J. Paleont., 80(2), 2006, pp. 212–228

0022-3360/06/0080-212$03.00

A NEW EARLY JURASSIC RHYNCHONELLID BRACHIOPOD FROM THE WESTERN TETHYS AND IMPLICATIONS FOR SYSTEMATICS OF RHYNCHONELLIDS FROM THE TRIASSIC–JURASSIC BOUNDARY

ADAM TOMAŠOVÝCH
Institut für Paläontologie, Würzburg Universität, Pleicherwall 1, 97070 Würzburg, Germany, <adam.tomasovych@mail.uni-wuerzburg.de>;
current address: Geological Institute, Slovak Academy of Sciences, Dubravská cesta 9, 840 05 Bratislava, Slovakia

ABSTRACT—A new multicostate rhynchonellid brachiopod *Jakubirhynchia* occurs in the Hettangian (Early Jurassic) carbonate deposits of the West Carpathians. A comparison with externally similar multicostate rhynchonellids from the Hettangian–Sinemurian carbonate deposits of the Alps shows their congeneric and conspecific status, indicating relatively wide regional distribution in the Early Jurassic of the western Tethys.

Diagnostic characters include conjunct deltidial plates, divided, vertically inclined inner hinge plates forming sessile septalium, and subfalciform crura with relatively complex, serrate terminations and broad outline in lateral view. Although the shape of hinge plates and crura may vary according to shell convexity and shell orientation during serial sectioning, two-dimensional restorations of cardinalia and crura show their distinctive morphology. It is important to note that some of the cardinalia details and crural shape can be detected only with very short between-section distances. Based on external characters, *Jakubirhynchia* is a homeomorph to another multicostate rhynchonellid, *Calcirhynchia*, typical of the Hettangian and Early Sinemurian of the northwestern Europe province and reported also from the Tethyan province. This suggests that original distribution of *Calcirhynchia* might not be so wide and postextinction multicostate rhynchonellids were taxonomically more diverse as was previously supposed. *Jakubirhynchia* consistently occupies offshore, low-energy, micritic-rich habitats below storm wave base. It is the first reported Hettangian member of the family Basiliolidae and may bridge the gap between the Carnian *Veghirhynchia* and Early Jurassic basiliolids. Preextinction, Norian and Rhaetian brachiopods that are close morphologic relatives of *Jakubirhynchia* are known from outside the western Tethyan area only.

INTRODUCTION

TAXONOMY OF Early Jurassic rhynchonellids from the Tethyan area is poorly known. Although knowledge about some rhynchonellid taxa from the Alps and Transdanubian Central Range was substantially enhanced in the last decade (Dulai, 1993, 1998, 2003b; Siblík, 1993, 1998; Böhm et al., 1999), identifications of multicostate rhynchonellids are still obscure or left in open nomenclature. Long-standing problems of taxonomy of Mesozoic rhynchonellids and their likely oversplitting (Williams and Hurst, 1977) are mainly related to the restricted range of their morphologic characters and time-consuming methodology of serial sections (making it difficult to evaluate intraspecific variation of internal characters).

Analyses of rhynchonellid species diversity patterns after the end-Triassic mass extinction that are of more than just local significance are not possible due to this taxonomic confusion. It seems that in contrast to some brachiopod clades which were strongly affected by the end-Triassic mass extinction, rhynchonellids crossed the Triassic–Jurassic boundary comparatively unscathed and became relatively diverse in the Jurassic. However, basic taxonomic and morphologic study of Hettangian rhynchonellids is a prerequisite for the end-Triassic mass extinction database. In addition, rhynchonellids with their conservative design form one of the most successful brachiopod orders, ranging from the Early Ordovician until present, and can provide possible tests of mass extinction control and selectivity on brachiopod evolution and distribution (Sandy, 1995; Hallam, 2002; Dulai, 2003a).

Hettangian multicostate rhynchonellids were recently found for the first time in carbonate deposits of the West Carpathians (Tomašových and Michalík, 2000). The main goal of this paper is to describe internal and external morphologic characters of these rhynchonellids in detail and to compare them to other Tethyan rhynchonellids of similar age. The implications of this find for the poorly known systematics of the Upper Triassic and Early Jurassic brachiopods in the Tethyan area are assessed.

GEOGRAPHIC AND STRATIGRAPHIC SETTING

In the Early Jurassic, the West Carpathians, affected by extensive rifting (Plašienka, 2000), were situated on the northwestern margin of the Tethys Ocean in the subtropical climatic belt, in an adjacent position to the depositional setting of the eastern Alps (Dercourt et al., 2000).

The Jakub section (old quarry) is situated in the Veľká Fatra Mountains (central Slovakia, Fig. 1.1, 1.2) and structurally belongs to the Fatric Unit. The basal part of the Jakub quarry is formed by massive and thick-bedded, light grey, well-sorted peloidal grainstones and packstones of the Svätý Jakub Formation (probably of Rhaetian age). Up-section, these limestones pass into the Nový Svet Formation, which is characterized by alternation of well-bedded, dark grey, spiculitic biopel-wackestones, pelbio-packstones, and bio-floatstones with very thin (0.5–1 cm), brownish marly wackestone interbeds or bedding plane pavements, slightly enriched in siliciclastic silt admixture (Tomašových and Michalík, 2000). In the upper part of the Nový Svet Formation, benthic assemblages with relatively abundant brachiopods and bivalves of Middle Hettangian age occur (Fig. 1.3). Three benthic assemblages may be distinguished on the basis of taxonomic composition and relative abundances of taxa. The lowermost is represented by a paucispecific assemblage dominated by terebratuloids, and is replaced higher by alternation of an oyster-dominated benthic assemblage with zeillerioid-rhynchonellid assemblage. These deposits are indicative of offshore, low-energy habitats below storm wave base.

The comparative material is derived from the Hierlatz (Hierlatz Limestone, Austria) of the eastern Alps. Here, red or pink coquinal biomicrites with abundant brachiopods and ammonites occur as dyke-infillings in the Upper Triassic Dachstein Limestone (Vörös, 1991). This setting was similarly situated below storm wave base. The specimens sampled by Miloš Siblík were derived from the Sinemurian part of the Hierlatz Limestone. The Hierlatz Limestone ranges from the *Arnioceras semicostatum* Zone up to the *Echioceras raricostatum* Zone (Rakús, personal commun., 2004).

METHODS

Five multicostate rhynchonellids from the Jakub quarry were sectioned. These specimens were partially silicified (Fig. 2.1, 2.2).

Based on an external character comparison (see below), ''*Rhynchonella*'' *latifrons* Geyer, 1889 from the Hierlatz Limestone (eastern Alps) of Sinemurian age is a possible candidate for species-level determination of these rhynchonellid specimens. As there are no data about internal characters of ''*R.*'' *latifrons*, two specimens sampled by Miloš Siblík (Prague) at the type locality of the Hierlatz Limestone, externally comparable to ''*R.*'' *latifrons*, were sectioned and compared with the specimens from the Carpathians. The specimens were oriented with the posterior part of lateral commissure in perpendicular position to the sectioned plane. The between-section distance used in brachiopod studies is mostly 0.1 mm or more. As was shown by Baker (1989), a section interval of approximately 0.02 mm can be used for a detection of early ontogenetic structures in the posteriormost parts of adult brachiopod shells. Although specimens were not tilted in order to observe juvenile structures (cf. Baker, 1972, 1989), cardinalia characters and crural terminations can be very fine even in adult brachiopods (e.g., Dewing, 2001). This can be especially important for relatively small species (below 20 mm). Therefore, a section interval of 0.025 mm was used in this study. An acetate peel of each section was taken and archived. The sections were drawn using high (50×) magnification under a binocular microscope with camera lucida. This was important as at the boundary between internal structures and a micritic matrix, microsparitic rims often develop and can obscure the final shape of internal structures. The posterior parts of the dorsal valve were reconstructed in a two-dimensional ventral and lateral view. Terminology of cardinalia follows Brunton et al. (1996). The shape of cardinalia and crura in cross sections is substantially affected by shell convexity, and it depends on tilting of a specimen during sectioning. This was clearly shown by Burri (1954), Westbroek (1967), Laurin (1974), and Singeisen-Schneider (1976). Therefore, two-dimensional restorations in ventral and lateral views were produced in order to recognize these effects.

SYSTEMATIC PALEONTOLOGY

Order RHYNCHONELLIDA Kuhn, 1949
Superfamily PUGNACOIDEA Rzhonsnitskaia, 1956
Family BASILIOLIDAE Cooper, 1959
Subfamily PAMIRORHYNCHIINAE Ovcharenko, 1983
Genus JAKUBIRHYNCHIA new genus

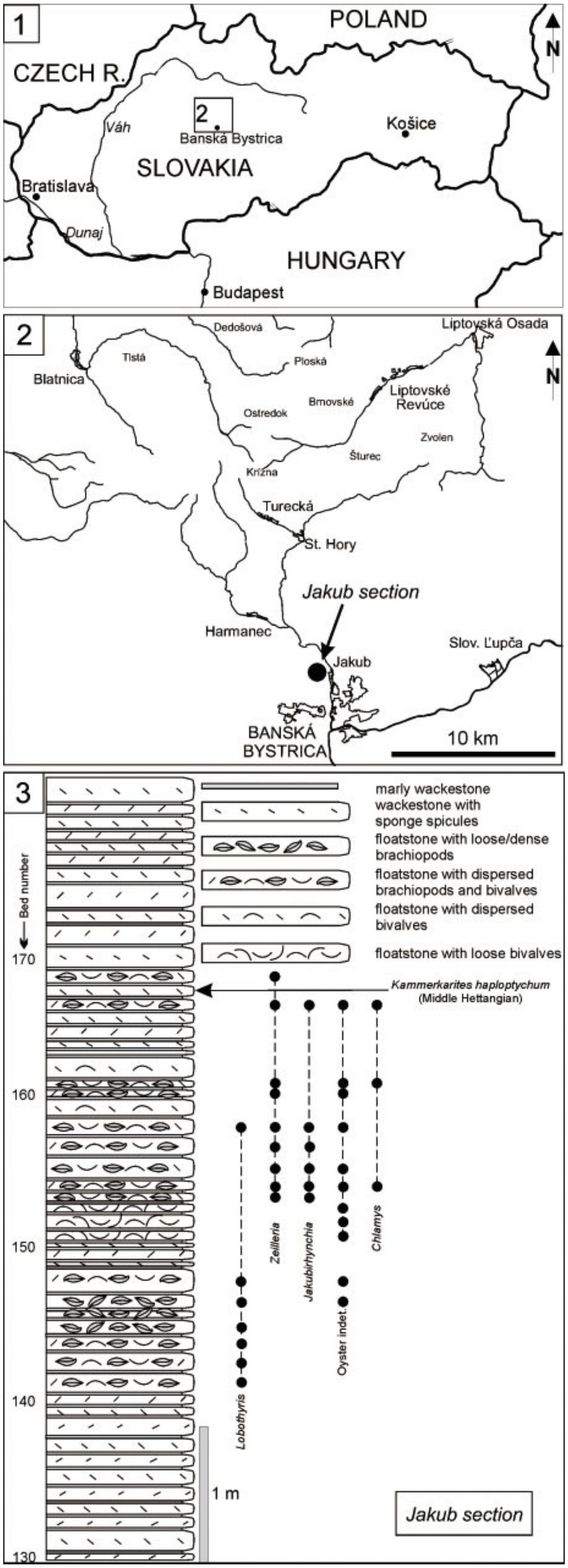
Type species.—*Jakubirhynchia latifrons* (Geyer, 1889).

Diagnosis.—Multicostate, moderately biconvex shells without planareas and anterior flattening, with bifurcating/intercalating costae. Conjunct and strengthened deltidial plates, submesothyrid foramen, and suberect beak. Short sessile septalium formed by steeply inclined inner hinge plates. Crura comparable to the subfalciform type, relatively broad in lateral outline, crescentic or flattened in cross section, substantially protruding into the dorsal valve, and possessing complex, serrate terminations at distal ends.

Etymology.—After the village of Jakub (central Slovakia), the locality of its most common occurrence.

Occurrence.—Middle Hettangian–Sinemurian, West Carpathians (Fatric Unit, Jakub), eastern Alps (Bajuvaric, Tirolic and Juvavic units, Fonsjoch, Adnet, Steinplatte, Hierlatz).

Discussion.—The typical characters of the superfamily Pugnacoidea Rzhonsnitskaia, 1956 include conjunct deltidial plates,



←

FIGURE *1*—Geographic position of the Jakub quarry near Banská Bystrica (Slovakia); *1*, overview map with the study area; *2*, geographic location of the Jakub section; *3*, simplified lithology with the distribution of brachiopods and bivalves in the Jakub section (Nový Svet Formation, West Carpathians).

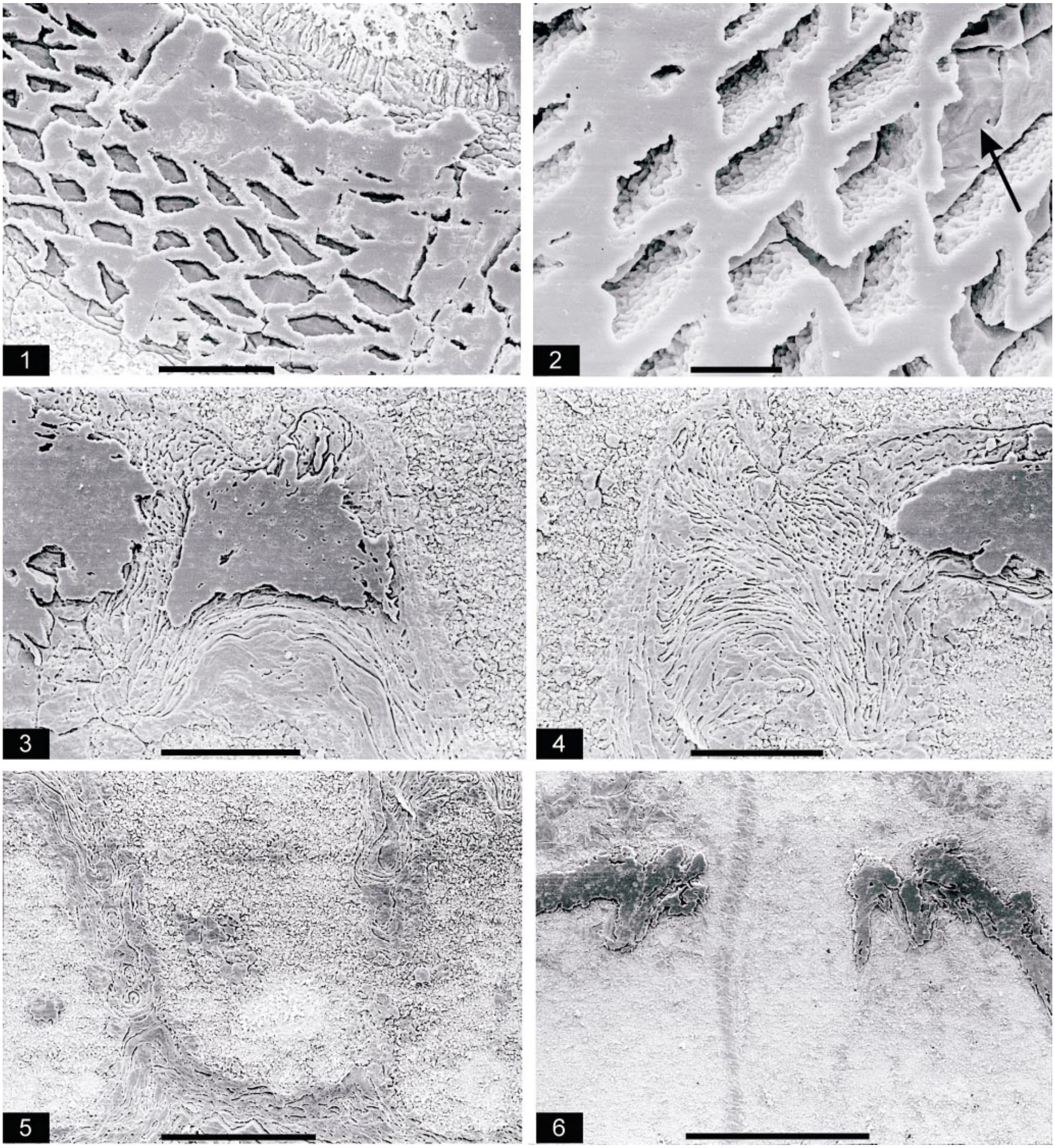


FIGURE *2*—Shell preservation and internal structures of *Jakubirhynchia latifrons* Geyer, 1889, Jakub quarry; *1*, incompletely silicified secondary shell layer with relicts of amalgamated/recrystallized calcite, the primary layer is not silicified, scale is 50 μm; *2*, detail of amalgamated calcitic relicts (arrow) surrounded by silica, scale is 20 μm; *3*, partially silicified crural base, gradually passing into the inner hinge plate, scale is 100 μm; *4*, well-preserved crural base, scale is 100 μm; *5*, contact of vertically inclined inner hinge plates with the valve floor (i.e., sessile septalium), scale is 200 μm; *6*, partially silicified crural bases, scale is 500 μm.

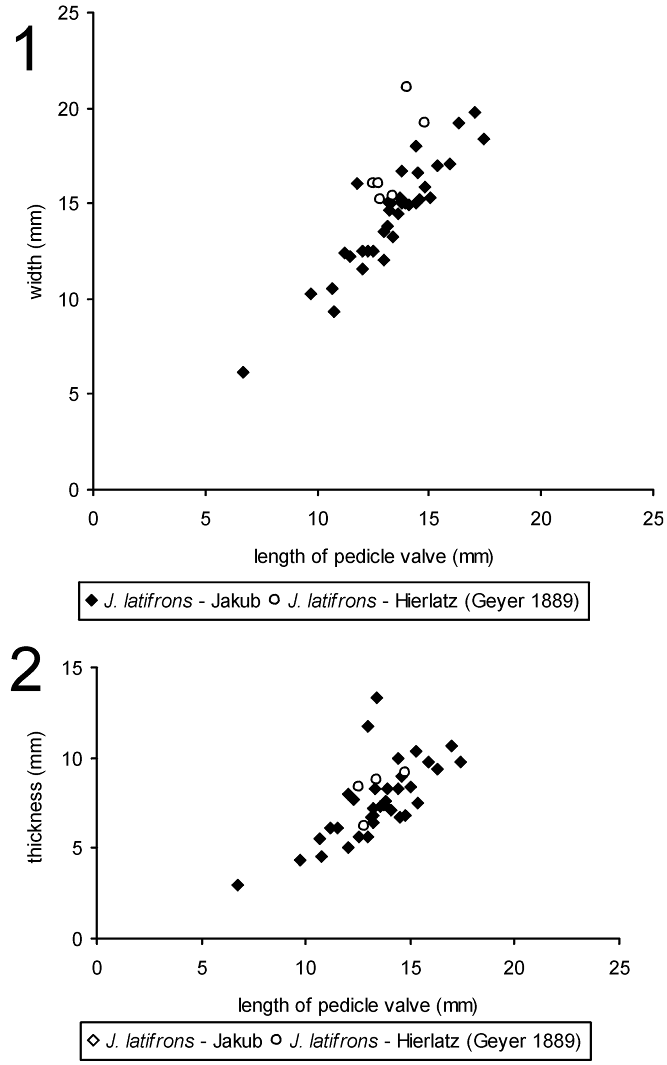


FIGURE *3*—Graph of *Jakubirhynchia latifrons* pedicle valve length versus width (*1*) and thickness (*2*); open circles represent the specimens figured by Geyer (1889).

divided, dorsally inclined hinge plates extending to the valve floor (i.e., sessile septalium), and septifal crural group (Manceñido and Owen, 2001; Savage et al., 2002). In addition, bifurcating and/or intercalating radial costae are typical of Basiliolidae Ovcharenko, 1983. The Devonian to Permian pugnacids are characterized by conjunct deltidial plates and dorsal inclination of inner hinge plates, sometimes connected to the floor of the dorsal valve (Savage, 1996).

Hamiform crural type (the subtype of the septifal group) is typical of superfamily Wellerelloidea Licharew, 1956 and their subfamily Cirpinae Ager, 1965 (Ager et al., 1972; Shi and Grant, 1993; Manceñido and Owen, 2001). However, the subfalciform crura of *Jakubirhynchia* represent a strong deviation from simple rodlike hamiform crura (which do not project so strongly in the dorsal valve). The presence of doubled/strengthened deltidial plates is supposed to be typical of Cirpinae. This character also occurs in *Pseudogibbirhynchia* Ager, 1962 (Basiliolidae) and is probably not unique to Cirpinae (Manceñido, personal commun., 2002). Cirpinae are characterized by well-developed planareas, a character missing in *Jakubirhynchia*. The family Allorhynchidae Cooper and Grant, 1976 (Wellerelloidea) is characterized by divided hinge plates, but the sessile septalium was not documented here. In summary, the conjunct deltidial plates, absence of planareas, and differences in the cardinalia morphology and crural type indicate higher affinity of *Jakubirhynchia* to the superfamily Pugnacoidea, family Basiliolidae, and subfamily Pamirorhynchiinae.

Most of the normally ribbed multicostate Hettangian rhynchonellids, without planareas or anterior flattening, are customarily assigned to the genus *Calcirhynchia* Buckman, 1918 (Gaetani, 1970; Dulai, 2003b). In contrast to *Jakubirhynchia*, *Calcirhynchia* possesses hamiform crura (Ager, 1962). The only known member of basiliolids from the Triassic is represented by the Carnian *Veghirhynchia* Dagys, 1974, which seems to be very similar to *Jakubirhynchia*. It possesses conjunct deltidial plates, inclined inner hinge plates connected with the valve floor (sessile septalium), and subfalciform crura. Dagys (1974) mentioned a smooth posterior part of shells, the main difference in comparison to *Jakubirhynchia*. Hettangian and Sinemurian multicostate rhynchonellids with subfalciform crura thus need to be assigned to *Jakubirhynchia*. In contrast to *Calcirhynchia*, this new genus belongs to a quite different lineage (Basiliolidae). There are some external differences between *Jakubirhynchia* and the type species of *Calcirhynchia*, including disjunct deltidial plates and an incurved beak in the latter genus. However, intrageneric variation and consistency of these external characters need to be further investigated and independently supported by the inspection of internal characters.

The first Jurassic representative of basiliolids is another multicostate genus *Pseudogibbirhynchia*, known since the Sinemurian (Manceñido, 2000). However, in contrast to *Jakubirhynchia*, the crural type is hamiform and a sessile septalium was not documented in this genus (Ager, 1962; Siblík, 1967; Alméras, 1996).

In addition, the genus *Hagabirhynchia* Hudson and Jefferies, 1961 from the Upper Triassic deposits of Oman shows some affinities to *Jakubirhynchia* (Hudson and Jefferies, 1961; Sandy and Aly, 2000). Shared external characters include multicostate shells without planareas and anterior flattening, ribs reaching from the umbo and dividing anteriorly, and a suberect beak with conjunct deltidial plates. In the figured interior (Hudson and Jefferies, 1961, text-fig. 1, sections 1.1–1.2 mm), there are relatively well-developed and vertically inclined inner hinge plates almost reaching to the valve floor. Crura were determined as radulifer (redescribed as hamiform in Savage et al., 2002), but due to long between-section intervals (in relation to the small specimen size), it is impossible to assess if the sections did record the whole crural morphology and their terminations. *Hagabirhynchia* was placed in the family Allorhynchidae by Savage et al. (2002). If sessile septalium and subfalciform crura would be supported by future research/revision, this genus should be shifted to basiliolids and would be morphologically very close to *Jakubirhynchia*.

JAKUBIRHYNCHIA LATIFRONS (Geyer, 1889) new combination

Rhynchonella latifrons GEYER, 1889, p. 54, pl. 6, figs. 25–31; PETERHANS, 1926, p. 362.
Calcirhynchia (?) *plicatissima* (QUENSTEDT, 1852); SIBLÍK, 1999, p. 966, pl. 1, fig. 4, text-fig. 2; BÖHM, EBLI, KRYSTYN, LOBITZER, RAKÚS, AND SIBLÍK, 1999, p. 194, pl. 29, fig. 4.
Calcirhynchia (?) cf. *plicatissima* (QUENSTEDT, 1852); SIBLÍK, 1999, p. 421, pl. 2, fig. 8, text-fig. 2.
Cirpa (?) *latifrons* (GEYER, 1889); BÖHM, EBLI, KRYSTYN, LOBITZER, RAKÚS, AND SIBLÍK, 1999, p. 194, pl. 29, fig. 5.
?*Rhynchonella plicatissima* QUENSTEDT; PETERHANS, 1926, p. 361, pl. 2, figs. 5–8.
?*Rhynchonella plicatissima salisburgiensis* NEUMAYR, 1879; PETERHANS, 1926, p. 361, pl. 2, figs. 9–12.
?*Cirpa* ? *latifrons* (STUR *IN* GEYER, 1889); DULAI, 1992, p. 43, pl. 1, fig.

FIGURE 4—*Jakubirhynchia latifrons*, Jakub quarry; *1–4*, Z24127, dorsal, ventral, anterior, and lateral views; *5–8*, Z24129, dorsal, ventral, anterior, and lateral views; *9–12*, Z24131, dorsal, ventral, anterior, and lateral views; *13–16*, Z24133, dorsal, ventral, anterior, and lateral views; *17–20*, Z24128, dorsal, ventral, anterior, and lateral views; *21–24*, Z24130; *25–27*, Z24136, ventral, anterior, and lateral views; *28–31*, Z24132, dorsal, ventral, anterior, and lateral views; *32*, Z24150 (sectioned specimen), dorsal view; *33–36*, Z24126, dorsal, ventral, anterior, and lateral views; *37–39*, Z24135, ventral, anterior, and lateral views; scale is 10 mm.

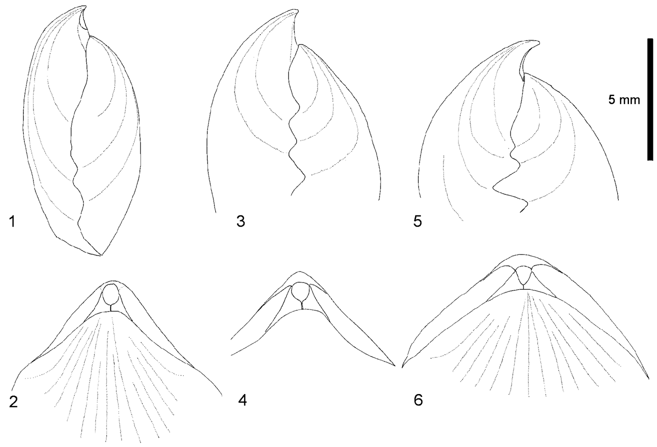


FIGURE 5—Lateral and dorsal views on the suberect beak, conjunct deltidial plates and submesothyrid pedicle foramen of *J. latifrons*; *1, 2,* specimen Z24147; *3, 4,* specimen Z24131; *5,* specimen Z24129; *6,* specimen Z24127.

2, text-fig. 3; VÖRÖS, SZABÓ, DULAI, SZENTE, EBLI, AND LOBITZER, 2003, p.70, pl. 6, figs. 16–18.

?''*Rhynchonella*'' sp.; SIBLÍK, 1999, p. 970, pl. 1, fig. 6.

nomen nudum *Rhynchonella salisburgiensis* NEUMAYR, 1879, p. 8, pl. 1, fig. 1.

non *Calcirhynchia plicatissima* (QUENSTEDT, 1852), DULAI, 1992, p. 44, pl. 1, fig. 3, text-figs. 4, 5; DULAI, 1993, p. 29, pl. 1, fig. 1, text-fig. 2.

Diagnosis.—As for genus.

Description.—In the following, the material from the Carpathians and Alps is separately described.

Jakub quarry (West Carpathians): Small to middle-sized biconvex shells, usually ranging up to 16 mm in length, 18 mm in width, and 10 mm in thickness (Fig. 3, Table 1). Subpentagonal to subtrigonal in outline, slightly wider than long, ovoid in lateral view and elliptic or subrectangular in anterior view (Fig. 4). The maximum width lying between the half and anterior third of the length. The apical angle ranging from 90° to 100°. Slightly concave posterolateral sides in dorsal view. Rounded or almost straight anterior margin, only with slightly extending median part. In smaller specimens, the anterior margin is relatively sharp in lateral view, with slightly protruding linguiform extension. In larger, 15 mm long specimens, it is more rounded. Well-developed and trapezoidal uniplication with a straight dorsal edge. Low fold (four to seven costae), only slightly raised and developed in the anterior third of the dorsal valve.

Slightly inclined or suberect, relatively long and wide beak, projecting markedly over the dorsal valve, with visible cardinal area. Subtriangular deltidial plates, conjunct near dorsal valve. Moderately large pedicle opening, submesothyrid in position (Fig. 5). Short and arcuate beak ridges; absent planareas.

No exposed smooth area. Between 13 and 18 moderately sharp costae. The costae arise by bifurcation in the umbonal area and locally also by intercalation in the anterior part.

Absent pedicle collar. Almost parallel or dorsally convergent dental plates. Slightly laterally expanded and dorsolaterally inserted teeth with lateral denticula. Relatively strengthened deltidial plates, in larger specimens completely coalesced near the dorsal valve. The pattern of fiber orientation is relatively complex, forming the structure usually termed as the doubling of deltidial plates (Fig. 6). In the anterior part, secondary fibers of deltidial plates are folded into short and sharp projections, bounding shallow hole or cavity which appears in cross section on internal (medioventral) side of deltidial plates.

The dorsal umbo is more deeply inserted into the ventral valve only in larger specimens with higher convexity. The notothyrial cavity has a mushroomlike outline in cross section, delimited by inner hinge plates and the posteriormost parts of inner socket ridges. In cross section, the inner hinge plates are straight and steeply dorsally convergent, attached either to very low median elevation (Figs. 6, 7) or directly to the valve floor (Fig. 8). Ventrally they are connected to the crural bases (Fig. 2.3, 2.4). This structure can be termed as a sessile septalium (Fig. 2.5). Its length reaches one-third or one-half of the length of cardinalia measured up to the distal end of the hinge plates. Here, inner hinge plates are detached from the valve floor and persist as narrow bands up to the beginning of crural processes (Fig. 2.6), medially to the crural bases, and bordered from the outer hinge plates by a relatively deep longitudinal furrow.

Relatively wide and subhorizontal outer hinge plates. Slightly ventrolaterally inclined, not very massive inner socket ridges. Massive and dorsally directed crural bases. In ventral view, crura are widely divergent in an anterior direction (Fig. 12.1, 12.3). In lateral view, they are very broad and in the anterior part serrated and expanded into keel (Figs. 6, 8, 12). The shape of crural terminations in cross sections in specimen Z24150 (Fig. 9) is enigmatic. From anteroventral part of each crus, short and slender projection extends in the posterior direction. From anterodorsal part, another broad projection is directed towards the dorsal valve in lateral view (Fig. 12.2). In cross section, crura have a sickle-shaped outline. According to relatively long and dorsally directed crural bases, their substantial protrusion into the dorsal valve and broad outline in lateral view (Fig. 12.2, 12.4, 12.6), crura are attributed to the subfalciform type.

Hierlatz (eastern Alps): Multicostate, moderately biconvex shells, subpentagonal in outline, without planareas and anterior flattening. High, suberect beak, exposed and conjunct deltidial plates. Relatively sharp costae, bifurcating near umbo, with some intercalations in the anterior part. Trapezoidal uniplication (five to eight costae) with straight dorsal margin.

Absent pedicle collar. In the smaller specimen, deltidial plates are thickened and doubled (Fig. 10). The cavities of elongate cross section are opened in the anterior direction. In the anteriormost part, each deltidial plate is divided into two, more or less parallel, plates which are not in contact in the anteromedian position.

A shape of notothyrial cavity in cross section depends on the valve convexity and specimen tilting. In ventral view, relatively short and slightly convergent/parallel inner hinge plates, forming the sessile septalium, are present in the posteriormost part of cardinalia of both specimens (Figs. 10, 11). Their length in ventral view attains approximately one-third of the length of the cardinalia. Due to the high convexity of dorsal valve and deep insertion of dorsal umbo, inner hinge plates are hidden in the smaller specimen (Fig. 10). Laterally to the inner hinge plates, relatively pronounced, dorsally directed crural bases are present. The outer hinge plates are horizontal in cross section, continuous with minute inner socket ridges. In lateral view, crura are very broad, protruding into both valves (Fig. 12.5, 12.8). On the one hand there is a slight but distinct rodlike prolongation in the dorsal direction in the anterior part of each crus (Fig. 12.5). On the other, there is a short, narrow prolongation in the ventral direction, approximately in the middle part of each crus in lateral view (Fig. 12.5). In cross section, secondary fibers of crura are zigzaglike or serrately arranged under high (50×) magnification (Figs. 10, 11).

Material examined.—Thirty-seven specimens (Z24126–24162) from Jakub quarry (beds 154–158, 167), two specimens from Hierlatz (Z24163–24164) and one specimen from Steinplatte. All

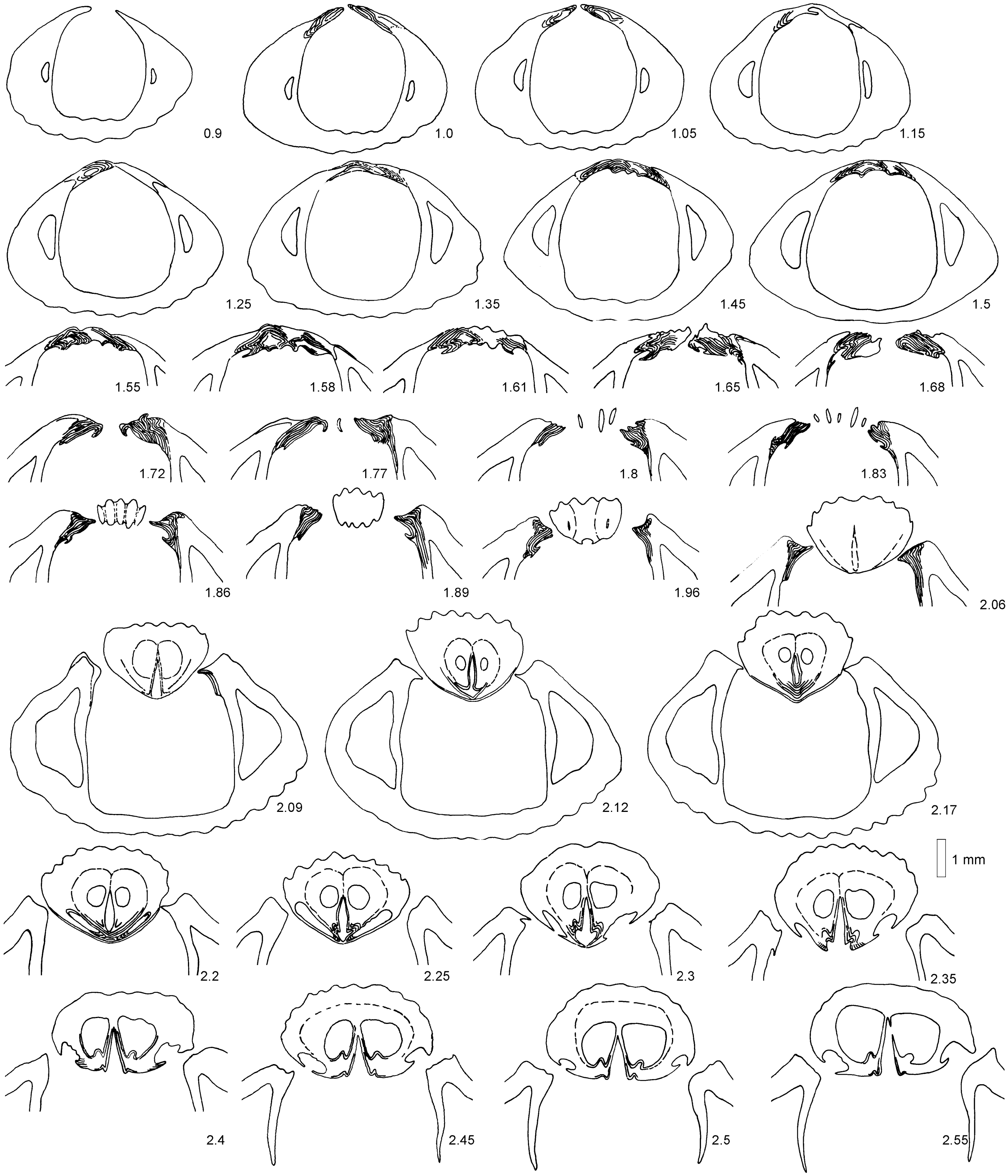


FIGURE 6—Transverse serial sections through beak and cardinalia of a specimen of *J. latifrons*, Jakub quarry, specimen Z24149. Length of dorsal valve is 15 mm.

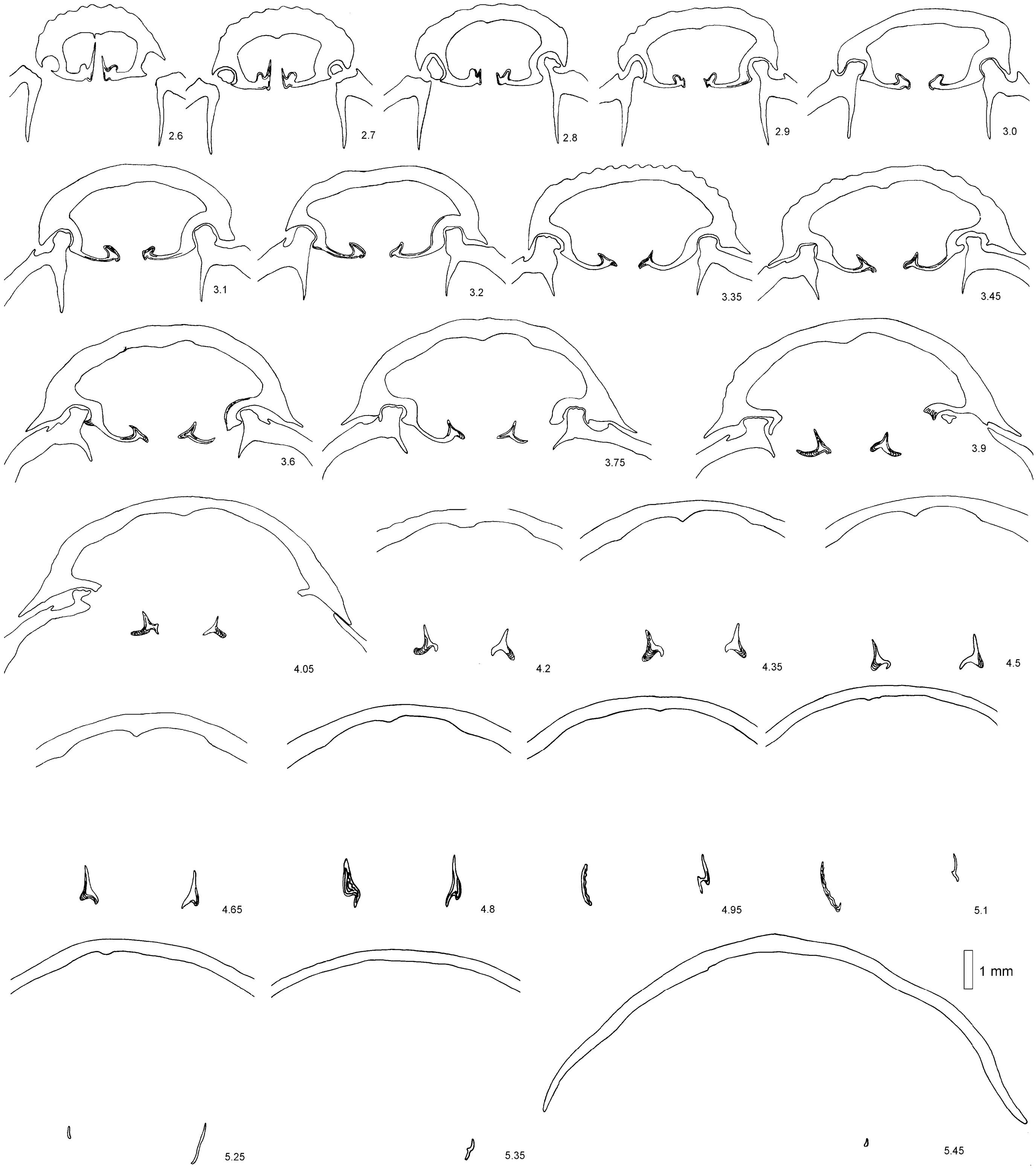


FIGURE 7—Transverse serial sections through an anterior part of hinge plates and crura of a specimen of *J. latifrons*, Jakub quarry, specimen Z24149. Length of dorsal valve is 15 mm.

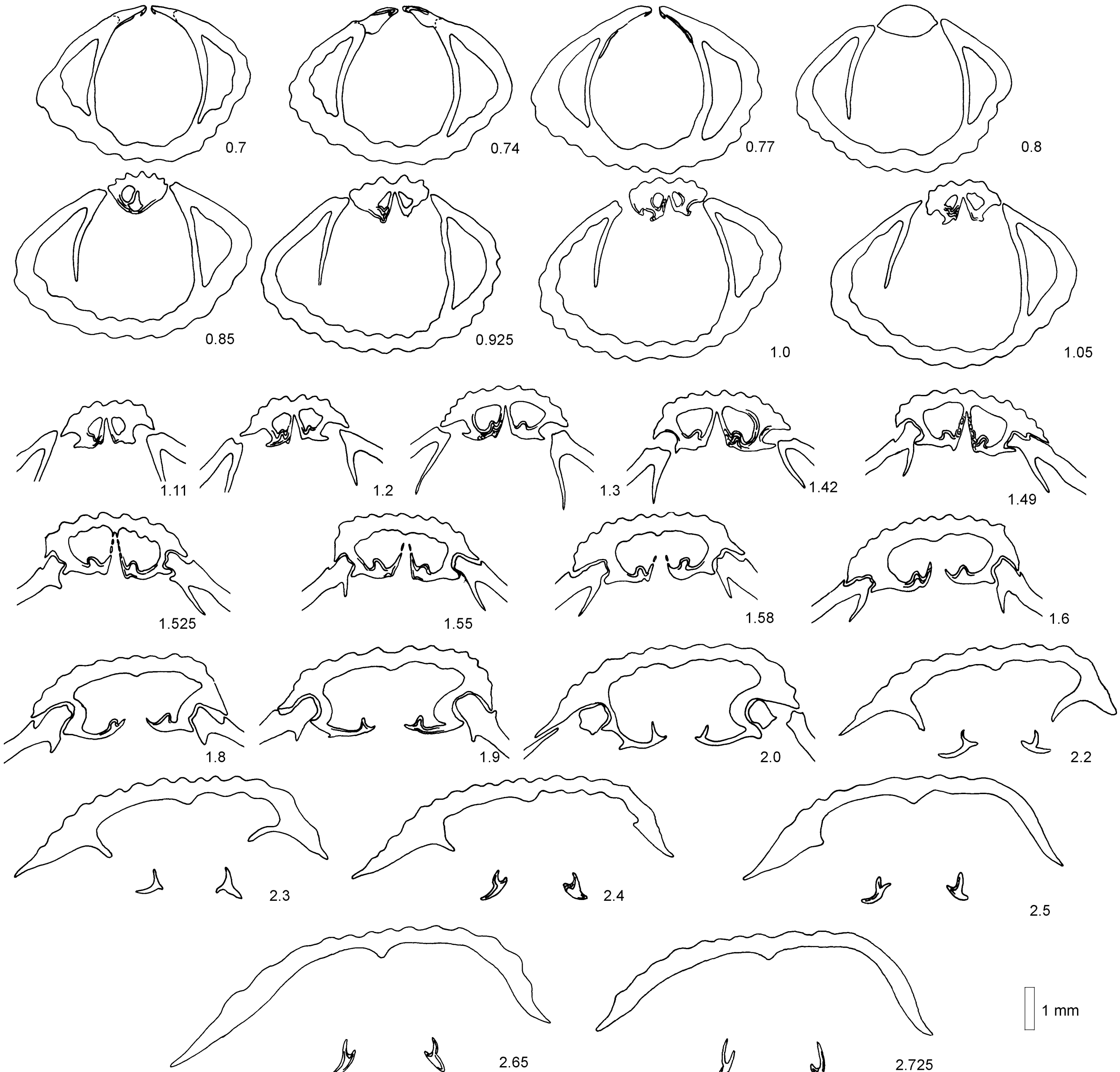


FIGURE 8—Transverse serial sections through beak, cardinalia, and posterior part of crura of a specimen of *J. latifrons*, Jacob quarry, Hierlatz, specimen Z24150. Length of dorsal valve is 12.1 mm.

specimens are deposited in the Slovak National Museum (Bratislava).

Occurrence.—Eastern Alps (Austria): Fonsjoch (Middle Hettangian, Siblík, 1999), Steinplatte (Enzesfeld Limestone, Upper Hettangian, Siblík, 1993), Adnet (Schnöll Formation, Middle Hettangian, Böhm et al., 1999), Hierlatz (Hierlatz Limestone, Sinemurian, Geyer, 1889; this paper), West Carpathians (Slovakia): Jakub (Nový Svet Formation, Middle Hettangian, this paper).

Discussion.—The comparison of internal and external features of the described rhynchonellids from the West Carpathians and the eastern Alps indicates their high similarity, suggesting that they are conspecific. The high variation in the shape of internal structures is intriguing (Fig. 12), but there are many examples of modern rhynchonellid and terebratulid species characterized by high internal morphologic variation (Foster, 1974; Boullier et al., 1986; Lee et al., 2001; Tort and Laurin, 2001; Tort, 2003). The shape of hinge plates in cross sections can be explained by variations in dorsal valve convexity (Fig. 10), which may be influenced by ontogenetic or adult intraspecific variation. In the shells with higher convexity, the shape of inner hinge plates and septalium is difficult to detect because these structures are not inclined in a perpendicular position to the section plane anymore (Fig. 12.7, 12.8). In the case when higher convexity is associated with preferential shell thickening in the posterior part, inner hinge plates can be buried under ontogenetically older shell material.

Based on the description of external characters by Geyer

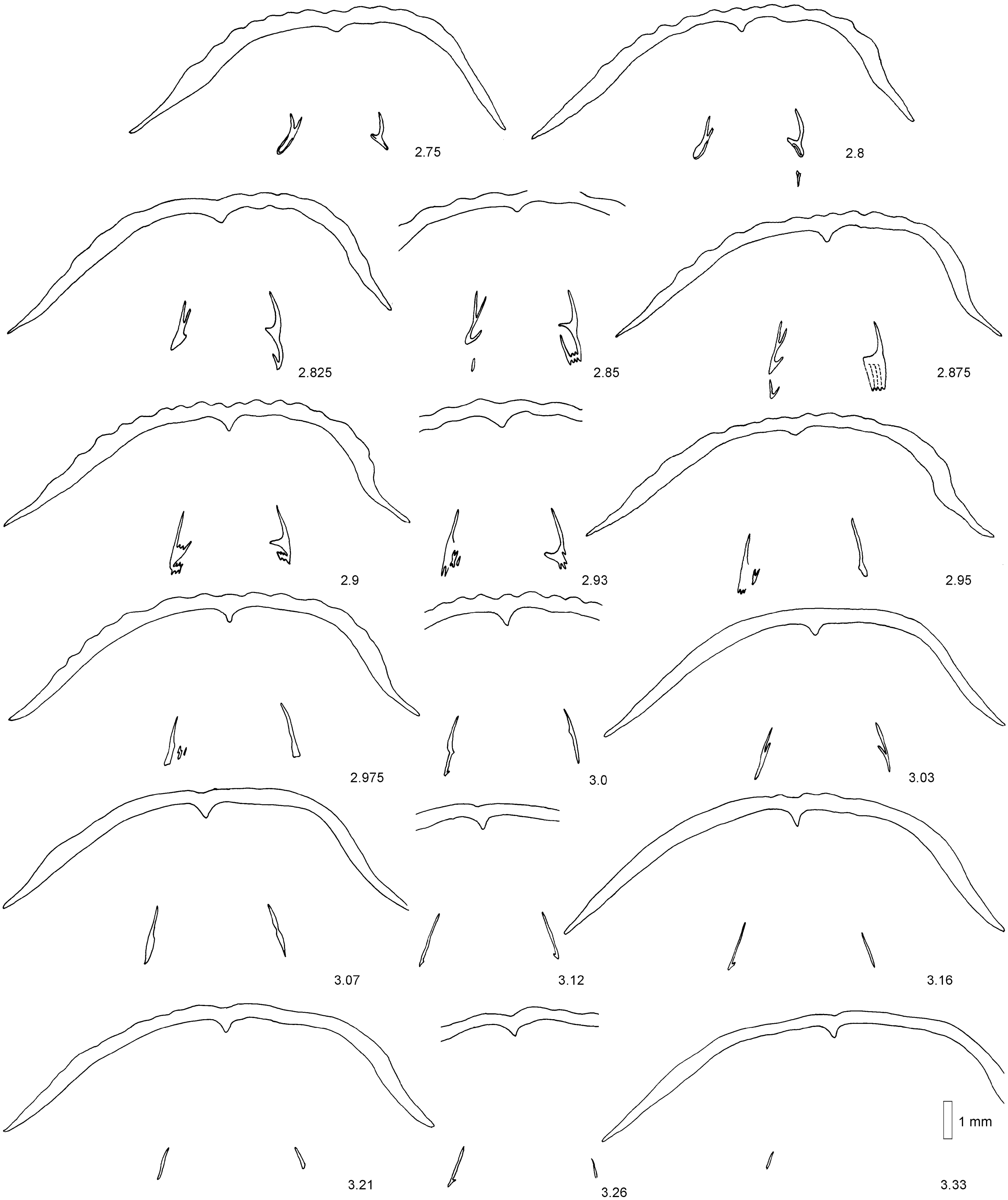


FIGURE 9—Transverse serial sections through an anterior part of crura of a specimen of *J. latifrons*, Jakub quarry, specimen Z24150. Length of dorsal valve is 12.1 mm.

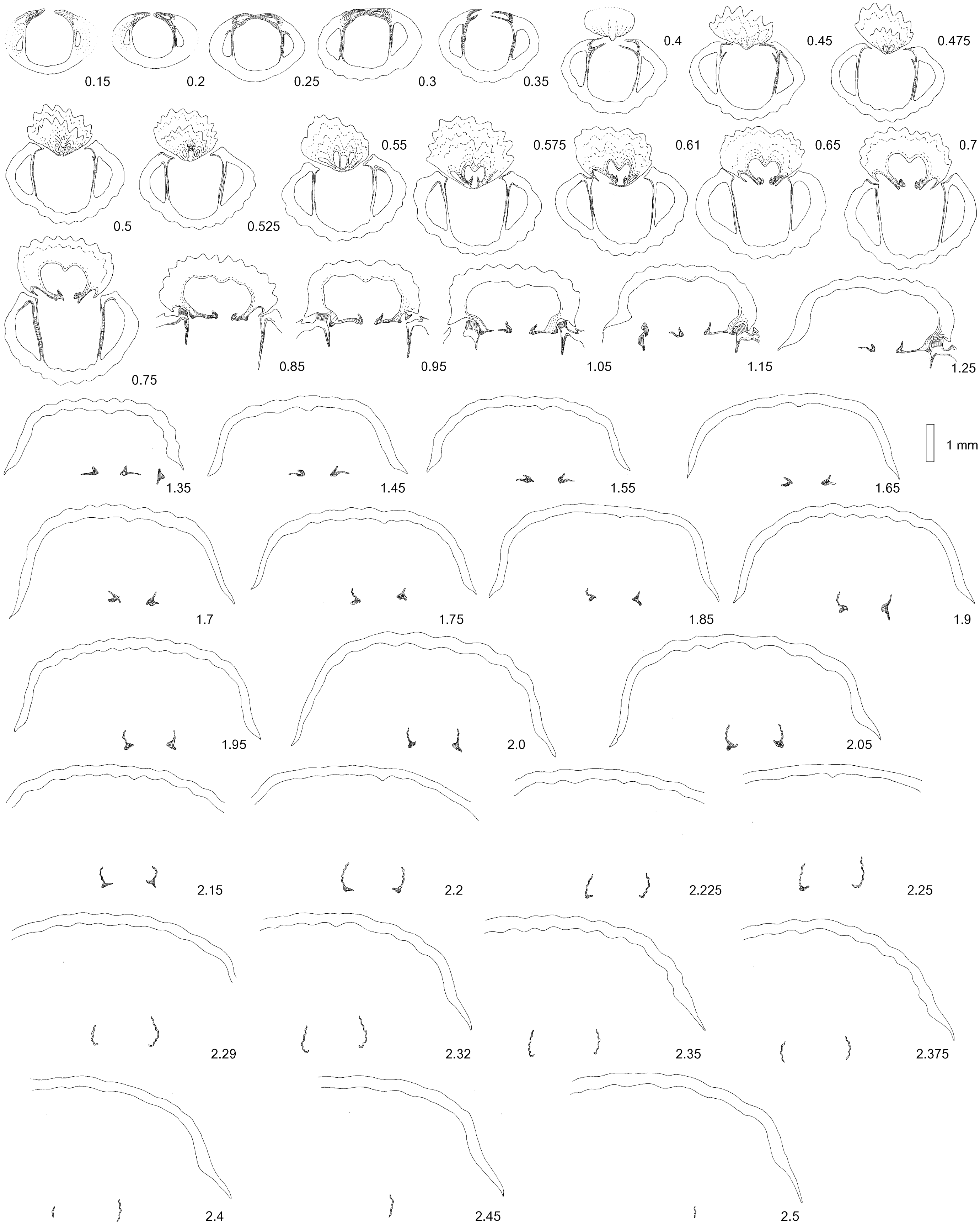


FIGURE *10*—Transverse serial sections through a specimen of *J. latifrons*, Hierlatz, specimen Z24164. Length of dorsal valve is 11.45 mm.

(1889), ''*R.*'' *latifrons* is characterized by a transversely oval outline with the width exceeding the length, conjunct deltidial plates delimiting submesothyrid foramen and suberect or slightly inclined ventral beak, and posterolateral margins of the dorsal valve forming a blunt apical angle. Shell ornamentation consists of relatively sharp, anteriorly bifurcating ribs. All these characters fully coincide with the external features of the described specimens and point to their conspecificity with ''*R.*'' *latifrons*. Based on the internal characters, they are thus assigned to the new genus *Jakubirhynchia*. Sacchi Vialli and Cantalupi (1967) assigned ''*R.*'' *latifrons* to *Prionorhynchia* Buckman, 1918, and Dulai (1992) and Siblík (*in* Böhm et al., 1999) to *Cirpa* de Gregorio, 1930. However, these genera are characterized by the presence of strong costae, planareas, and the latter genus also by anterior flattening, in contrast to''*R.*'' *latifrons*. Pearson (1977) gave ''*R.*'' *latifrons* as a possible candidate for assignment into his new genus *Fissirhynchia* with calcarifer crura, but this is not the case.

''*Rhynchonella*''*salisburgiensis* Neumayr, 1879 was described from the Kendlbach Formation of the eastern Alps (locality Breitenberg, Lower Hettangian, *Psiloceras psilonotum* Zone, equivalent to the *Psiloceras planorbis* Zone of the northwestern Europe). The diagnosis, based on two specimens only, included dorsobiconvex subtrigonal shells, wider than long, about 20 relatively sharp ribs reaching to apex, anteriorly bifurcating, shallow and wide sulcus on the ventral valve, rounded or slightly flattened anterior margin, and a small pointed and suberect beak. Although some external characters point to some distinctiveness (i.e., the high rib number and tendency to anterior rounding), they were also seen in some very large specimens of *Jakubirhynchia*. A potential relationship between ''*R.*'' *salisburgiensis* and *Jakubirhynchia* is also noticeable from the adjacent paleogeographic position of their original habitats (eastern Alps and West Carpathians). Peterhans (1926) revised several brachiopod species from the Sinemurian of the Prealps (southwestern Switzerland) which had been described by Haas (1887). He attributed some multicostate rhynchonellids to ''*R.*'' *salisburgiensis* on the subspecific level. However, due to the insufficient original description of the type material, ''*R.*'' *salisburgiensis* is here regarded as nomen nudum.

Siblík (1999) described *Calcirhynchia* (?) cf. *plicatissima* from the Middle Hettangian of the eastern Alps (locality Fonsjoch), finding that it was characterized by multicostate subpentagonal shells with normal rib bifurcations, a shallow sulcus, and trapezoidal uniplication. Internal sections revealed the presence of sessile septalium and very broad, most probably subfalciform crura, which agree with internal characters of *Jakubirhynchia latifrons*. In addition, Hettangian brachiopods from the Steinplatte and Adnet sections (eastern Alps) described by Siblík (1993) and Siblík (*in* Böhm et al., 1999) as *Calcirhynchia* (?) *plicatissima* Quenstedt, 1852, ''*Rhynchonella*'' sp., and *Cirpa* (?) *latifrons* are also assigned to *Jakubirhynchia latifrons*. One specimen from the Steinplatte section identified by M. Siblík as *Calcirhynchia* (?) *plicatissima* was sectioned in the posterior shell part and also showed the sessile septalium (not shown). However, this is tentative because another sectioned specimen from Steinplatte figured by Siblík (1993, text-fig. 2) does not show this internal character. The specimens from Steinplatte and Adnet are externally indistinguishable from *J. latifrons* from Jakub and Fonsjoch and occur in similar stratigraphic levels (i.e., Middle and Upper Hettangian).

Siblík (*in* Böhm et al., 1999) illustrated sections of *Cirpa* aff. *latifrons* (Geyer, 1889) from the Schnöll Formation of the Hettangian age of the eastern Alps, but the described specimens were externally different from the type material of Geyer (1889). Other published occurrences of ''*R.*'' *latifrons* (see synonymy in Dulai, 2003b) are difficult to evaluate at this stage without further knowledge about internal and external morphologic variation.

In contrast to *J. latifrons*, Hettangian and Lower Sinemurian specimens from the Transdanubian Central Range described as *Calcirhynchia* ? *plicatissima* show a small beak, uniplication of variable, commonly arched curvature, and the absence of linguiform extension on the anterior margin (Dulai, 1992, 1993). This, together with the presence of an elevated pedicle collar, indicates that they probably do not belong to *Jakubirhynchia*. ''*R.*'' *plicatissima* Quenstedt, 1852 was originally described from the Sinemurian deposits of the Swabian Alb (Germany). Several authors identified this species from the Tethyan area (Geyer, 1889; Dulai, 1992, 1993; Vörös et al., 2003), but internal and external characters of the northwestern European material figured by Quenstedt (1852, 1858, 1871) are different from the Tethyan specimens. Gaetani (1970) described the internal structure of ''*R.*'' *plicatissima*, showing that the high dorsal median septum supporting the posterior part of cardinalia forms a short shallow septalium. Manceñido (1993) supposed that Gaetani's specimen belonged in fact to *Rudirhynchia calcicosta* Quenstedt, 1852. However, that specimen was obtained from Kuhwasen near Ofterdingen (Swabian Alb, Sinemurian, *Asteroceras obtusum* Zone), which is the type locality of ''*R.*'' *plicatissima*. *Rudirhynchia calcicosta* is rarely known from the Upper Sinemurian *Echioceras raricostatum* Zone, typically starts at the Sinemurian/Pliensbachian boundary, and occurs in stratigraphically younger deposits (Quenstedt, 1871; Rau, 1905). In addition, there is an important external difference, because ''*Rhynchonella*'' *plicatissima* specimens, figured by Quenstedt (1871) and deposited in Tübingen, do have marked planareas (personal obs.). Unfortunately, Quenstedt (1852, 1858, 1871) did not figure any lateral view of ''*R.*'' *plicatissima*, thus making it impossible to assess the presence of this character solely from his monograph. The presence of planareas is visible also in Gaetani's sectioned specimen. ''*R.*'' *plicatissima* with planareas, sharp costae, a high median septum, and shallow septalium thus most probably belongs to *Prionorhynchia*.

MULTICOSTATE HETTANGIAN RHYNCHONELLIDS

One of the most common Hettangian rhynchonellid in Europe is the multicostate genus *Calcirhynchia*. Its type species, *C. calcaria* Buckman, 1918, typically occurs in the Upper Hettangian and Lower Sinemurian deposits, but its first appearance is reported from the Lower Hettangian *Psiloceras planorbis* Zone. In the northwestern European province, it is present in offshore micrites in the St. Marys Well Bay Formation (Blue Lias) of South Glamorgan (Warrington and Ivimey-Cook, 1995). In the northern Tethyan province, it occurs in low-energy bioclastic facies associated with coral patch reefs in the lower part of the ''Calcaires nodules cendrés'' of the southeastern France (Alméras and Elmi, 1987). Since the Late Hettangian, *C. calcaria* is known from the northwestern European province only. It occurs in the offshore Blue Lias Formation and the Calcaires à Gryphеés of the Anglo-Paris Basin (Lang, 1924; Hallam, 1960; Wobber, 1968; Almerás and Hanzo, 1991; Hanzo et al., 2000). Rhynchonellids described as ''*Terebratula*'' *ammonitica* by Quenstedt (1871), most probably conspecific with *C. calcaria*, occur in low-energy deposits of the Lias alpha 2 in the Swabian Alb, Germany (e.g., Vaihinger Nest, Engel, 1908; Schloz, 1972; Bloos, 1976; Grüner, 1997). Interestingly, some members of this genus probably occupied the Tethyan habitats during the Rhaetian. Based on short septalium and crura, Pearson (1967) identified ''*Rhynchonella*'' *subrimosa* Schafhäutl, 1851 as a member of *Calcirhynchia*.

In the Tethyan area, Hettangian and Early Sinemurian multicostate rhynchonellids show a higher taxonomic diversity (Dulai, 2001, 2003a) and higher morphologic disparity (Siblík, 1999).

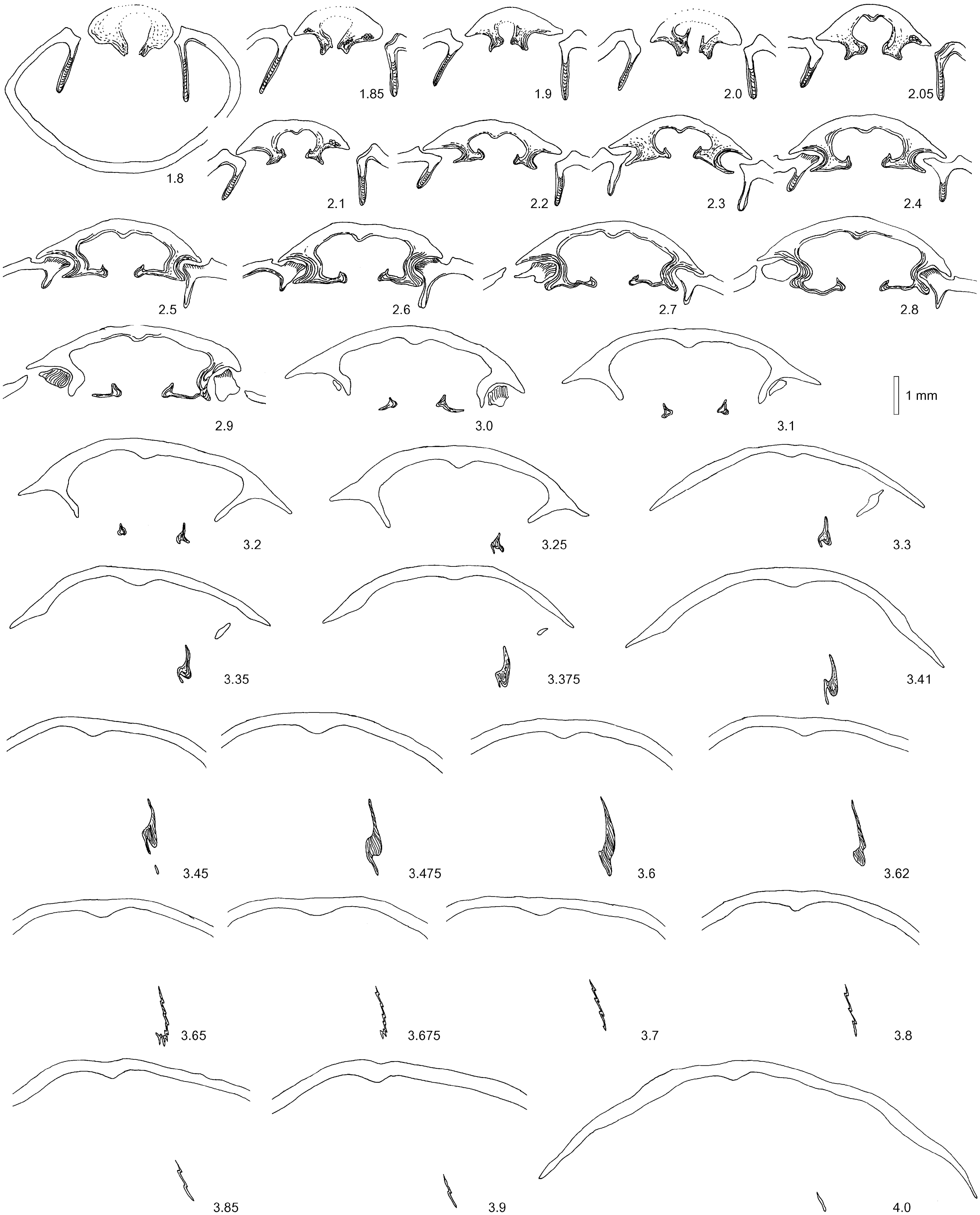


FIGURE *11*—Transverse serial sections through a specimen of *J. latifrons*, Hierlatz, specimen Z24163. Length of dorsal valve is 11.95 mm.

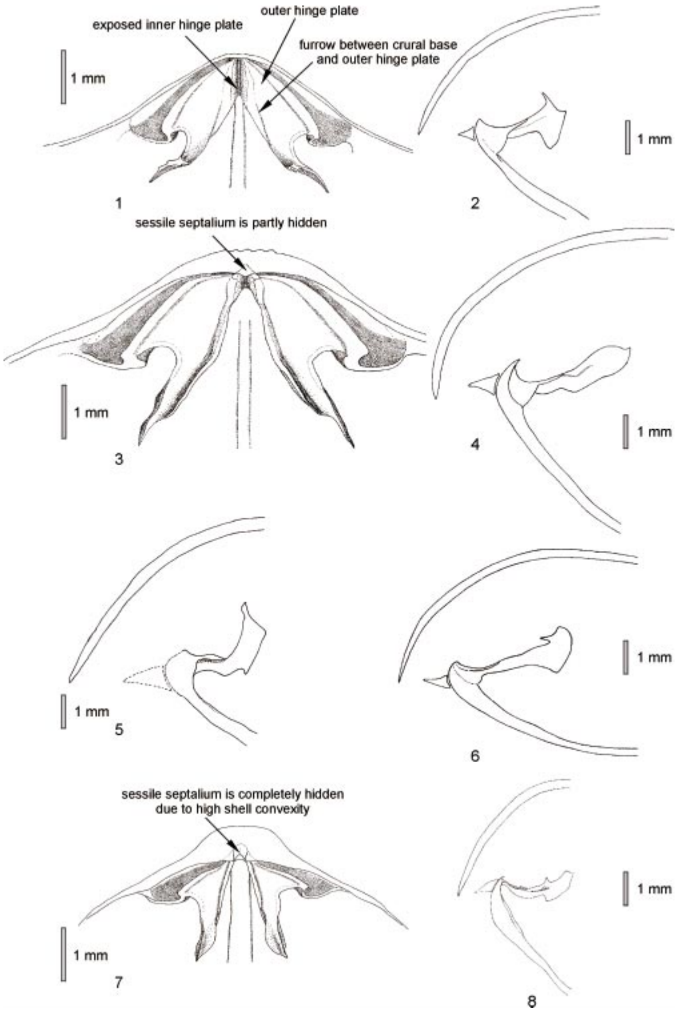


FIGURE *12*—Ventral and lateral views of cardinalia and crura of *J. latifrons*; *1, 2,* specimen Z24150 (see Figs. 8, 9, Jakub); *3, 4,* specimen Z24149 (see Figs. 6, 7, Jakub); *5,* specimen Z24163 (see Fig. 11, Hierlatz); *6,* specimen Z24137 (Jakub); *7, 8,* specimen Z24164 (see Fig. 10, Hierlatz).

The typical characters include strongly developed/concave planareas in *Prionorhynchia* [e.g., *P. fraasi* (Oppel, 1861), *P. greppini* (Oppel, 1861), *P. polyptycha* (Oppel, 1861); see Dulai, 1992, 2003b; Siblík *in* Böhm et al., 1999], and *Salgirella* Moiseev, 1936 (Dulai, 1993). The planareas coassociated with anterior flattening are typical of *Cirpa* (e.g., Siblík, 1993; Siblík *in* Böhm et al., 1999). Strongly dorsobiconvex shells with high uniplication and small planareas, associated with a specific crural type, are typical of *Grestenella* Siblík, 1999. The multicostate rhynchonellids, with the absence of these distinctive characters, were mostly identified as *Calcirhynchia* (e.g., *C. rectemarginata* Gaetani, 1970). MacFarlan (1992) described two new Early Jurassic species of *Vincentirhynchia* MacFarlan, 1992, which are multicostate rhynchonellids. However, Savage et al. (2002) suggested that these two species may belong rather to *Prionorhynchia* or *Cirpa*. The type species of *Vincentirhynchia* has a smooth area in the posterior shell part.

Jakubirhynchia n. gen. thus represents a new Early Jurassic multicostate genus. Although there are some external differences, the inspection of internal characters is needed for the distinction of *Jakubirhynchia* from *Calcirhynchia*. Importantly, it remains to be verified whether *Calcirhynchia* co-occurs together with *Jakubirhynchia* in the western Tethyan area, or if there are other, not yet described genera of multicostate rhynchonellids. This paper shows that the Hettangian multicostate rhynchonellids without planareas and anterior flattening from the eastern Alps and West Carpathians in fact belong invariably to *Jakubirhynchia*. Sandy (1995) supposed that *Calcirhynchia* consists of opportunistic species which are typical of low-diversity, postextinction fauna. In the light of the finding that there are other, unrelated Hettangian multicostate rhynchonellids like *Jakubirhynchia*, the distribution of *Calcirhynchia* is probably not as wide as was originally supposed. In addition, *Calcirhynchia calcaria* does not occur across different facies and is typical of offshore, low-energy marlstones/limestones (i.e., it is restricted to some facies types only). Most of the occurrences of *Jakubirhynchia* similarly indicate rather low-energy conditions below a storm wave base, but the deposits are uniformly pure carbonates. In the eastern Alps, in addition to the Hierlatz Limestone, specimens from Adnet and Steinplatte tentatively identified as *Jakubirhynchia* occur similarly in carbonate-rich, crinoidal wackestones and floatstones of the Schnöll Formation. Dulai (2003a) showed that Hettangian multicostate rhynchonellids preferentially occur in the deeper, micritic-rich settings. This indicates that the generalistic character of postextinction Hettangian rhynchonellid fauna can be more apparent than real. The occupation of the shallow, high-energy habitats is more typical of the Sinemurian and Pliensbachian multicostate rhynchonellids (Tchoumatchenco, 1972, 1993; Dulai, 2003a).

None of the known Rhaetian rhynchonellids described from the western Tethyan area demonstrates any relationship to *Jakubirhynchia*. Typical Rhaetian multicostate rhynchonellids of the western Tethyan area, represented by *Fissirhynchia fissicostata* (Suess, 1854) and *Osmarella starhembergica* (Zugmayer, 1880), belong, according to the cardinalia and crural morphology (Pearson, 1977; Siblík, 1998), to different rhynchonellid clades. Although their lineages continue into the Jurassic, at the specific level they do not occur in post-Triassic deposits. The data about the occurrence of *F. fissicostata* in the Early Jurassic (e.g., cited in Pearson, 1977; Manceñido, 1980; Siblík, 1988) were not supported by later investigations. *Jakubirhynchia latifrons* probably represents the lineage which immigrated into the western Tethyan area after the end-Triassic mass extinction. *Veghirhynchia*, known also from the Alps, occurs in the Carnian deposits and thus there is a substantial gap until the end of Triassic. If *Hagabirhynchia* from the Norian is the close relative of *Jakubirhynchia*, this may point to the migration from the southern Tethys. No representatives of Basiliolidae are known from the Hettangian, and *Jakubirhynchia* may thus bridge the gap between the Carnian *Veghirhynchia* and Early Jurassic members of Basiliolidae.

CONCLUSIONS

1. Important details about cardinalia and crural morphology are recognizable only using a very small between-section interval (below 0.1 mm). Although serial sectioning is a time-consuming technique, it is suggested that in small species, at least the posteriormost parts of the cardinalia and anterior crural terminations should be investigated in small-scale between-section intervals. In addition, due to diagenetic overprint (microsparitic crusts at the boundary between shell and matrix), crural terminations are clearly recognizable only under relatively high (50×) magnification.

2. Hettangian and Sinemurian multicostate rhynchonellids from the West Carpathians and eastern Alps, characterized by subfalciform crura, are assigned to the new genus *Jakubirhynchia*. *Jakubirhynchia* belongs to the lineage of the superfamily Pugnacoidea and is the first reported Hettangian member of the family Basiliolidae. In addition to the crural type, the diagnostic characters are the presence of well-developed and dorsally inclined

TABLE *1*—Data set with measurements of 37 specimens of *J. latifrons* from the Jakub section. Shortcut: r—rectimarginate commissure.

Specimen number	Bed number	Length of pedicle valve (mm)	Length of brachial valve (mm)	Width (mm)	Thickness (mm)	Width of anterior margin (mm)	Width of fold (mm)	Width of sulcus (mm)	Height of sulcus (mm)	Number of costae in fold	Total number of ribs
Z24126	155	14.6	12.5	15.2	9.0	6.7	6.3	7.0	4.1	6	18
Z24127	141	12.3	10.2	12.5	7.7	—	5.7	6.8	3.9	5	14
Z24128	167	15.9	13.5	17.1	9.8	8.4	8.0	9.8	5.3	6	16
Z24129	debris	13.3	11.0	15.0	8.3	6.9	5.2	7.7	5.2	4	13
Z24130	167	13.2	10.4	15.0	6.4	7.3	7.2	8.2	2.5	7	19
Z24131	167	13.7	11.4	15.3	7.4	7.4	5.9	7.7	2.9	6	18
Z24132	167	17.4	14.4	18.4	9.8	9.2	11.4	13.3	5.6	7	17
Z24133	167	13.2	11.2	14.6	6.8	6.2	6.1	7.4	3.1	5	17
Z24134	debris	13.1	11.2	13.8	6.7	6.5	5.8	7.3	1.7	5	15
Z24135	155	14.4	12.6	18.0	10.0	8.2	8.5	10.0	6.5	6	19
Z24136	155	13.8	11.3	15.1	7.6	5.3	5.8	8.0	4.5	5	17
Z24137	167	13.0	10.5	12.0	11.7	6.4	6.4	7.7	2.5	6	18
Z24138	155	15.4	12.8	17.0	7.5	7.6	5.2	9.5	5.6	6	16
Z24139	155	14.1	12.1	14.9	7.1	6.3	7.0	9.0	2.9	6	18
Z24140	156	13.4	11.0	13.2	13.3	7.8	7.1	8.1	3.5	6	20
Z24141	167	13.9	10.9	15.0	8.3	6.4	7.3	9.8	5.1	7	17
Z24142	167	13.8	—	15.0	—	6.2	—	9.0	4.7	6	—
Z24143	167	13.0	11.3	13.5	5.6	—	—	—	3.0	6	20
Z24144	155	16.3	14.5	19.2	9.4	8.6	8.6	10.3	4.6	7	21
Z24145	155	12.0	10.0	11.6	8.0	6.2	4.6	7.0	5.8	4	10
Z24146	155	10.7	9.0	10.5	5.5	—	—	—	—	—	—
Z24147	155	12.0	10.5	12.5	5.0	—	—	—	1.5	5	17
Z24148	158	13.6	10.8	14.5	7.3	6.4	5.4	7.9	3.0	5	13
Z24149	155	17.0	15.0	19.8	10.7	10.3	11.6	11.3	7.4	7	17
Z24150	167	13.2	12.1	15.1	7.2	8.3	6.4	8.8	3.5	6	18
Z24151	167	—	13.0	17.3	9.3	9.2	6.1	7.5	5.1	6	18
Z24152	155	15.3	13.5	—	10.4	—	—	—	—	—	—
Z24153	167	9.7	8.2	10.3	4.3	4.6	4.7	5.2	1.5	6	18
Z24154	167	—	13.3	16.0	9.2	6.8	7.3	8.4	4.8	7	19
Z24155	155	14.8	13.4	15.9	6.8	6.8	7.9	9.5	4.2	5	15
Z24156	167	11.2	9.8	12.5	6.1	6.3	4.9	5.8	3.4	5	15
Z24157	157	15.1	13.3	15.3	8.4	8.1	5.8	9.6	6.5	5	16
Z24158	167	10.8	9.4	9.3	4.5	—	—	—	—	—	—
Z24159	155	6.7	6.1	6.2	3.0	3.5	r	r	r	5	13
Z24160	155	—	10.6	11.3	6.9	5.5	5.1	7.8	4.8	5	13
Z24161	158	—	11.1	14.8	6.5	8.2	6.5	8.3	4.2	6	16
Z24162	155	14.5	13.0	16.6	6.7	—	—	—	—	7	19

inner hinge plates forming the sessile septalium, and conjunct deltidial plates.

3. Based on external characters, *Jakubirhynchia* is the homeomorph to *Calcirhynchia*, another multicostate rhynchonellid genus known from the Hettangian and Sinemurian. *Calcirhynchia* is widely distributed in the northwestern European province, although several occurrences were reported from the Tethyan province. *Jakubirhynchia*, known from the western Tethyan area, is typical of offshore, low-energy, micritic-rich carbonates deposited below a storm wave base.

ACKNOWLEDGMENTS

Thanks to A. Dulai and S. Carlson for reviews and L. Vermaas and K. Dewing for editorial comments. Also thanks to M. Siblík for the discussions on the systematics of Early Jurassic rhynchonellids and loaning of the specimens from Hierlatz, J. Michalík and M. Schlirf for introduction into the serial sectioning technique, and M. Manceñido for several suggestions about rhynchonellid phylogeny and systematics. A. Liebau, F. Stojaspal, and M. Aberhan provided the access to the type material of F. A. Quenstedt (University of Tübingen), G. Geyer (Geologische Bundesanstalt, Vienna), and A. Oppel (Museum für Naturkunde, Berlin). I am indebted to J. Schlögl for help with photographs. This paper was supported by the Systematic Association and German Science Foundation (Fu-131/26–1) and is a contribution to the IGCP project 458: Triassic–Jurassic boundary events.

REFERENCES

AGER, D. V. 1962. A monograph of the British Liassic Rhynchonellidae, Pt. III. Palaeontographical Society of London Monograph, 116:85–136.

AGER, D. V. 1965. Mesozoic and Cenozoic Rhynchonellacea, p. H597–H625. *In* R. C. Moore (ed.), Treatise on Invertebrate Paleontology. Pt. H. Brachiopoda. The Geological Society of America and the University of Kansas Press, Lawrence.

AGER, D. V., A. CHILDS, AND D. A. PEARSON. 1972. The evolution of the Mesozoic Rhynchonellida. Geobios, 5:157–235.

ALMÉRAS, Y. 1996. Les Brachiopodes Toarciens et Aaléniens inférieurs du bassin du Rhône. Documents des Laboratoires de Géologie Lyon, 138:1–123.

ALMÉRAS, Y., AND S. ELMI. 1987. Evolution des peuplements de brachiopodes en fonction de lenvironment dans le Lias Ardechois. Les Cahiers de l'Université Catholique de Lyon, 3:21–56.

ALMÉRAS, Y., AND M. HANZO. 1991. Les Rhynchonellidés du Calcaire à grypheés dHettange (Sinémurien-NE France): Étude des peuplements et enregistrement des variations du paléoenvironment. Palaeogeography, Palaeoclimatology, Palaeoecology, 86:313–329.

BAKER, P. G. 1972. The development of the loop in the Jurassic brachiopod *Zeilleria leckenbyi*. Palaeontology, 15:82–85.

BAKER, P. G. 1989. Location and interpretation of ontogenetic relics in the shell of adult brachiopods. Lethaia, 22:241–245.

BLOOS, G. 1976. Untersuchungen über Bau und Entstehung der Feinkörnigen Sandsteine des Schwarzen Jura alpha–Hettangium und tiefstes Sinemurium im schwäbischen Sedimentationsbereich. Arbeiten aus dem Institut für Geologie und Paläontologie an der Universität Stuttgart, 71:1–269.

BÖHM, F., O. EBLI, L. KRYSTYN, H. LOBITZER, M. RAKÚS, AND M. SIBLÍK. 1999. Fauna, stratigraphy and depositional environment of the Hettangian–Sinemurian (Early Jurassic) of Adnet (Salzburg, Österreich). Abhandlungen der geologischen Bundesanstalt, 56:143–271.

BOULLIER, A., J.-H. DELANCE, C. C. EMIG, L.-L. D'HONDT, D. GASPARD, AND B. LAURIN. 1986. Les population actuelles de *Gryphus vitreus* (Brachiopoda) en Corse. Implications paléontologiques, p. 179–196. *In*

P. R. Racheboeuf and C. C. Emig (eds.), Les Brachiopodes fossiles et actuels. Biostratigraphie du Paléozoique, 4.

BRUNTON, C. H. C., F. ALVAREZ, AND D. I. MACKINNON. 1996. Morphological terms used to describe the cardinalia of articulate brachiopods: Homologies and recommendations. Historical Biology, 11:9–41.

BUCKMAN, S. S. 1918. The Brachiopoda of the Namyau Beds, Northern Shan States, Burma. Memoirs of the Geological Survey of India, Palaeontologia Indica (n.s.), 3, 299 p.

BURRI, F. 1954. Die Morphogenese von Sulcirhynchia valangiensis (Brachiopoda). Eclogae Geologicae Helvetiae, 47:419–425.

COOPER, G. A. 1959. Genera of Tertiary and recent rhynchonelloid brachiopods. Smithsonian Miscellaneous Collections, 139:1–90.

COOPER, G. A., AND R. E. GRANT. 1976. Permian brachiopods of West Texas, IV. Smithsonian Contributions to Paleobiology, 21:1293–2607.

DAGYS, A. 1974. Triassic brachiopods (morphology, classification, phylogeny, stratigraphical significance and biogeography). Sibirskoe Otdelenie Izdatelstvo Nauka, Novosibirsk, 214, 387 p. (In Russian)

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

DERCOURT, J., M. GAETANI, B. VRIELYNCK, E. BARRIER, B. BIJU-DUVAL, M. F. BRUNET, J. P. CADET, S. CRASQUIN, AND M. SANDULESCU. 2000. Atlas Peri–Tethys. Palaeogeographical maps. Commission for the Geologic Map of the World, Paris.

DEWING, K. 2001. Hinge modifications and musculature of strophomenoid brachiopods: Examples across the Ordovician–Silurian boundary, Anticosti Island, Quebec. Canadian Journal of Earth Sciences, 38:125–141.

DULAI, A. 1992. The Early Sinemurian (Jurassic) brachiopod fauna of the Lókút Hill (Bakony Mts., Hungary). Fragmenta Mineralogica et Palaeontologica, 15:41–94.

DULAI, A. 1993. Hettangian (Early Jurassic) brachiopod fauna of the Bakony Mts. (Hungary). Fragmenta Mineralogica et Palaeontologica, 16:27–50.

DULAI, A. 1998. Hettangian and Early Sinemurian (Early Jurassic) brachiopod fauna of the Pisznice Limestone in the Eastern Gerecse Mts. and in the Kálvária Hill at Tata. Földtani Közlöny, 128:237–263. (In Hungarian)

DULAI, A. 2001. Diversification of Mediterranean Early Jurassic brachiopods after the end-Triassic mass extinction—new results from Hungary, p. 411–423. *In* C. H. C. Brunton, L. R. M. Cocks, and S. L. Long (eds.), Brachiopods: Past and Present. A Systematic Association Special Volume Series, 63.

DULAI, A. 2003a. Taxonomic composition of Mediterranean Early Jurassic brachiopod faunas from Hungary: Niche replacement and depth control. Fragmenta Palaeontologica Hungarica, 21:43–50.

DULAI, A. 2003b. Hettangian and Early Sinemurian (Early Jurassic) brachiopods of the Transdanubian Central Range (Hungary) II. Resultationes investigationum Rerum Naturalium Montium Bakony, 27, 146 p. (In Hungarian)

ENGEL, T. 1908. Geognostischer Wegweiser durch Wurttemberg. Anleitung zum Erkennen der Schichten und zum Sammeln der Petrefakten (third edition). Stuttgart, 645 p.

FOSTER, M. W. 1974. Recent Antarctic and Subantarctic Brachiopods. Antarctic Research Series, 21, 189 p.

GAETANI, M. 1970. Faune hettangiane della parte orientale della provincia di Bergamo. Rivista Italiana Paleontologia, 76:355–442.

GEYER, G. 1889. Über die liasischen Brachiopoden des Hierlatz bei Hallstatt. Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt, 15:1–88.

GRÜNER, M. 1997. Dynamische Paläoökologie und taxonomische Bearbeitung des Unterjura (Hettangium bis unteres Sinemurium) auf der Schwäbischen Alb. Profil, 11:1–197.

HAAS, H. 1887. Étude monographique et critique des Rhétiens et Jurassiques des Alpes Vaudoises et des contreés environnantes. Mémoires de la Société Paléontologique Suisse, 14:67–126.

HALLAM, A. 1960. A sedimentary and faunal study of the Blue Lias of Dorset and Glamorgan. Philosophical Transactions of the Royal Society, London, B243:1–44.

HALLAM, A. 2002. How catastrophic was the end-Triassic mass extinction? Lethaia, 35:147–157.

HANZO, M., B. LATHUILIÉRE, Y. ALMÉRAS, G. DAGALLIER, S. GUERIN-FRANIATTE, F. GUILLOCHEAU, V. HUAULT, L. NORI, AND R. RAUSCHER. 2000. Paléoenvironnements dans le Calcaire à grypheés du Lias de Lorraine, de la carrière de Xeuilley au Bassin Parisien. Eclogae Geologicae Helveticae, 93:183–206.

HUDSON, R. G. S., AND R. P. S. JEFFERIES. 1961. Upper Triassic brachiopods and lamellibranchs from the Oman Peninsula, Arabia. Palaeontology, 4:1–41.

KUHN, O. 1949. Lehrbuch der Paläozoologie. E. Schweizerbartische Verlagsbuchhandlung, Stuttgart, 326 p.

LANG, W. D. 1924. The Blue Lias of the Devon and Dorset coasts. Proceedings of the Geologist's Association, 35:169–185.

LAURIN, B. 1974. Étude sur la structure et la variabilité de l'espèce *Burmirhynchia latiscensis* nov. sp. (Rhynchonellidae du Callovien inférieur de Bourgogne). Bulletin de la Societé Géologique de France, 16:396–404.

LEE, D. E., S. J. CARLSON, N. BUENING, AND C. R. SAMSON. 2001. Variation in the loops of the Recent species of *Liothyrella* (Brachiopoda; Terebratuloidea) from New Zealand and South Orkney Islands, p. 65–70. *In* C. H. C. Brunton, L. R. M. Cocks, and S. L. Long (eds.), Brachiopods: Past and Present. A Systematic Association Special Volume Series, 63.

LICHAREW, B. K. 1956. Superfamily Rhynchonellacea Gray, 1848, p. 56–61. *In* L. D. Kiparisova, B. P. Markowskii, and P. Radchenko (eds.), Materials for Paleontology, New Families and Genera. Vsesoiuznyi Nauchnoissledovatel̆skii Geologicheskii Institut (VSEGEI), Materialy (Paleontologia), 12. (In Russian)

MACFARLAN, D. A. B. 1992. Triassic and Jurassic Rhynchonellacea (Brachiopoda) from New Zealand and New Caledonia. The Royal Society of New Zealand Bulletin, 31:1–310.

MANCEÑIDO, M. O. 1980. Nota sobre la validez de *Fissirhynchia* Pearson, 1977 (Brachiopoda, Rhynchonellida). Ameghiniana, 17:335–338.

MANCEÑIDO, M. O. 1993. Early Jurassic brachiopods from Greece: A review, p. 79–100. *In* J. Pálfy and A. Vörös (eds.), Mesozoic Brachiopods of Alpine Europe. Hungarian Geological Society, Budapest.

MANCEÑIDO, M. O. 2000. A systematic summary of the stratigraphic distribution of Jurassic rhynchonellid genera (Brachiopoda). Georesearch Forum, 6:387–396.

MANCEÑIDO, M. O., AND E. F. OWEN. 2001. Post-Paleozoic Rhynchonellida (Brachiopoda): Classification and evolutionary background, p. 189–200. *In* C. H. C. Brunton, L. R. M. Cocks, and S. L. Long (eds.), Brachiopods: Past and Present. A Systematic Association Special Volume Series, 63.

MOISEEV, A. S. 1936. Les nouveaux genres Rhynchonellidae du Triassique et Liassique. Travaux de la Société Naturale de Leningrad (Section Géologie et Mineralogie), 65:39–50. (In Russian with French abstract)

NEUMAYR, M. 1879. Zur Kenntniss der Fauna des untersten Lias in den Nordalpen. Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt, 7:1–46.

OPPEL, A. 1861. Ueber die Brachiopoden des untern Lias. Zeitschrift der deutschen geologischen Gesellschaft, 13:529–550.

OVCHARENKO, V. N. 1983. Jurassic brachiopods of the Pamirs. Akademia Nauk Tadzhikiskoi SSR, Institut Geologii, Dushanbe, 196 p. (In Russian)

PEARSON, D. A. B. 1967. Rhaetian articulate brachiopods of Europe. Unpublished Ph.D. dissertation, Imperial College of Science and Technology, London, 354 p.

PEARSON, D. A. B. 1977. Rhaetian brachiopods of Europe. Neue Denkschriften des Naturhistorischen Museums in Wien, 1:9–45.

PETERHANS, E. 1926. Révision des brachiopodes liasiques du Grammont, des Tours d'Aï, du Pissot et de Rossinière figurés dans l'ouvrage de M. H. Haas. Mémoires de la Société Vaudoise des Sciences Naturelles No. 13, 2:353–384.

PLAŠIENKA, D. 2000. Paleotectonic controls and tentative palinspatic restoration of the Carpathian realm during the Mesozoic. Slovak Geological Magazine, 6:200–204.

QUENSTEDT, F. A. 1852. Handbuch der Petrefaktenkunde. Tübingen, 755 p.

QUENSTEDT, F. A. 1858. Der Jura. Tübingen, 842 p.

QUENSTEDT, F. A. 1871. Petrefactenkunde Deutschlands. Abteilung 1, Band 2. Die Brachiopoden. Leipzig, 748 p.

RAU, K. 1905. Die Brachiopoden des mittleren Lias Schwaben mit Ausschluss der Spiriferinen. Geologische und Paläontologische Abhandlungen (neue Folge), 4:263–355.

RZHONSNITSKAIA, M. A. 1956. Systematization of Rhynchonellida, p. 125–126. *In* E. Guzmán and others (eds.), Resumenes de Los Trabajos Presentados. International Geological Congress, Mexico, Report, 20.

SACCHI VIALLI, G., AND G. CANTALUPPI. 1967. I nuovi fossili di Gozzano (Prealpi Piemontesi). Memorie della Societa Italiana di Scienze Naturali, 16:63–127.

SANDY, M. 1995. Early Mesozoic (Late Triassic–Early Jurassic) Tethyan brachiopod biofacies: Possible evolutionary intra-phylum niche replacement within the Brachiopoda. Paleobiology, 21:479–495.

SANDY, M. R., AND M. F. ALY. 2000, A southern Tethyan brachiopod fauna from the Late Triassic of the United Arab Emirates. Geobios, 33: 561–567.

SAVAGE, N. M. 1996. Classification of Paleozoic rhynchonellid brachiopods, p. 249–260. *In* P. Copper and J. Jin (eds.), Brachiopods, Proceedings of the 3rd International Brachiopod Congress. A. A. Balkema, Rotterdam-Brookfield.

SAVAGE, N. M., M. O. MANCEÑIDO, E. F. OWEN, S. J. CARLSON, R. E. GRANT, A. S. DAGYS, AND S. DONG-LI. 2002. Rhynchonellida, p. 1027–1377. *In* Treatise on Invertebrate Paleontology, Pt. H, Brachiopoda (revised). Volume 4. Rhynchonelliformea (Part). Geological Society of America and University of Kansas, Lawrence.

SCHAFHÄUTL, K. E. F. 1851. Über einige neuen Petrefakten des Südbayerischen Vorgebirges. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefactenkunde, 1851:407–421.

SCHLOZ, W. 1972. Zur Bildungsgeschichte der Oolithenbank (Hettangium) in Baden-Wurttemberg. Arbeiten aus dem Institut für Geologie und Paläontologie an der Universität Stuttgart, 67:101–212.

SHI, XIAO-YING, AND R. E. GRANT. 1993. Jurassic rhynchonellids: Internal structures and taxonomic revisions. Smithsonian Contributions to Paleobiology, 73, 190 p.

SIBLÍK, M. 1967. New species of Domerian rhynchonelloids from Slovakia. Geologický Sborník, 18:151–168.

SIBLÍK, M. 1988. Brachiopoda mesozoica (a) Brachiopoda triadica, p. 1–145. *In* H. Zapfe (ed.), Catalogus Fossilium Austriae. Österreichische Akademie der Wissenschaften, 5c.

SIBLÍK, M. 1993. Lower Liassic brachiopods from the Steinplatte-Kammerköhralm area near Waidring (northern Calcareous Alps, Salzburg). Jahrbuch der geologischen Bundesanstalt, 136:965–982.

SIBLÍK, M. 1998. A contribution to the brachiopod fauna of the ''Oberrhätkalk'' (northern Calcareous Alps, Tyrol-Salzburg). Jahrbuch der geologischen Bundesanstalt, 141:73–95.

SIBLÍK, M. 1999. New data on the Hettangian brachiopod fauna of the Northern Calcareous Alps (Austria, Bavaria). Abhandlungen der geologischen Bundesanstalt, 56:419–438.

SINGEISEN-SCHNEIDER, V. 1976. Interpretation von Serienschliffen bei Brachiopoden, am Beispiel von Dogger-Terebratuliden aus dem Basler Jura. Eclogae Geologicae Helvetiae, 69:93–110.

SUESS, E. 1854. Über die Brachiopoden der Kössener Schichten. Denkschriften der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften, 7:29–65.

TCHOUMATCHENCO, P. 1972. Thanatocoenoses and biotopes of Lower Jurassic brachiopods in central and western Bulgaria. Palaeogeography, Palaeoclimatology, Palaeoecology, 12:227–242.

TCHOUMATCHENCO, P. 1993. The horizontal distribution of brachiopods during the *Zeilleria quadrifida* Zone (Late Carixian–Early Domerian, Early Jurassic) in Bulgaria, p. 143–150. *In* J. Pálfy and A. Vörös (eds.), Mesozoic Brachiopods of Alpine Europe. Hungarian Geological Society, Budapest.

TOMAŠOVÝCH, A., AND J. MICHALÍK. 2000. Rhaetian/Hettangian passage beds in the carbonate development in the Krí na Nappe (central western Carpathians, Slovakia). Slovak Geological Magazine, 6:241–249.

TORT, A. 2003. Morphological plasticity of the outline and the internal structures of the shell of the recent *Terebratella tenuis* sp. nov. (Brachiopoda, Terebratulida). Zoomorphology, 122:47–54.

TORT, A., AND B. LAURIN. 2001. Intra- and interspecific variation in internal structures of the genus *Stenosarina* (Brachiopoda, Terebratulida) using landmarks. Journal of Paleontology, 75:261–273.

VÖRÖS, A. 1991. Hierlatzkalk–a peculiar Austro-Hungarian Jurassic facies, p. 145–154. *In* H. Lobitzer and H. Császár (eds.), Jubiläumsschrift 20 Jahre Geologische Zusammenarbeit Österreich-Ungarn. Wien.

VÖRÖS, A., J. SZABÓ, A. DULAI, I. SZENTE, O. EBLI, AND H. LOBITZER. 2003. Early Jurassic fauna and facies of the Schafberg area (Salzkammergut, Austria). Fragmenta Palaeontologica Hungarica, 21:51–82.

WARRINGTON, G., AND H. C. IVIMEY-COOK. 1995. The late Triassic and early Jurassic of coastal sections in west Somerset and South and Mid-Glamorgan, p. 9–30. *In* P. D. Taylor (ed.), Field Geology of the British Jurassic. Geological Society of London, London.

WESTBROEK, P. 1967. Morphological observations with systematic implications on some Paleozoic Rhynchonellida from Europe, with special emphasis on the Uncilulidae. Leidse Geologische Mededelingen, 41:1–82.

WILLIAMS, A., AND J. M. HURST. 1977. Brachiopod evolution, p. 79–121. *In* A. Hallam (ed.), Patterns of Evolution as Illustrated by the Fossil Record. Elsevier, Amsterdam.

WOBBER, F. J. 1968. A faunal analysis of the Lias (Lower Jurassic) of South Wales (Great Britain). Palaeogeography, Palaeoclimatology, Palaeoecology, 5:269–308.

ZUGMAYER, H. 1880. Untersuchungen über rhätische Brachiopoden. Beiträge zur Paläontologie und Geologie Österreichs-Ungarns, 1:1–42.

ACCEPTED 22 FEBRUARY 2005