea perierii* Deslongchamps, 1853, a possible representative of *Cadomella* according to Rollier (1916), is excluded herein on the basis of its smooth shell. The misattribution of *Leptaena davidsonii* Deslongchamps, 1853 to *Cadomella* by Muir-Wood and Williams (1965), Cowen and Rudwick (1966), and Brunton and MacKinnon (1972) was corrected by MacKinnon (2006); it is a *Koninckodonta* Bittner, 1893.

Cadomella moorei (Davidson in Davidson and Morris, 1847)
(Text-figs 2–4)

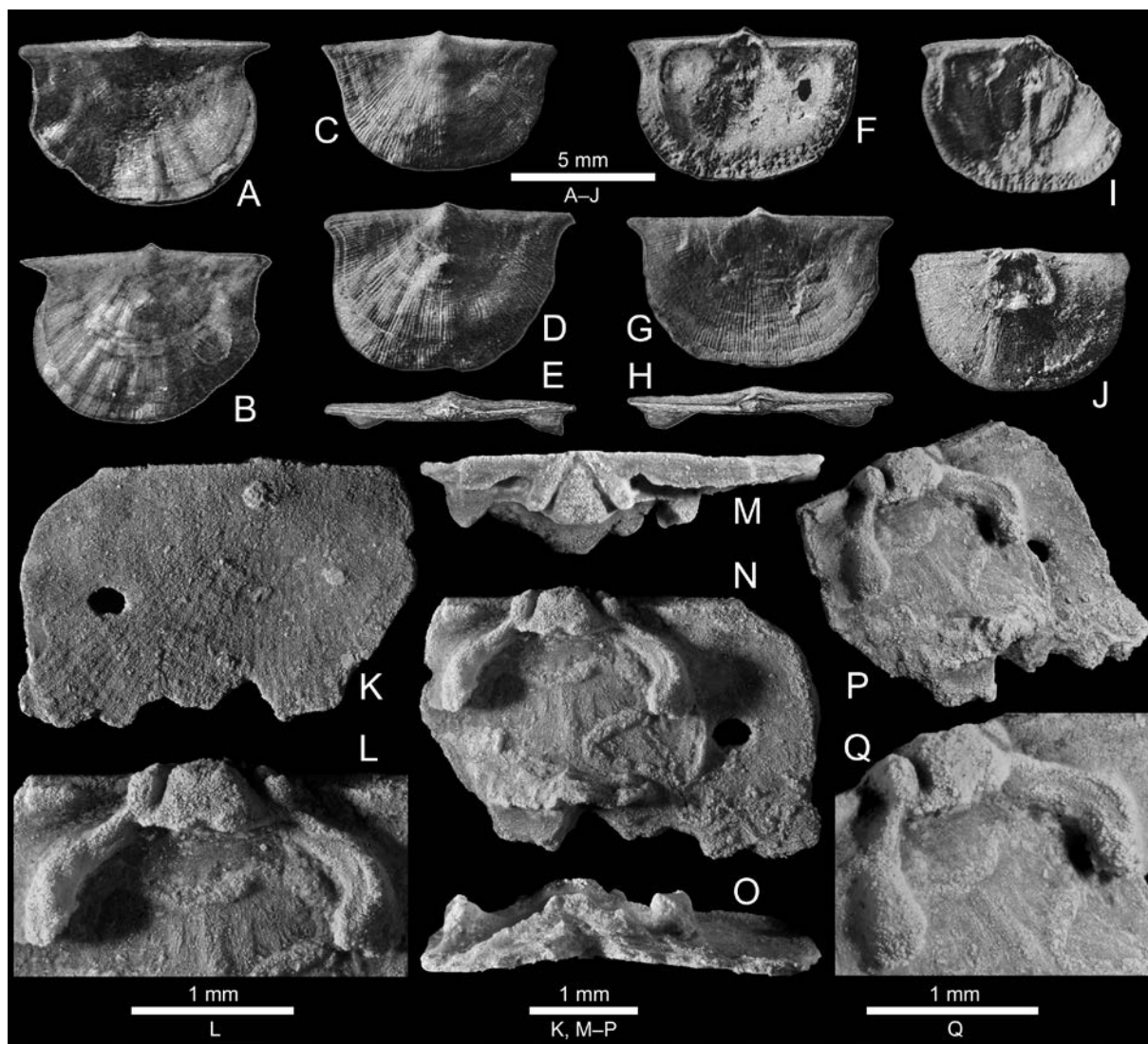
- *1847. *Leptaena Moorei*, Davidson; Davidson and Morris, p. 251, pl. 18, fig. 1a–c.
- 1849. *Leptaena Moorei*, Davidson; Davidson, figs 4, 4a.
- 1849. *Leptaena Moorei*, Davidson, 1847; d'Orbigny, p. 220.
- 1851. *Leptaena Moorei*, Dav.; Davidson, p. 17, pl. 1, figs 18, 18a–e.
- 1858. *Leptaena Moorei* Dav.; Deslongchamps and Deslongchamps, pp. 136, 138, 161, pl. 2, fig. 20.
- 1871. *Leptaena Moorei*; Quenstedt, p. 535, pl. 54, figs 131, 132.
- 1876. *Leptaena Moorei*, Dav.; Davidson, p. 93.
- 1887. *Cadomella Moorei*, Davidson; Ehlert and Ehlert, p. 1285, fig. 1051.

- v. 1905. *Cadomella Quenstedti* n. sp.; Rau, pp. 7–9, pl. 1, figs 1–21.
- 1905. *Cadomella Moorei* Dav. sp.; Rau, pl. 1, figs 22–25.
- 1916. *C. [=Cadomella] Quenstedti* K. Rau; Rollier, p. 45.
- 1916. *C. [=Cadomella] Moorei* Davidson; Rollier, p. 45.
- 1965. *Cadomella moorei* (Davidson); Muir-Wood and Williams, pp. H438, H439, fig. 295.1.
- non 1988. *Cadomella cf. moorei* (DAVIDSON); Alméras *et al.*, p. 695, pl. 1, fig. 6.
- 1988. *Cadomella moorei* (DAVIDSON), 1852; Raouiat, pp. 105–107, text-figs 46, 47, pl. 1, figs 1–2.
- 2006. *C. [=Cadomella] moorei* Davidson; MacKinnon, p. 2251, fig. 1498a–d.
- ?2007. *Cadomella moorei* (DAVIDSON, 1847); Alméras *et al.*, p. 34.
- ?2009. *Cadomella cf. moorei* (Davidson); Elmi *et al.*, p. 40.
- 2020. *Cadomella moorei* (Davidson 1847); Höflinger, p. 122, unnumbered text-figs.

MATERIAL: Eight articulated shells, eight dorsal valves, and six ventral valves, GPIT-PV-124544–124564 [formerly 76859, 76860], 93567; 'Leptaenenbett', *Pleuroceras spinatum* Zone, upper Pliensbachian, Lias; Wilflingen, Baden-Württemberg, Germany. These specimens are syntypes of *Cadomella quenstedti*, out of which the articulated shell GPIT-PV-124544 [formerly one of several specimens under the catalogue number GPIT-PV-76860] (Text-fig. 2A, B; see also Rau 1905, pl. 1, fig. 1) is selected herein as the lectotype.

DESCRIPTION: Shell up to 9.3 mm in width, transverse (width-to-length ratio 1.2–1.4 in specimens smaller than 4 mm, 1.4–1.8 in larger ones), sometimes mucronate, very low (usually 1.4–1.6 mm thick, often thinner), concavo-convex to nearly plano-convex. Maximum width at hinge line. Ventral interarea triangular, low; delthyrium in some cases mostly open, with strong but narrow deltidial plates; sometimes deltidial plates covering a large part of the delthyrium, leaving a narrow groove in the middle; sometimes deltidial plates conjunct, thus forming a symphytium. Pedicle foramen hypothyrid. Dorsal valve with an interarea of similar height as the ventral one; notothyrium filled by the cardinal process.

Ornamentation of very fine, rounded costae and costellae, (7–)10–12(–14) per mm, separated by narrow furrows. Costae begin within less than 1 mm



Text-fig. 2. Morphology of *Cadomella moorei* (Davidson in Davidson and Morris, 1847). A, B – articulated shell GPIT-PV-124544, lectotype of *C. quenstedtii* Rau, 1905 in dorsal and ventral views; C – articulated shell GPIT-PV-124550 in ventral view; D, E – articulated shell GPIT-PV-124548 in ventral and posterior views; F – ventral interior GPIT-PV-124563; G, H – articulated shell GPIT-PV-124546 in dorsal and posterior views; I – ventral interior GPIT-PV-124562; J – dorsal interior GPIT-PV-124552; K–Q – fragmentary dorsal valve GPIT-PV-93567 in exterior (K), posterior (M), interior (N), anterior (O), and oblique (P) views, with enlargements of cardinalia in dorsal (L) and oblique (Q) views (specimen prior to sectioning, see Text-fig. 3). All specimens are from the Lower Jurassic (Lias δ , uppermost Pliensbachian) of Wilflingen (Baden-Württemberg), coll. Karl Rau. All specimens, except the lectotype, are paralectotypes of *C. quenstedtii* Rau, 1905. A–J are images in visible light (modified after Rau 1905, pl. 1, figs 1[a], 1[b], 7, 5, 5a, 20, 3, 3a, 19, 9); K–Q are SEM micrographs.

from the beak. Costellae appearing by both intercalation and bifurcation. A single shell also has broad, low undulations.

Dorsal interior: Cardinal process stark, bifid, separated by narrow, deep notches from inner socket ridges (Text-fig. 2L, M). These are prolonged by thick rims bordering the posterior part of the muscle field; rims are coalescent with the valve floor, and in their distal (anterior) parts curve towards the plane of the

symmetry and get elevated over the valve floor (Text-fig. 2Q); the rims laying on the valve floor are interpreted as crural bases, and their slightly elevated endings as the proximal part of the crura. Muscle field occupying slightly less than half of the valve length, elevated over the valve floor (Text-fig. 2J), variable in details. The anterior half of the muscle field sometimes bisected by a septum, sometimes developed as a low rim, and sometimes as a narrow and relatively

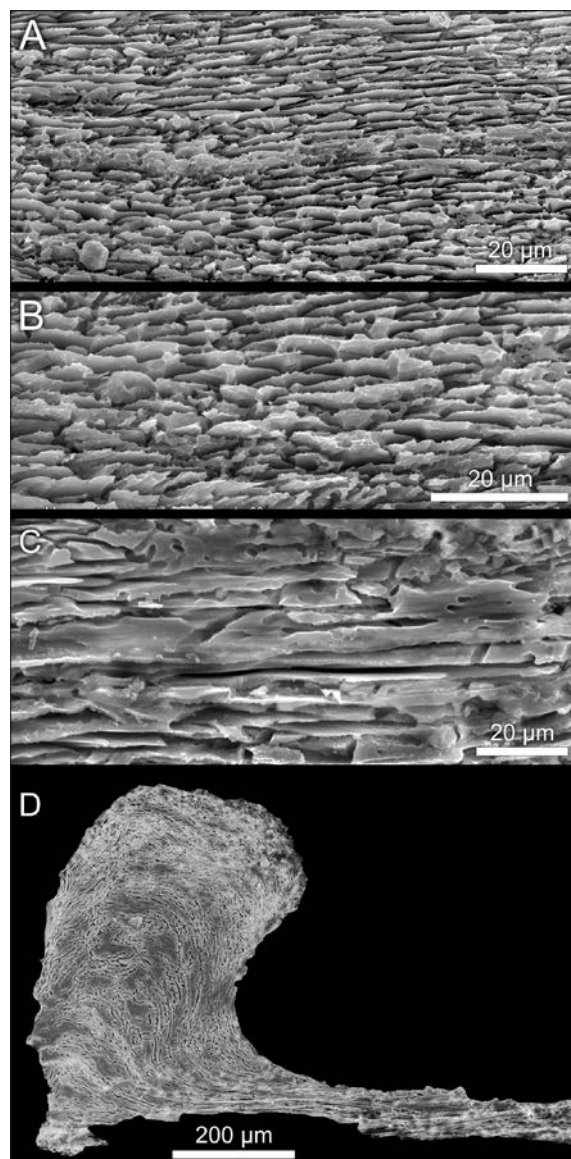
high blade-like structure. The septum is anteriorly coalescent with a strong transverse rim bordering the muscle field (arms of the septum *sensu* Rau 1905; Text-fig. 2N, P). In a single specimen there is an anteriorly open hollow at the anterior end of the septum.

Ventral interior: Valve surrounded by a marginal rim which is somewhat broader under the delthyrium, forming a kind of small platform. Teeth stark. Muscle field occupying from a little less than half the valve length (Text-fig. 2F) to about $\frac{2}{3}$ of the valve length (Text-fig. 2I); two large, elliptical muscle scars separated by a low and indistinct median elevation.

Microstructure: The single specimen examined shows fibrous fabric of the secondary layer (Text-fig. 3); primary layer not preserved. Secondary fibres display a typical parallel stacking and cross-sectional shape. They measure up to 13–25 μm in width and 1.2–2.2 μm in thickness. Important to note, no signs of shell punctation were found.

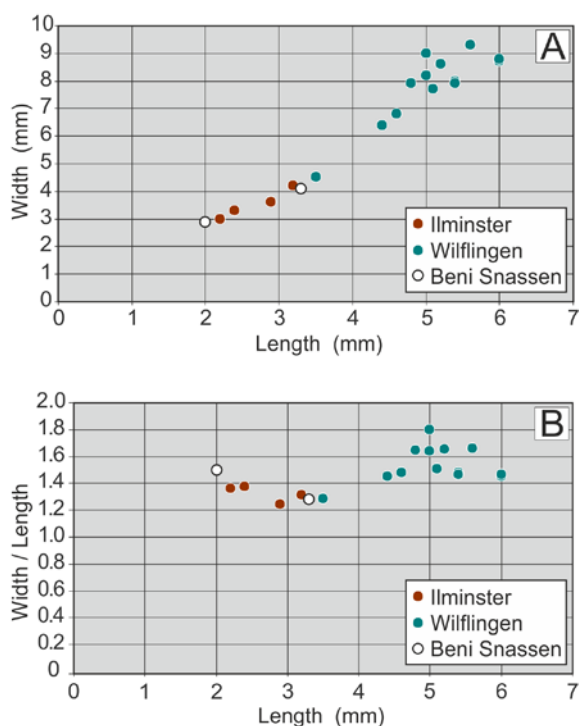
REMARKS: The question of specific distinction between *Cadomella* from Somerset and Normandy, on the one hand, and that from the Swabian Alb, on the other hand, was discussed several times with different conclusions. Quenstedt (1871) described the material from Hechingen (Württemberg) under *Leptaena moorei*. Conversely, Rau (1905, p. 9) described *Cadomella quenstedti* on the basis of the following differences with *C. moorei*: larger size, stronger mucrons, higher width-to-length ratio, more rounded outline, larger umbo, tuberculate shell margin less pronounced, shorter median septum. The two species were estimated to be distinct by Rollier (1916), at least in part on the basis of overestimated stratigraphic difference (*C. moorei* would be middle to upper Toarcian). The distinction at species level was upheld by Alm  ras *et al.* (2007) who listed the specimens from England studied by Rau (1905) in the synonymy of *C. moorei*, but excluded those identified as *C. quenstedti*. In turn, H  flinger (2020) considered that separation of *C. quenstedti* is based on characters of marginal significance and thus doubtful.

Indeed, the difference in size between *C. quenstedti* and *C. moorei* is striking, the maximum recorded width being 9.3 mm in the former (measured on a specimen from Rau's collection) and 4.2 mm in the latter (Davidson 1847, given as '2 lines', recalculated here taking one line to be equal to $\frac{1}{12}$ of an inch; additional three specimens measured on photographs in MacKinnon 2006). However, a biometric analysis shows that the size variability can be conveniently treated as continuous (Text-fig. 4A), whereas the differences in shape (greater width-to-length ratio in



Text-fig. 3. Microstructure of the shell of *Cadomella moorei* (dorsal valve GPIT-PV-93567 from the upper Pliensbachian of Wilflingen). A, B – Transverse section of the valve near the anterior margin showing the typical arrangement of fibres in the secondary layer; the valve exterior is to the bottom. C, D – Subradial section of the of the valve showing fibrous secondary layer (C) and arrangement of fibres in the thickened crural base (D); the valve exterior is to the bottom and posterior is to the left. All figures are SEM micrographs.

Swabian specimens) can be explained by allometric growth (Text-fig. 4B). In view of the above, the present authors consider that the specific distinction of the two species is unwarranted and *C. quenstedti* is herein proposed to be a synonym of *C. moorei*. This opinion is strengthened by the fact that the age dif-



Text-fig. 4. Biometric comparison of samples of *Cadomella moorei* from the upper Pliensbachian of Wilflingen (Baden-Württemberg, Germany; the so-called *C. quenstedti*) and the lower Toarcian of Ilminster (Somerset, England) and Beni Snassen (Northern Morocco): shell width to shell length (A) and shell width-to-length ratio to shell length (B). Data for Wilflingen new, for Ilminster after Davidson (1847) and MacKinnon (2006; see text), for Beni Snassen after Raouiat (1998).

ference between the two samples is relatively small (under 2.5 Ma, see below and Text-fig. 1E). A similar case of the same brachiopod species, the shells of which strongly differ in size between regions is that of *Kerpina vineta* Struve, 1961 (Atrypida, Devonian), found in Europe and Africa (Halamski and Baliński 2013, p. 277).

STRATIGRAPHIC AND PALAEOBIOGEOGRAPHIC DISTRIBUTION OF *CADOMELLA*

Cadomella has a relatively limited stratigraphic and palaeogeographic distribution. It is known from a few occurrences of assemblages of micromorphic brachiopods discovered first at the same time in England and southern France (Pic de St. Loup, southern Massif Central, Hérault department; see a letter from Thomas Davidson quoted by Wright 1863 in

1863–1880, p. 88) and since then called ‘*Leptaena* fauna’ (Deslongchamps 1853; Mouterde *et al.* 1979), ‘*Leptaena* bed’ (Deslongchamps and Deslongchamps 1858), ‘*Koninckella* bed’ (Riout 1980), or ‘*Koninckella* fauna’ (Almérás and Fauré 1990; Vörös 2002). Several comments are necessary. First, such assemblages are not rare in Western Europe, but in many (if not most) of them *Cadomella* is absent, like in eastern France (Delsate 1997), in Portugal both at Peniche (Comas-Rengifo *et al.* 2014) and at Zambujal (Mouterde *et al.* 1964; Comas-Rengifo *et al.* 2013), and, more generally, in several sections of the Iberian Peninsula (Gahr 2002). Secondly, *Cadomella* occurrences, when dated with satisfactory precision, albeit not synchronous, are confined to a short time interval – the Swabian ‘*Leptaenenbett*’ is late Pliensbachian (*costatum* Zone) in age, whereas the English and French ‘*Leptaena* bed’ is early Toarcian (Arkell 1933, p. 170; Ager 1967, p. 139; see also Vörös 2002, pp. 347–349); the difference in age is thus about one to two and a half million years (Hesselbo *et al.* 2020, p. 980). The Sinemurian record of *Cadomella moorei* (d’Orbigny 1849, p. 220) is an error which was corrected by Davidson (1851, p. 17). No brachiopod related to *Cadomella* is known from older strata, which is in stark contrast with the koninckinids, the eponymous representatives of the ‘*Koninckella* fauna’, reported from several Sinemurian and Carixian assemblages (Vörös 2002, p. 347).

Cadomella was first described from Ilminster in Somerset, England (Davidson and Morris 1847), where it is reported to be relatively frequent (Davidson 1851, p. 17) and where the specimens illustrated by MacKinnon (2006) also came from. Subsequently, it was found in Normandy, at Curcy near Caen by Deslongchamps and Deslongchamps (1858). The specimen sectioned by Brunton and MacKinnon (1972, pl. 76, figs 5–6) came also from Curcy [misspelt as Curey]. *Cadomella* was reported from the Swabian Alb first from Hechingen by Quenstedt (1871), then from Wilflingen, Hechingen, Erzingen, and Reutlingen by Rau (1905). *Cadomella* was also found at Geisingen (material in SMNS; see also Schmidt 1922). Four additional localities are listed by Höflinger (2020, p. 122): Dormettingen (origin of the specimen illustrated by Höflinger 2020, p. 122), Ziegelwasen b. Weilstetten, Sondelfingen, and Theta b. Bayreuth.

Several other occurrences of *Cadomella moorei* are listed by Almérás *et al.* (2007, p. 34), with reference to Riout (1980). However, this is likely to have resulted from a misunderstanding: the localities given by Riout (1980, p. 82) are those where the

‘*Koninckella* bed’ crops out, whereas, as observed earlier, *Cadomella* is not present in all the localities where the *Koninckella* fauna occurs, quite the contrary. For example, among the rich collection of micromorphic brachiopods from the ‘couche à *Leptaena*’ of May-sur-Orne (Calvados, France) kept at the University of Caen (Louis Boutillier’s collection; see Brignon 2020) there are several dozens of specimens belonging to at least eight species of thecideides (coll. examined, April 2026), but not a single *Cadomella*.

The issue of the presence of *Cadomella* in Africa requires a somewhat more extensive discussion. *Cadomella moorei* is reported from the Lalla Menanou locality (Beni Snassen, Rif Mountains, northern Morocco) in the unpublished Ph.D. memoir by Raouiati (1998). The illustrations leave no doubt that the identification is correct and measurements provided in this work have been used by the present authors in the biometric analysis (Text-fig. 4). However, brachiopods reported as *Cadomella moorei* from the same region of Beni Snassen by Alméras *et al.* (1988) are misidentified: the specimen (FLS 306568; material examined) is a biconvex, coarsely costate shell. Brachiopods reported as *Cadomella moorei* from the Monts des Traras (Trara Mts., Tell Atlas, NW Algeria) by Alméras *et al.* (2007) and then mentioned, this time as *Cadomella* cf. *moorei*, by Elmi *et al.* (2009) were never illustrated and, in the Alméras collection kept in Lyon, under the inventory number FSL 309044 cited in the published work (Alméras *et al.* 2007), there is another species and no *Cadomella* anywhere (E. Robert, written communications 4.02.2026 and 6.03.2026); so this information is considered as uncertain. To sum up, *Cadomella* is undoubtedly present in Beni Snassen, Morocco, despite unrelated brachiopods being also published from that region under that name, whereas the report from Trara Mts., Algeria is unconfirmed.

It may be noted that the distribution of *Cadomella* is thus limited to the western part of the Tethys that also hosted the last known occurrences of the athyrinids and the relict diversity of the spiriferinides (Baeza-Carratalá *et al.* 2015; Vörös *et al.* 2016, p. 240; García Joral *et al.* 2024, p. 134; spiriferinides post-dating the extinction of this order in Europe were reported from New Zealand, MacFarlan 2023).

CONCLUSIONS

Biometric analysis of *Cadomella quenstedti* Rau, 1905, described from the upper Pliensbachian (*spina-*

tum Zone) of the Swabian Alb, leads to the conclusion that it is best treated as a synonym of *Cadomella moorei* (Davidson in Davidson and Morris, 1847), described from the lower Toarcian of England.

The systematic position of *Cadomella* among the rhynchonellates (the class-level position is undoubted due to the fibrous microstructure of the shell) cannot be further elucidated at the present stage of research. There are several similarities with some thecideides (concavo-convex shell, features of the dorsal valve), but important differences (microstructure) exist too.

The authorship of the genus *Cadomella* should be attributed to Daniel Ehlert and Pauline Ehlert (credited on the title page of the original work under the abbreviation D.-P. Ehlert), the first to publish the name and diagnosis, even though the authors themselves attributed the name to Ernest Munier-Chalmas. This solution is forced by current rules of zoological nomenclature.

The confirmed localities for *Cadomella* are Ilminster (type locality in Somerset), Curcy (Normandy, France), Beni Snassen (Northern Morocco) and eight localities in the Swabian Alb (Germany). For all other localities mentioned in the literature primary data and/or specimens are lacking. The confirmed stratigraphic range of *Cadomella* is upper Pliensbachian (Germany) to lower Toarcian (elsewhere).

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