Jurassic Rhynchonellids: Internal Structures and Taxonomic Revisions

SHI, XIAO-YING
and
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ABSTRACT

Shi, Xiao-ying and Richard E. Grant. Jurassic Rhynchonellids: Internal Structures and Taxonomic Revisions. *Smithsonian Contributions to Paleobiology*, number 73, 190 pages, 83 figures, 18 plates, 1993.—Jurassic brachiopods of the order Rhynchonellida are classified according to modern concepts and techniques, with special attention to internal structures. They are grouped into 6 families and 16 subfamilies of which three are new: the Acanthorhynchiinae, the Cryptorhynchiinae, and the Piarorhynchiinae. Subfamilies emended or revised are the Acanthothyridinae Schuchert (1913) raised to family rank, Davanirhynchinae Ovtsharenko (1983), Dzhangirhynchinae Ovtsharenko (1983), Erymnariinae Cooper (1959), Indorhynchiinae Ovtsharenko (1975), Septocurellinae Ager, Childs, and Pearson (1972), and Striirhynchiinae Kamysan (1968). New genera are *Aalenirhynchia* (type-species *Rhynchonella subdecorata* Davidson, 1853), *Bradfordirhynchia* (type-species *Cryptorhynchia bradfordensis* Buckman, 1918), and *Sharpirhynchia* (type-species *Kallirhynchia sharpi* Muir-Wood, 1938). A new subgenus is *Burmirhynchia* (*Hopkinsirhynchia*) (type-species *Burmirhynchia hopkinsi* Davidson, 1854). The only new species is *Pycnoria depressa*. Eleven genera are revised, and many are transferred among the subfamilies; lectotypes are designated where needed.

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Introduction

The order Rhynchonellida, one of the major groups among the Jurassic brachiopods, presents challenges of long standing. Although it has been more than two hundred years since Linnaeus (1767) recorded the first species of Jurassic rhynchonellid, and more than 160 Jurassic rhynchonellid genera have been named, the classification has not been established solidly and many genera are still not properly studied in the terms of internal structures. Jurassic rhynchonellids are important not only in stratigraphical and paleontological studies, or for their abundance and diversity in the marine sediments, but also for their widespread distribution and rapid evolution and their ecological adaptation to different environments.

The basic systematics of the Jurassic rhynchonellids were laid out by Buckman (1918). As a result of the limitation in techniques, equipment, and knowledge at that time, Buckman's system is far from satisfactory in the view of present knowledge. Most of his genera were established without knowledge of internal characters, and many of them were not defined clearly on any consistent feature, so that much confusion has resulted. Buckman did, of course, contribute a great deal to the systematics, and his monograph is still used as one of the most important standard books on the Brachiopoda. In later years, tremendous work was done on the Jurassic rhynchonellids, and great advances were achieved in studies of their taxonomy, paleoecology, biostratigraphy, and paleobiogeography as well as in some facets of their evolution. However, the inadequacy of materials and the paucity of regions studied have left a number of problems still unsolved.

When we initially became involved in the study of Jurassic

rhynchonellids, we realized that most of the genera are ordinary looking forms, they are similar in external morphology and not easy to distinguish. It is almost impossible to put some species into their relevant genera confidently without studying the internal structures. In the "Treatise" (Williams and Rowell, 1965) a tentative classification was suggested for the Mesozoic and Cenozoic Rhynchonellida and many genera were presented with some interior information; however, a lot of uncertainty remained and many genera that were not sufficiently known internally had to be grouped solely on their external appearances. Because of insufficient study of the internal structures, much confusion in the taxonomy has arisen, and homonyms and synonyms are not rare in the literature. Comprehensive study of Jurassic rhynchonellids reveals that species or generic names vary from country to country, or even from area to area. These problems in taxonomy, in turn, produce new difficulties and confusion in the studies of biostratigraphy, paleobiogeography, and evolution. Therefore, as the basis of paleontology and its related subjects, taxonomic study should still be emphasized and the study of interiors, which is of great importance in the classification, should receive especially close attention.

Here we attempt to revise the Jurassic rhynchonellid genera, clarify the confusion in taxonomy, and lay out a reliable basis for the classification in terms of anatomic structures. Most genera studied in this paper have been based on their type-species by aid of either silicified specimens or serial sections, with emphasis especially on the internal structures of the dorsal valve. For some genera, such as *Rhactorhynchia* and *Kutchirhynchia*, our diagnoses had to be based on forms closely related to their type-species or on information available in the literature because of the scarcity of available specimens. The Early and Late Jurassic rhynchonellids are not handled in depth in this paper, because most of them have been studied and revised in detail by Ager (1956–1967) and Childs (1969). The interior characters of those forms are relatively clear. This

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paper, therefore, concentrates mainly upon the Middle Jurassic ones (the majority of Jurassic rhynchonellids) that have not previously been studied sufficiently. It focuses on internal structures and resultant taxonomic revisions. Some Early and Late Jurassic genera had to be studied in order to trace trends in evolution.

With the rapid accumulation of data resulting from the expansion in areas and subjects studied, ever more new taxa have been created. We judge that this is an opportune time to revise and synthesize the classification before too many homonyms, synonyms, and confused classifications result from insufficient study, while recognizing that much remains to be done.

PREVIOUS WORK.—Although the first Jurassic rhynchonellid species was described by Linnaeus in 1767, the systematic study of Jurassic rhynchonellids did not progress significantly until the last century. Among the workers of the early nineteenth century, Von Buch (1831–1839), Fischer de Waldheim (1809), Lamarck (1819), Roemer (1835–1839), Schlotheim (1813–1820), Sowerby (1812–1829), and Zieten (1830–1833) are usually considered as the most important researchers on Jurassic rhynchonellids. During this period most of the species were recorded under the names "*Terebratula*" (Muller, 1776) or "*Rhynchonella*" (Fischer de Waldheim, 1809). Generally no information on the internal structures was presented, and the species were recognized primarily on their exterior morphology, especially the shell shape and ornament.

From the middle to the end of nineteenth century, much was accomplished toward understanding this subject, most notably by Brown (1837–1849), Buckman (1882–1899), Davidson (1850–1886), Eudes-Deslongchamps (1853–1887), Greppin (1890–1900), Haas (1886–1893), Haas and Petri (1882–1891), Oppel (1853–1863), d'Orbigny (1850–1852), Quenstedt (1851–1885), Rothpletz (1886), and Szajnocha (1879–1881). Many of these important monographs remain indispensable standard works for current research. During this period, the generic terms *Rhynchonellina* and *Apringia* were respectively created by Gemmellaro (1871) and Gregorio (1886), however, most species were still described as "*Terebratula*" or "*Rhynchonella*." Little information on interior characters was provided, so internal structures could not be used as important characters for the recognition of taxa, although Rothpletz (1886) recognized several basic types of crura. During this period the important genus *Acanthothiris* was proposed by d'Orbigny (1850). In the nineteenth century, a large amount of data was accumulated and many species were described. The family Rhynchonellidae was founded in 1848 by Gray. In general, however, not much attention was paid to the study of internal structures in that century. The taxonomy was largely based on the exterior appearance and some other easily observed characters. During this period, the research work was, geographically, restricted mainly to Europe, especially to the industrial countries.

In the early part of the twentieth century, many paleontologists considered the Jurassic rhynchonellids. A wealth of data

concerning this topic was accumulated as the result of expansion in geological investigation and exploration. Only a few monographs, however, were published. Notable works of that period are by Bigot (1934–1936), Buckman (1901–1927), Douglas and Arkell (1928–1932), Dubar (1925–1938), Kitchin (1900), Leidhold (1921), Lissajous (1905–1923), Muir-Wood (1925–1939), Richardson (1904–1919), Roche and Arcelin (1936–1939), Rollier (1910–1919), Weir (1925–1938), and Wisniewska (1932). Buckman (1918) and Rollier (1917–1919) are the scholars to be mentioned most prominently. The former created many genera, and systematically summarized and revised most of the genera. The latter made a detailed emendation of the species erected by that time. During this period, although increased attention was paid to internal structures in taxonomic studies, it was really not enough. Most genera were scarcely known internally. The classification on the supra-generic level was still not efficiently organized, but Jurassic terrains studied spread to a world wide scale, and important advances were attained.

Since the 1940s, the study of this subject has been greatly improved and accelerated not only in the areas studied but also in depth and understanding. Important developments took place in the taxonomy, paleoecology, paleobiogeography, biostratigraphy, and evolutionary aspects. Tremendous work has been done on regional faunas world wide, but comprehensive and emendation work still are not enough, compared with the accelerating accumulation of new taxa. We do not intend to evaluate all the research on Jurassic rhynchonellids of this period, but several important monographs should be mentioned here.

D.V. Ager (1956–1967) summarized systematically the Lower Jurassic rhynchonellids of Britain. Many important genera were very well studied and emended with adequate descriptions of their type-species. The detailed study of internal structures makes this one of the most important studies of Lower Jurassic rhynchonellids. Makridin (in Rzonstnizkaja, Likharew, and Makridin, 1960) and Ager (1965a) respectively summarized the Mesozoic rhynchonellid genera briefly in the "Osnovy" and the "Treatise." The rhynchonellid classification was significantly rearranged in the "Treatise" and many genera were defined with reference to internal structures. Ager, Childs, and Pearson (1972) dealt with all the Mesozoic rhynchonellid genera in the sense of evolution and complemented the systematic classification of the Mesozoic Rhynchonellida. This is one of the most important summary works in the recent study of rhynchonellids.

Childs (1969) made a good summary work on the Upper Jurassic rhynchonellids of Northwestern Europe. His monograph emended several important genera that were thoroughly studied and revised through detailed investigation of interiors. Another important work was that by Makridin (1964), although it was basically a study of regional faunas.

Although Almeras' (1964–1988) primary focus has been on Jurassic terebratulids, he has contributed importantly to understanding of internal features and the taxonomic arrange-

ment of Middle Jurassic rhynchonellids, especially those of the Aalenian to the Bajocian. Laurin (1972–1984) also made significant contributions to the study of Middle Jurassic rhynchonellids. His monograph of 1984, contributed importantly to the study of interior structures and taxonomic revisions of many important Bathonian to Callovian genera and species from western Europe.

Beside the major works mentioned above, shorter treatments of regional brachiopod faunas also must be considered. Cooper (1989), Dagis (1968–1972), Dubar (1938–1967), Fischer (1961–1969), Ching [Jing] and Sun (1976–1982), Kamyshan (1967–1973), Makridin (1954–1964), Ovtsharenko (1967–1983), Prossorovskaya (1962–1985), Rousselle (1962–1983), Seifert (1963), Shi (1985–1990), Siblik (1964–1968), Sucic-Protic (1969–1985), Tchoumatchenko (1966–1988), Voros (1983–1985), and Wisniewska-Zelichowska (1978) have all done some work dealing with the taxonomy and systematics of Jurassic rhynchonellids.

The latest monograph to deal with Jurassic rhynchonellids is by Cooper (1989) on Jurassic (Callovian) brachiopods of Saudi Arabia. This work treats terebratulids and spiriferids as well, but 13 new genera of rhynchonellids are established. He follows the conventional classification, but reveals many significant details of internal structures, by sections, skillful excavations, and well-preserved silicified specimens.

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Internal Structures

Internal structures are very important for the classification of the Rhynchonellida and for the recognition of its taxa. As mentioned earlier, most of the Mesozoic and Cenozoic rhynchonellids, except for a few genera that have unusual appearances and are easily distinguished, are ordinary forms. Their external appearances are similar and can be characterized as having a "conventional" brachiopod look. The correct recognition of most genera or even subfamilies depends heavily on interior characters. Generally, the interiors of the ventral valve are less important and can only be used for the recognition of the lower level taxa. Some structures, such as a persistent median septum, may be important at the generic level. The presence or absence of dental plates may be valuable for recognition of genera or even subfamilies. The pedicle collar, the shape and the development of the dental plates, and the teeth, are less useful, or can be used only at the species level. The internal structures of the dorsal valve have proved to be the most valuable characters for the rhynchonellids. Among these structures, the crura are the most important because they are fairly complicated (many characters to utilize) and are generally persistent throughout genera and subfamilies. The dorsal septum is next in importance; together with the crura and the septalial plates (or crural plates) they form the major structure inside the dorsal valve. Although the hinge plates and the inner socket ridges are of importance in the classification to some extent, they are relatively variable and so are more useful for lower level taxa. The septalium, although useful in a general sense, has proved to be a highly variable structure in the Jurassic rhynchonellids. In some groups, it proves a useful character, while in some others it varies even at the species level. The sockets and the accessory denticles of the dorsal valve are of minor importance, even at the species level. The secondary thickenings and callus within the valves were usually taken as useful characters for the recognition of genus and species. We suggest, however, that these characters might be more closely related to the ecological and the environmental factors of the shells rather than to their genetic heritage. It might be better to use them as the characters of populations or species rather than of genera.

In this paper, therefore, the classification of the rhynchonellids has relied heavily on interior features of the dorsal valve, although for lower level taxa those of the ventral valve have

also receive thoughtful consideration. The present study shows that the basic crural types can be used as keys to the families of the Rhynchonellacea, while the variations of each basic crura type can be generally used to classify the subfamilies. The general characters of the septum, septalial plates, and to a lesser extent the septalium, can be used for the recognition of the subfamily and genus, while the hinge plates and inner socket ridges can be used only for the lower taxa. The following discussions, therefore, deal mainly with the interiors of the dorsal valve.

Terminology

This paper essentially uses the definitions of morphological terms used in the "Treatise" (Williams and Rowell, 1965). For terms used in describing the character of internal structures in section, we have also adopted those used by Ager, Childs, and Pearson (1972), Almeras (1966a, 1971, 1979a, b, 1987), Childs (1969), and Laurin (1974, 1984a). Some other things about the internal structures of the rhynchonellids are discussed in greater detail in the following sections.

Definition of abbreviations for measurements and counts, and explanation of the format for serial section drawings are given on page 25.

CRURA

The crura are the most complex structures of the rhynchonellid interior, and also are the most important characters in their classification. They are especially important in the grouping of families and subfamilies and in the determination of genera. Many previous studies neglected these structures, particularly the shapes of the crural terminations in section. Many published serial sections are incomplete, failing to show the characteristics of crural terminations, which often are key points in determining the crural type. Many genera are distinguishable by the shapes of crura ends, despite external similarities.

According to Ager's (1965a) summary, 11 crural types have been recognized in Mesozoic and Cenozoic rhynchonellids. Among these the radulifer, falcifer, and septifer are regarded as the basic and most distinct types. The others, namely, arcuifer, calcarifer, canalifer, maniculifer, spinulifer, prefalcifer, mergifer, and cilifer, are treated as variations on the three basic types. Roughly, the radulifer crura and their variants are borne by the family Rhynchonellidae, the falcifer and variants are

borne by Basiliolidae, and the septifer crura are found in Erymnariidae. There are a few exceptions to these general rules, and some genera are not linked properly with known crura. Mitra and Ghosh (1973) and Ovtsharenko (1983) proposed respectively another two crural types: pseudocalcarifer and subfalcifer. In this paper, however, the former has been rejected and the latter has been redefined as a variant of the falcifer. Only 7 crural types are recognized here, they are: radulifer, calcarifer, canalifer, subfalcifer, prefalcifer, falcifer, and septifer.

Radulifer is one of the basic crural types, and is also the most common type occurring in the Mesozoic rhynchonellids. It is generally borne in the subfamilies Rhynchonellinae, Tetrarhynchinae, Piarorhynchiinae, and Striirhynchiinae of the family Rhynchonellidae as well as in the Acanthothyridinae of the family Acanthothyridinae. Radulifer crura are unspecialized hook- or rod-like structures that project variably toward the pedicle valve from the inner margins of the hinge plates. Their terminations vary considerably in shape in cross section, but usually lack specialized processes or heads. Previous research has generally neglected variations in the crural ends because of breakage of the distal parts, incomplete or improperly oriented serial sections, or variations in the distal ends that produce different shapes in cross section. Generally the radulifer crura curve somewhat ventrally forward. When the crura extend almost along the plane of commissure they show two points in the sections (Figure 1A,B). The same kinds of crura may have different shapes in cross section, the commonest being subcircular and subtrigonal (e.g., in *Cymatorhynchia*, *Sphenorhynchia*, *Costirhynchia*, *Lacunaerhynchia*, and *Rhynchonelloidea*). When the crura are curved sufficiently toward the ventral valve, in serial section they may appear as vertical plates or parentheses (Figure 1C,D). If the crura simply diverge forward gently, they may appear as subparallel vertical plates (e.g., in *Ptilorhynchia*, *Isjuminella*, and *Quadratorhynchia*). If the crura not only curve in toward the ventral valve but also converge at their anterior ends toward each other, they may appear as parentheses in section (e.g., in *Burmiorhynchia*, *Kallirhynchia*, and *Hopkinsirhynchia*). Crura of trigonal shape in cross section that curve strongly toward the ventral valve may appear not only as vertical plates or parentheses, but also may appear to have short hooks at the tips of the crural ends in sections (Figure 1E,F; e.g., in *Homoeorhynchia* and Figures 2, 3 in *Kutchirhynchia*). The angle of sectioning also influences the appearance of crura in sections. The crura vary in three

FIGURE 1.—Terminal variations of radulifer crura (not in natural proportion).

FIGURE 2.—Serial sections of *Kutchirhynchia* sp.; Y13244, L 23.6, W 19, T 16, A 87; from the Matuo Formation (Bathonian), South of Wenquan, Southern Qinghai, China. Showing strongly incurved radulifer crura.

dimensions and will show different shapes in serial sections depending on the orientation. Inattention to these factors may produce spurious crural shapes that result in incorrect interpretations.

Mitra and Ghosh (1973) proposed a new type of crura based on those in *Kutchirhynchia kutchiensis* (Kitchin), and named it pseudocalcarifer. They mentioned (1973:181, footnote) that "Muir-Wood (1934), while describing *Kallirhynchia* introduced calcarifer type crura. According to her, calcarifer crura are ventrally terminated in a hook-shaped process. The crura in *Kutchirhynchia* have all the elements of calcarifer type crura, except the hook-shaped termination. Thus in the present work, the crura in *Kutchirhynchia* have been termed pseudocalcar-

ifer." Their definition and analysis along with comparison of their serial sections (Mitra and Ghosh, 1973:178, fig. 1) with those presented here (Figures 2, 3) and the serial sections made by E.F. Owen at the Natural History Museum, London, indicate that the so-called pseudocalcarifer crura are actually radulifers whose distal ends curve strongly inward toward the ventral valve, so that in the sections they appear as vertical plates (Figures 2, 3). The crura are similar to prefalCIFer and subfalCIFer crura in appearance, and are easy to confuse. Generally, radulifer crura arise from the inner margins of the distal ends of the hinge plates, many specimens having the crural bases very narrow or poorly formed. PrefalCIFer and subfalCIFer crura, in contrast, rise from the dorsal sides of the

FIGURE 3.—Serial sections of *Kutchirhynchia* sp.; H124464, L 18, W 16.4, T 13.2, A 79; from the Matuo Formation (Bathonian), Nardigangre, Northern Tibet, China. Showing strongly incurved radulifer crura.

inner margins of hinge plates, with broad and well-formed crural bases that begin much earlier in ontogeny. The origin and the growth of these crural types are different (compare Figure 2 with Figures 15–19 of *Bradfordirhynchia*, new genus, *Cirpalangi* Ager (1958:59, text-fig. 33), and *Pseudogibbirhynchia moorei* (Davidson) Ager, 1962:111, text-fig. 67).

Calcarifer crura are specialized varieties of the radulifer type that characterize the subfamily Ivanoviellinae. This crural type was defined by Muir-Wood (1934) based on *Kallirhynchia yaxleyensis* (Davidson). She also described this type of crura in *Rhynchonelloidella* and figured several sets of serial sections (Muir-Wood, 1936). Unfortunately, Muir-Wood (1934) defined calcarifer crura mainly on the basis of longitudinal sections of *Kallirhynchia yaxleyensis* (Davidson), so it is difficult to determine their real shapes. Transverse sections of *Kallirhynchia yaxleyensis* (Davidson) illustrated by Muir-Wood (1934:535, fig. 2) are incomplete, failing to show the anterior parts of the crura. Muir-Wood (1936) illustrated another two sets of serial sections of *Kallirhynchia*, of which

those of *Kallirhynchia superba* Buckman are also incomplete. The serial sections of *Kallirhynchia platiloba* Muir-Wood show that this species should be transferred into the *Rhynchonelloidella* rather than remain in *Kallirhynchia* as was originally recognized by Muir-Wood (see Muir-Wood, 1936:41, text-fig. 11; 43, text-fig. 12). For a long time, therefore, the crura of *Kallirhynchia* were actually not known. Laurin (1984a), after study of French specimens, pointed out that the crura of *Kallirhynchia* are radulifer rather than calcarifer. Our study of the topotypes also demonstrates that *Kallirhynchia yaxleyensis* (Davidson), *K. concinna* (Sowerby), and *K. multicostata* Douglas and Arkell all have radulifer crura as understood by most brachiopod workers, even though the calcarifer crura (Muir-Wood, 1934) were defined from crura of *Kallirhynchia yaxleyensis* (Davidson).

Muir-Wood (1936) illustrated several sets of serial sections of the calcarifer type of crura among the *Rhynchonelloidella*, but only those of *Rhynchonelloidella smithi* (Davidson) were complete (Muir-Wood, 1936:56, text-fig. 15). Ager

(1965a:H599, fig. 478-5) reconstructed the calcarifer crura based on serial sections of *Kallirhynchia platiloba* by Muir-Wood (1936:41, fig. 11) and thought the calcarifer crura to be close to the falcifer. As a result, he mistakenly put *Kallirhynchia*, *Rhynchonelloidella*, and *Thurmannella* all into the subfamily Lacunosellinae, although he later corrected this mistake (Ager, Childs, and Pearson, 1972). By comparing the crura in *Rhynchonelloidella*, *Thurmannella*, *Lotharingella*, and *Cardinirhynchia* with those in *Lacunosella* as well as *Orbirhynchia*, which have typical falcifer crura, it has been demonstrated that the calcarifer crura are quite different from the falcifer in their origin, and in subsequent adult shapes in transverse sections. Nevertheless, the calcarifer crura share some resemblances with prefalcifer, even though they have different origins. The major differences between them are that the calcarifer crura have dorsally directed hooks or expanded heads at their distal ends, and the crural bases do not project strongly dorsally. Several varieties of crural terminations have been noticed within the calcarifer type (Figure 4).

The canalifer type of crura also is a specialized form of radulifer. It was defined by Ager (1965a:H600) as "in the canalifer type the ventrally directed radulifer crura are folded longitudinally in the form of a dorsally facing channel or gutter. In other words, the crura are V- or U-shaped in cross-section." This type of crura has been proved to be one of the best criteria for recognizing the subfamily Cyclothyridinae. This crural type has been recorded to date only in genera later than Triassic, occurring mainly in the Middle-Late Jurassic and Cretaceous; probably it is at a high level in rhynchonellid evolution. Owing to variable curvature toward the ventral valve and the convergence of the crural ends, the canalifer crura exhibit wide

variation in transverse sections. When the crura project almost along the commissure plane or curve gently in toward the ventral valve, the crura may be U- or V-shaped in cross section, as in *Flabellirhynchia*, *Granulirhynchia*, and *Lamellaerhynchia*. These variations depend largely on the angle between the two folded lamellae and the gutter depth (Figure 5A,B). When the crura curve strongly in toward the ventral valve, they may be Y-shaped, fork-shaped, or even appear as four vertical plates, if the furrows on the dorsal sides of each crus are deep and wide enough (Figure 5C-E), as in *Globirhynchia*, *Bicepsirhynchia*, *Septaliphoria*, and *Moquellina*. Some of these crura exhibit peculiar shapes in cross section (Figure 5F), as in *Pararhactorhynchia trigona* (Shi, 1987b:59, fig. 14; 1990:313, fig. 4; and Figure 72 of this paper). All these varieties of the canalifer crura can be used to distinguish genera or species, although they vary in appearance depending upon the orientation of the section.

Although the canalifer crura normally are distinguished easily from the calcarifer type, there are transitional forms between them, especially in the Late Bathonian to Callovian genus *Moquellina* and its closely related form *Tanggularella* from North Qinghai-Tibetan Plateau, China. Most species of *Moquellina* have crura of the canalifer type, but some specimens have crura fairly similar to the calcarifer type. Generally in canalifer crura, the two folded lamellae of each crus are symmetrical and have nearly the same length. While in calcarifer crura, each crus distally consists of a primary lamella that is much longer and a very short secondary lamella that is either directed dorsally or exists simply as an expanded head. The angle between these two lamellae generally is very small (Figures 6-8, compare with Figures 4, 5).

FIGURE 4.—Terminal variations of calcarifer crura (not in natural proportion).

FIGURE 5.—Terminal variations of canalifer crura (not in natural proportion).

FIGURE 6.—Serial sections of *Moquellina circulata* Shi; Y152219, L 17.5, W 18.3, T 11.9, A 99; from upper part of the Tuotuohe Formation (Upper Bathonian), Yanshiping, Southern Qinghai, China. Showing calcarifer crura.

FIGURE 7.—Serial sections of *Moquellina trilobata* Shi; Y152133, L 19.0, W 19.1, T 13.1, A 100; from upper part of the Tuotuohe Formation (Upper Bathonian to Lower Callovian), Yanshiping, Southern Qinghai, China. Showing canalicifer crura.

FIGURE 9.—Serial sections of *Lacunosella rhombica* Shi; D232529, L >21.5, W 21.3, T 16.2, A 85; from the Suwa Formation (Middle to Upper Oxfordian), Dogai Coring, Northern Tibet, China. Showing falcifer crura.

Subfalcifer crura are similar to the falcifer type in some ways, but differ in the later stages of ontogeny. This crural type was proposed by Ovtsharenko (1983:49, footnote), who commented that, “by subfalcifer we understand crura that are close in form to falcifer, but with distal tips strongly grown in a dorsal direction.” However, from his illustrations (Ovtsharenko, 1983:72, fig. 14a; 75, fig. 15a,b; 77, fig. 16a; 80, fig. 17a,b), it seems that the subfalcifer crura are not much wider than the falcifer distally in the dorsal-ventral direction so this can not be used as a key point to distinguish subfalcifer from falcifer crura. Comparing the crura in *Dzhangirhynchia* Ovtsharenko and in *Bradfordirhynchia*, new genus, both of which possess typically subfalcifer crura, with those in *Lacunosella* and *Orbirhynchia* with typically falcifer crura, it has been found that the main differences between them are that the subfalcifer extension occurs much later in ontogeny, arising dorsally from the distal ends or anterior parts of the hinge plates. The falcifer form begins much earlier and arises from the preliminary parts of the hinge plates or forms directly from the prolongations of the septalial plates or crural plates (Figures 9–11; compare with Figures 15–19 of *Bradfordirhynchia*).

FIGURE 8 (facing page).—Serial sections of *Moquellina globosa* Shi; G15822, L 15.7, W 14.3, T 13.8, A 80; from the Xiali Formation (Middle to Upper Callovian), Geladandong, Southern Qinghai, China. Showing canalifer crura.

FIGURE 10.—Serial sections of *Lacunosella rhombica* Shi; D232525, L 26.5, W 21, T 15, A 75; from the Suwa Formation (Middle to Upper Oxfordian), Dogai Coring, Northern Tibet, China. Showing falcifer crura.

FIGURE 11.—Serial sections of *Lacunosella trilobatiformis* Wisniewska; D232530, L >25.5, W 23.5, T 18.2, A 87; from the Suwa Formation (Upper Oxfordian), Dogai Coring, Northern Tibet, China. Showing falcifer crura and the tapering hinge plates anteriorly.

Generally, the falcifer crural bases are much wider (dorsal-ventral direction) than those in subfalcifer. The falcifer crura, on the other hand, are generally shorter (crural length/dorsal valve = 0.28–0.31) than the subfalcifer crura (crural length/dorsal valve length = 0.31–0.34).

Subfalcifer crura are similar in appearance to prefalcifer

crura in transverse sections, so the two types may be easy to confuse. Most prefalcifer crural bases are narrower (dorsal-ventral direction) than those of the subfalcifer, and are differentiated later in ontogeny than are the subfalcifer. This distinction in terms, is useful because the subfalcifer type is transitional in development from prefalcifer to falcifer. The

prefalcifer crura particularly characterize an important Triassic to Early Jurassic rhynchonellid subfamily, the Cirpinae, and the falcifer crura are very distinctive in an important Late Jurassic to Cretaceous rhynchonellid subfamily, the Lacunosellinae. Subfalcifer crura have been recognized only in Middle Jurassic rhynchonellids, especially in the subfamily Dzhangirrhynchinae. This does not necessarily mean that these subfamilies are closely related, however, in fact they have been placed consistently in separate families, the Wellerellidae and Basiloididae. Apparently, this is a matter of how researchers evaluate the criteria in classification. The Cirpinae are put under the family Wellerellidae mainly because many genera have united hinge plates, which were taken as one of the main characters of the family. The subfamily Cirpinae is, so far as concerns the Mesozoic–Cenozoic Rhynchonellida, the only higher taxon that has been put in a Paleozoic family and is supposed to be directly related to the Paleozoic rhynchonellids. If we stressed the crural type, the subfamily Cirpinae would be put in the family Basiloididae, which is characterized by having falcifer crura or its varieties.

Septifer is one of the basic crura types and characterizes the family of Erymnariidae. This kind of crura was originally distinguished by Rothpletz (1886:86), and later was more clearly defined by Wisniewska (1932:6) and Cooper (1959:9). Wisniewska defined septifer crura as, “Crura short with the crural plates supported at the bottom of the valve and extending for about one-third the valve length,” recognizing them especially in the Jurassic genus *Septocrurella*. Cooper further commented that this is an extremely rare type of crura that is known only in a few genera. He recorded this type of crura especially in the Tertiary genus *Erymnaria* and was so impressed by the crura that a family, the Erymnariidae, was created on the basis of the genus. In this paper, the septifer crura have been recognized in *Cryptorhynchia* Buckman, 1918, and in *Aethirhynchia* Shi, 1990. This type of crura has been recognized only in a few genera, however, it also shows a considerable variation in appearance in transverse section. In *Septocrurella*, *Caucasella*, and *Erymnaria*, the crural plates are parallel, extending downward and sitting directly on the dorsal valve floor. Crural plates of *Crurirhynchia*, *Aethirhynchia*, and *Sulcirostra* are relatively short, partly fused with the socket fulcral plates posteriorly, becoming separate from the latter anteriorly, leaving small chambers between them. In *Cryptorhynchia*, however, the crural plates are completely fused with the fulcral plates, so the crura seem to arise directly from the fulcral plates at the anterior. These characters and development of the crural plates divide the Erymnariidae into three subfamilies here.

SEPTALIUM

In the “Treatise” (Williams and Rowell, 1965:H152) the septalium was defined as: “trough-like structure of brachial valve between hinge plates (or homologues), consisting of

septalial plates (or homologues) enveloping and buttressed by median septum; does not carry adductor muscles.” This definition has been used widely and is the description of a normally shaped septalium in the Mesozoic rhynchonellids. Although Childs (1969) discussed the septalium in detail and some others (Delance and Laurin, 1973; Laurin, 1984a; Rousselle, 1965a, b; Westbroeck, 1968) also gave some comments on this structure, the topic needs further discussion.

The term septalium was originally introduced by Leidhold (1921) in describing *Thurmannella orbtrita* and *Septaliphoria arduennensis* of the Upper Jurassic rhynchonellids, referring to the V-shaped cavity that unites the hinge plates in the dorsal valve. He illustrated the septalium by several silicified specimens (Leidhold, 1921, pl. v: figs. 2d, 3d, 5a, 6). Prior to Leidhold, Weller (1910:502) described this kind of structure as the “Crural Cavity” in Paleozoic rhynchonellids. As the term “Crural Cavity” was thought to be misleading, the term “septalium” has been accepted as the formal name for this structure. Wisniewska (1932:6, fig. 1a,b,c) illustrated the septalium in transverse sections and regarded it as a trough-like structure formed by the plates derived from the hinge plates and the septum, generally in the shape of a Y. This is surely the concept of the septalium that has become widely used. Wisniewska (1932:26, fig. 6) also mentioned that sometimes the septalium is not supported by a septum, but appears to rest directly on the dorsal valve floor. Muir-Wood (1934:518, fig. 1; 551, fig. 11) gave a detailed description of the septalium and illustrated it by transverse sections of *Digonella*. She pointed out that the floor of a septalium is formed by two septalial plates that converge and fuse together to form a septum. This septum supports the hinge plates, and appears to be distinct from the true median septum in many species (Muir-Wood, 1934:528–529). From all these descriptions mentioned above, it seems clear that a septalium should have the following three key points: first, it should be formed by the septalial plates; second, it should be supported by the septum; and third, it should be trough-like and located between the hinge plates. Childs (1969), on the other hand, thought that the structure in which the septalial plates sit directly on the dorsal floor instead of being supported by a septum should also be regarded as a septalium. One of the main reasons for this is that in *Septaliphoria arduennensis* (Oppel) the septalium is developed only at the extreme posterior end of the dorsal valve and is either supported by a very low septum or appears to rest directly on the floor (Childs, 1969:88, fig. 31 and also Figures 6, 7, 8, 12 in this paper). One of Childs’ illustrations (1969:88, fig. 31) of *Septaliphoria arduennensis* (Oppel) shows a very short and narrow septalium-like structure, where the two septalial plates are parallel and rest directly on the dorsal floor. The other (Childs, 1969:89, fig. 32) has no septalium at all. Another illustration of *Septaliphoria paucicosta* Childs (Childs, 1969:92, fig. 33) does not show a septalium either, instead the pendant septalial plates are parallel, neither united with the septum nor forming a trough. Childs (1969) also

FIGURE 12.—Serial sections of *Septaliphoria arduennensis* (Oppel); G151022, L 19.6, W 19.2, T 15, A 103; from the Lower part of Suwa Formation (Lower Oxfordian), Geladandong, Southern Qinghai, China. Showing septalial plates resting directly on the floor, canalifer crura incurved ventrally.

illustrated two sets of serial sections of *Thurmannella*, one of which, *Thurmannella obtrita* (Defrance) (Childs, 1969:48, fig. 19), has no recognizable septalium, but has very short and pendant septalial plates; another, *Thurmannella acuticosta* Childs (1969:52, fig. 20), has no septalium either, but the septalial plates are longer, pendant, and parallel. All these species, however, were described as “septalium present” in the paper by Childs (1969). It becomes clear that Childs regarded both the structures in which the septalial plates are pendant, not united with the septum to form a trough, and in which the septalial plates rest directly on the dorsal floor, as the septalium. Laurin (1972, 1974, 1984a) also used the septalium in a broad sense, and those in which the septalial plates sit on the floor and do not constitute a V-shaped trough have also

been included. To avoid perpetuating misleading definitions in the literature, it is necessary to present a clear definition of the septalium and to assign terms to the variously related parts. Rousselle (1965b) suggested that depending on whether or not it appears “trough-shaped” in cross section, the septalium may be described as either “apparent” or “non apparent.” These terms are still not sufficient to express clearly the real nature and shape of the septalium.

We suggest here that only when the septalial plates converge and join with the septum to form a U- or V-shaped trough, will they be described as a septalium; or when the septum is very short, the septalial plates converge and join with it at the dorsal floor, so that the septum could not be recognized definitely, this structure will also be described as a septalium. In other words,

the floor of a septalium is constituted by the septalial plates, not by the dorsal valve floor. If the septalial plates are parallel and pendant, the septum inserts between them, or the septalial plates are subparallel and set on the dorsal floor directly, the combination of structures will not be called a septalium, because a trough is not present. This suggestion basically agrees with that of the "Treatise." In this paper the septalium and its related structures have been described as in Figure 13.

Components A–D in Figure 13, show the septalium fully developed and complete, and illustrate the condition of "septalium present": A, septalium wide and deep; B, septalium narrow and deep; C, septalium narrow and shallow; D, septalium wide and shallow. Component E shows an incomplete septalium, it is generally very short and disappears rapidly forward. Components F–H, show no troughs formed and will be described as no septalium or septalium not developed. In components I and J, the septalial plates go down all the way to the dorsal floor directly and the septum is extremely reduced (only in a few specimens of *Moquellina* a very short septum can be seen at the very posterior of the umbonal cavity, e.g., in component I). We suggest the term "septoidium" for this kind of structure in order to separate it from the true septalium. The septoidium usually is very short (posterior–anterior direction), less than 1.5 mm long and disappears rapidly forward. It differs from the septalium in mode of formation and probably possesses importance in evolution of the rhynchonellids. This structure has been recorded only in the Late Bathonian to Callovian genus *Moquellina* Jin, Sun, and Ye, 1979 (Figures 6–8), and some specimens of the Oxfordian genus *Septaliphoria* Leidhold, 1921 (Figure 12). In transverse section, the septoidium has an appearance similar to septifer crura in some Mesozoic and Cenozoic rhynchonellids (the family Erym-

nariidae Cooper, 1959), but they are totally different. The septoidium is formed by the downward prolongations of the septalial plates, generally very short in the posterior–anterior dimension and occurs only at the posteriormost part of the dorsal umbonal cavity, having nothing to do with the crura. In contrast, the septifer crura are formed by the extremely extended crural bases that are much longer in the posterior–anterior dimension and could partly or completely fuse with the socket fulcral plates.

The septalium was previously thought to be important in the classification of the rhynchonellids for subfamily and genus (Cooper, 1970). The present study, however, has shown that all the elements that together constitute a septalium are capable of considerable variation in genus or even at the species level, although this by no means implies that they are useless for classification. Generally speaking, the septalium could only be used to subdivide certain groups in a rough sense. In some subfamilies the septalium is constant, while in others it is highly variable. In some genera, the septalium has proved to be important and constant, but in some others it varies from species to species or even from specimen to specimen. Usually the septalium tends to be present in the juvenile individuals of some species and to be reduced in the adults. In a particular genus, the primitive and early species more often have a well developed septalium, while the advanced and late species tend to have the septalium reduced. In general, most rhynchonellids of the Triassic and Early Jurassic have the septalium present, most of the Late Jurassic and Cretaceous ones lack a well developed septalium, while the Middle Jurassic forms vary. This seems to be true also at the subfamily and family levels. Within the Rhynchonellidae, most of the genera of the subfamily Rhynchonellinae, which is a relatively primitive and

FIGURE 13.—Septalium and its related structures (not in natural proportion).

earlier subfamily, have a well developed and V-shaped septalium. In the advanced and later subfamily Cyclothyridinae, only a few early genera have the septalium; while in the subfamily Tetrarhynchiinae, most genera have a variably developed septalium. Comparison of adequately studied genera and different lineages with reference to their ages, produces the strong impression that the septalium is a gradually obsolescent structure both in ontogeny and in phylogeny, although there are some exceptions and the interiors of many genera are not yet clearly understood.

In this paper, the septalium, especially for the subfamily Tetrarhynchiinae, has not been regarded as a very valuable criterion in classification even at the species level, although the presence or absence of a septalium may be useful among species within a particular genus.

Classification

The classification used here basically follows the system suggested by Ager, Childs, and Pearson (1972), but present research into the intricacies of internal structures requires many genera to be transferred among the families and subfamilies. Several new genera and subfamilies have had to be established on the same basis.

Ager, Childs, and Pearson (1972) noted that a total of 90 Jurassic rhynchonellid genera had been established by 1970. After that to the middle of 1990, 56 more genera were named (including possible synonyms). Therefore we now have 147 genera of Jurassic rhynchonellids, which have been grouped into two superfamilies: Dimerellacea Buckman, 1918, containing 14 valid genera, and the Rhynchonellacea Gray, 1848, with 133 named ones (including synonyms). All genera considered in this paper belong to the Rhynchonellacea, so the following discussion focuses mainly on that superfamily.

Although there are some distinctively shaped genera, most of the Rhynchonellacea are ordinary looking forms. Some exterior characters, such as shell shape, ornamentation, smooth areas, beak, foramen, deltidial plates, uniplication, as well as sulcus and fold have proved to be valuable in classification. In general, they are relatively more variable compared with the internal structures. Because most rhynchonellids are marine benthic sessile animals, their shell shapes and some other exterior characteristics were influenced by the substrate, water depth, temperature, and other environmental factors. It is not surprising, therefore, to find that the same genus or even same species from different areas and different sedimentary facies could vary considerably in morphology. Internal structures, like the exteriors, also vary through ontogeny and in different populations, but they are influenced less strongly by external conditions and so are relatively stable and hence more important in the classification. The crural types, septum, septalial plates, dental plates, hinge plates, as well as the septalium in general have proved to be significant for recognition of family, subfamily, and genus. The importance of

the muscle scars for genera was overly emphasized by Buckman (1918), nevertheless they have some corroborative value in the grouping of subfamilies and families.

The classification used here is based on the comprehensive characters of the rhynchonellids, wherein we stress the internal structures more than the exteriors, especially the crural types and the septum and their related structures. After studying all the information available on the internal structures of the Jurassic rhynchonellaceans, it is clear many of the 133 named genera of Rhynchonellacea still have not been investigated properly in the terms of internal structures, so uncertainties remain. Clearly the present work is by no means the final word on this subject.

New families and subfamilies have been proposed recently, but it appears that not all of these are well founded. Russian paleontologists use a somewhat different classification system, although some of their higher taxa do not differ significantly from those of the "Treatise." Of course, we do not imply that the system used in the "Treatise" is perfect or could not be changed, but mean that in high level classification overlapping names should be avoided as far as possible. Our view is that Jurassic rhynchonellaceans can be tentatively grouped into 6 families and 16 subfamilies (a family or subfamily that does not include Jurassic genera is not counted here). The systematic positions of the 133 Jurassic nominal rhynchonellacean genera (including new genera proposed here) have been rearranged as follows.

RHYNCHONELLID HIERARCHICAL SYNOPSIS

Including All Nominal Genera

- Superfamily RHYNCHONELLACEA Gray, 1848
 - Family WELLERELLIDAE Likharev, 1956
 - Subfamily CIRPINAE Ager, 1965
 - Genus *Bodrakella* Moisseev, 1936
 - Genus *Calcirhynchia* Buckman, 1918
 - Genus *Caucasorhynchia* Dagis, 1963
 - Genus *Cirpa* Gregorio, 1930
 - Genus *Lokutella* Voros, 1983
 - Genus *Neocirpa* Prossorovskaya, 1985
 - Genus *Prionorhynchia* Buckman, 1918
 - Genus *Pseudogibbirhynchia* Ager, 1962
 - Genus *Salgirella* Moisseev, 1936
 - Genus *Squamirhynchia* Buckman, 1918
 - Family BASILIOLIDAE Cooper, 1959
 - Subfamily DAVANIRHYNCHIIINAE Ovtsharenko, 1983
 - Genus *Almorhynchia* Ovtsharenko, 1983
 - Genus *Davanirhynchia* Ovtsharenko, 1983
 - Subfamily DZHANGIRHYNCHIIINAE Ovtsharenko, 1983
 - Genus *Bradfordirhynchia*, new genus
 - Genus *Dzhangirhynchia* Ovtsharenko, 1983
 - Genus *Ptyctorhynchia* Buckman, 1918
 - Genus *Rahouiarhynchia* Tchoumatchenko, 1987
 - Subfamily LACUNOSELLINAE Smirnova, 1936
 - Genus *Aidynkulirhynchia* Ovtsharenko, 1983
 - Genus *Dichotomosella* Tchoumatchenko, 1987

- ?Genus *Isjuminelina* Makridin, 1960
 Genus *Kericserella* Voros, 1983
 Genus *Kolhidaella* Moisseev, 1939
 Genus *Lacunosella* Wisniewska, 1932
 Genus *Pamirorhynchia* Ovtsharenko, 1983
 Genus *Praelacunosella* Wisniewska-Zelichowska, 1978
 Genus *Stolmorhynchia* Buckman, 1918
- Family RHYNCHONELLIDAE Gray, 1848
 Subfamily RHYNCHONELLINAE Gray, 1848
 Genus *Apringia* Gregorio, 1886
 Genus *Costirhynchia* Buckman, 1918
 Genus *Fusirhynchia* Dagens, 1968
 Genus *Homoeorhynchia* Buckman, 1918
 Genus *Korjakirhynchia* Smirnova, 1990
 Genus *Laevigatirhynchia* Wisniewska-Zelichowska, 1978
 Genus *Ptilorhynchia* Crickmay, 1933
 Genus *Planirhynchia* Sucic-Protic, 1969
 Genus *Rhynchonella* Fischer de Waldheim, 1809
 Genus *Rhynchonelloidea* Buckman, 1918
 Genus *Rudirhynchia* Buckman, 1918
 Genus *Roturhynchia* Sun, 1981
 Genus *Snezhnorhynchia* Smirnova, 1990
 Genus *Slovenirhynchia* Siblik, 1967
 Genus *Uralorhynchia* Dagens, 1968
- Subfamily PIARORHYNCHIINAE, new subfamily
 Genus *Bihendulirhynchia* Muir-Wood, 1935
 Genus *Cuneirhynchia* Buckman, 1918
 Genus *Grandirhynchia* Buckman, 1918
 Genus *Orlovirhynchia* Dagens, 1968
 Genus *Piarorhynchia* Buckman, 1918
 Genus *Pseudomonticlarella* Smirnova, 1987
 Genus *Scalpellirhynchia* Muir-Wood, 1936
 Genus *Tropiorhynchia* Buckman, 1918
- Subfamily IVANOVIELLINAE Makridin, 1964
 Genus *Cardinirhynchia* Buckman, 1918
 Genus ?*Ivanoviella* Makridin, 1955
 Genus *Lotharingella* Laurin, 1984
 Genus *Mediterranirhynchia* Sucic-Protic, 1969
 Genus *Microrhynchia* Muir-Wood, 1952
 Genus *Rhynchonelloidea* Muir-Wood, 1936
 Genus *Sharpirhynchia*, new genus
 Genus *Thurmannella* Leidhold, 1921
- Subfamily TETRARHYNCHIINAE Ager, 1965
 Genus *Aalenirhynchia*, new genus
 Genus *Amydroptychus* Cooper, 1989
 Genus *Baeorhynchia* Cooper, 1989
 Genus *Burmiorhynchia* Buckman, 1918
 Subgenus *B.* (*Hopkinsirhynchia*), new subgenus
 Genus *Colpatoria* Cooper, 1989
 Genus *Conarosia* Cooper, 1989
 Genus *Cymatorhynchia* Buckman, 1918
 Genus *Daghanirhynchia* Muir-Wood, 1935
 Genus *Deltarhynchia* Cooper, 1989
 Genus *Druganirhynchia* Tchoumatchenko, 1983
 Genus *Echyrosia* Cooper, 1989
 Genus *Eurysites* Cooper, 1989
 Genus *Formosarhynchia* Seifert, 1963
 Genus *Gibbirhynchia* Buckman, 1918
 Genus *Goniorhynchia* Buckman, 1918
 Genus *Heteromychus* Cooper, 1989
 Genus *Isjuminella* Makridin, 1955
 Genus *Kallirhynchia* Buckman, 1918
 Genus *Kutchirhynchia* Buckman, 1918
- Genus *Lacunaerhynchia* Almeras, 1966
 Genus *Lirellarina* Cooper, 1989
 Genus *Mediterranirhynchia* Sucic-Protic, 1969
 Genus *Mosquella* Makridin, 1955
 Genus *Nastosia* Cooper, 1989
 Genus *Nyalamurhynchia* Ching, Sun, and Rong, 1976 (Subjective synonym of *Lacunaerhynchia* Almeras, 1966)
 Genus *Obsoletirhynchia*, Shi, 1992
 Genus *Praecyclothyrus* Makridin, 1955 (?Subjective synonym of *Somalirhynchia* Muir-Wood, 1935)
 Genus *Quadratirhynchia* Buckman, 1918
 Genus *Rhactorhynchia* Buckman, 1918
 Genus *Robustirhynchia* Seifert, 1963
 Genus *Rostrirhynchia* Sucic-Protic, 1969
 Genus *Russirhynchia* Buckman, 1918
 Genus *Sardorhynchia* Ruggiero and Ungaro, 1983 (Subjective synonym with *Isjuminella* Makridin, 1955)
 Genus *Schizoria* Cooper, 1989
 Genus *Septulirhynchia* Almeras, 1966 (Subjective synonym of *Lacunaerhynchia* Almeras, 1966)
 Genus *Somalirhynchia* Weir, 1925
 Genus *Sphenorhynchia* Buckman, 1918
 ?Genus *Strongyloria* Cooper, 1989
 Genus *Tetrarhynchia* Buckman, 1918
- Subfamily INDORHYNCHIINAE Ovtsharenko, 1975
 Genus *Indorhynchia* Ovtsharenko, 1975
 Genus *Moquellina* Jin, Sun, and Ye, 1979
 Genus *Tanggularella* Shi, 1990
- Subfamily CYCLOTHYRIDINAE Makridin, 1955
 Genus *Bicepsirhynchia* Shi, 1990
 Genus *Bilaminella* Babanova, 1964
 ?Genus *Blochmannella* Leidhold, 1921
 Genus *Curtirhynchia* Buckman, 1918
 Genus *Cyclothyrus* M'Coy, 1844
 Genus *Flabellirhynchia* Buckman, 1918
 Genus *Globirhynchia* Buckman, 1918
 Genus *Granulirhynchia* Buckman, 1918
 Genus *Oriensellina* Smirnova, 1986
 Genus *Pararhactorhynchia* Shi, 1990
 Genus *Pycnorhynchia* Cooper, 1989
 Genus *Septaliphoria* Leidhold, 1921
 Genus *Sulcirhynchia* Burri, 1953
 Genus *Torquirhynchia* Childs, 1969
 ?Genus *Trichorhynchia* Buckman, 1918
 ?Genus *Yunnshanella* Li and Gu, 1982
- Subfamily STRIIRHYNCHIINAE Kamyshan, 1968
 Genus *Capillirhynchia* Buckman, 1918
 Genus *Cubanirhynchia* Kamyshan, 1968
 Genus *Furcirhynchia* Buckman, 1918
 Genus *Lineirhynchia* Buckman, 1918
 ?Genus *Parvirhynchia* Buckman, 1918
 Genus *Rimirhynchia* Buckman, 1918
 Genus *Striirhynchia* Buckman, 1918
- Family ACANTHOTHYRIDIDAE Schuchert, 1913
 Subfamily ACANTHOTHYRIDINAE Schuchert, 1913
 Genus *Acanthothiris* d'Orbigny, 1850
 Genus *Acanthothyropsis* Kamyshan, 1973
- Subfamily ACANTHORHYNCHIINAE, new subfamily
 Genus *Acanthorhynchia* Buckman, 1918
 Genus *Echinirhynchia* Childs, 1969
 Genus *Paraacanthothyris* Kamyshan, 1973
- Family ERYMNARIIDAE Cooper, 1959
 Subfamily ERYMNARIINAE Cooper, 1959
 Genus *Erymnaria* Cooper, 1959

Subfamily CRYPTORHYNCHIIDAE, new subfamily

Genus *Aethirhynchia* Shi, 1990Genus *Crurirhynchia* Dagis, 1961Genus *Cryptorhynchia* Buckman, 1918?Genus *Sulcirostra* Muir-Wood and Cooper, 1951

Subfamily SEPTOCRURELLINAE Ager, Childs, and Pearson, 1972

Genus *Caucasella* Moisseev, 1934Genus *Gnathorhynchia* Buckman, 1918Genus *Omolonella* Moisseev, 1936Genus *Septocrurella* Wisniewska, 1932

Family SEPTIRHYNCHIIDAE Muir-Wood and Cooper, 1951

Genus *Septirhynchia* Muir-Wood, 1935

Comparison of the classification system above with that proposed by Ager, Childs, and Pearson (1972), reveals that many genera have been placed in different subfamilies. This is partly a result of the recent several years' study and partly a problem of different opinions. At the family level, the only major changes are the replacement of Pugnacidae Rzhonsnitskaya, 1956, by Basiliolidae Cooper, 1959, and raising the subfamily Acanthothyridinae Schuchert, 1913, to family rank. Four new subfamilies have been added because they are recognizable both in interior and exterior morphology and are clustered together both in the evolutionary lineage and in the chronology. Some genera have to be grouped on the basis of the exteriors and by comparison with closely related forms, because of the lack of adequate information on internal structures. The main characteristics of the families and subfamilies are summarized briefly as follows.

CHARACTERISTICS OF RHYNCHONELLID SUPRAGENERIC TAXA

Superfamily RHYNCHONELLACEA Gray, 1848

Rhynchonellida with impunctate shell; commonly lacking spondylia and camarophorium. Crura usually short, cardinal process commonly absent (except in Septirhynchiidae). Dorsal valve uniplicate instead of sulcate, deltidial plates present.

Family WELLERELLIDAE Likharev, 1956

Commonly uniplicate, costae usually strong. No cardinal process and septalium, hinge plates generally entire; dental plates and dorsal septum variously developed.

This family is represented in the Mesozoic only by the subfamily Cirpinae, which constitutes a very important rhynchonellid group in the Triassic and Early Jurassic.

Subfamily CIRPINAE Ager, 1965

Beak generally small and short, with well developed planoareas; deltidial plates usually thick and strengthened, foramen small. Costae strong, generally no smooth areas. Crura prefalcifer, hinge plates usually united or fused; septum reduced, septalium usually absent.

This subfamily is characterized internally by prefalcifer crura, fused hinge plates, and a reduced septum. The deltidial plates of some genera may be doubled and strengthened. This subfamily is close to the subfamily Lacunosellinae of the Basiliolidae, especially in having prefalcifer crura that have been regarded as a variety of falcifer crura. Externally it is also similar to that subfamily in having strong costae, a small beak, and no smooth stage. Some genera in this subfamily, such as *Pseudogibbirhynchia*, have well developed and distinct prefalcifer crura that are somewhat similar to falcifer crura and show a close relation to the subfamily Lacunosellinae. Clearly this is a matter of interpretation; the subfamily was placed in the Wellerellidae mainly because many of the genera have fused hinge plates, a condition that characterizes the Paleozoic Wellerellinae.

Prionorhynchia was put in this subfamily and was thought to be closely related to *Cirpa*. Externally the two are similar in having well developed planoareas and strong costae. However, the present study shows that internally *Prionorhynchia* has well separated hinge plates and simple deltidial plates.

Family BASILIOLIDAE Cooper, 1959

Smooth, semicostate or costae rhynchonellacean having conjunct deltidial plates and small auriculate foramen. Crura falcifer or its varieties; dorsal septum reduced into ridge or absent; no cardinal process.

This family was originally defined by Cooper (1959:15) for the Cenozoic rhynchonellids. Later it was shown that some Mesozoic forms are also closely related to them, especially the subfamily Lacunosellinae, which has the same crural character and very reduced septum. Ovtsharenko (1983) erected the family Pamirorhynchiidae, which included two new subfamilies, Pamirorhynchiinae and Dzhangirhynchiinae. He took it as a parallel family with Basiliolidae under the superfamily Basilioloidea Cooper, 1959 (there he treated Basiliolidae as a superfamily). To us, the subfamily Pamirorhynchiinae is not significantly different from the Lacunosellinae, while the subfamily Dzhangirhynchiinae can be juxtaposed with the latter. Whether the subfamily Lacunosellinae and the family Basiliolidae should be promoted respectively to family and superfamily rank is just a matter of interpretation. We treat the Basiliolidae as a family with three Jurassic subfamilies.

Subfamily DAVANIRHYNCHIIDAE Ovtsharenko, 1983

EMENDED DIAGNOSIS.—Small, semicostate anteriorly; long and distinct smooth areas present or with very fine, feeble capillae posteriorly. Crura subfalcifer to falcifer; septum reduced, no septalium.

This subfamily was established by Ovtsharenko to include only the genus *Davanirhynchia*, which was said to have spinulifer-radulifer crura, and was placed in the family Praecyclothyridiloidae Makridin, 1964 (although this family

now is regarded as the same as Rhynchonellidae Gray, 1848). After observing the serial sections of the genus (the only set of serial sections illustrated by Ovtsharenko, 1983:44, fig. 10, *Davanirhynchia davanienensis* Ovtsharenko), it became evident that the crura actually are subfalcifer, as that type is commonly understood. This genus is similar to *Almorhynchia* Ovtsharenko, 1983, but the latter has falcifer to subfalcifer crura and no capillae on posterior smooth areas. This subfamily, as emended above, differs from the Lacunosellinae in having subfalcifer to falcifer crura, small size, clearly developed smooth areas, and feeble semicostation anteriorly.

Subfamily DZHANGIRHYNCHIIINAE Ovtsharenko, 1983

EMENDED DIAGNOSIS.—Small to medium, multicostellate; fold low; smooth areas either very short or absent. Crura subfalcifer; dorsal septum either present or reduced into ridge, septalium generally not developed.

The subfamily Dzhangirhynchiinae was proposed by Ovtsharenko (1983) to include only the genus *Dzhangirhynchia*; here three more genera have been added to it. At that time, the subfamily was placed under the Family Pamirorhynchiidae Ovtsharenko, 1983. To us the family is basically the same as the Basiliolidae. The subfamily Dzhangirhynchiinae, as emended here, has essentially the characters of Basiliolidae and is easily distinguished from the other subfamilies of the family in having subfalcifer crura, clear septum, and fully developed multicostellae. This kind of crura is characteristically intermediate between the prefalcifer and falcifer types, and probably represents the median status of crural development from prefalcifer to falcifer. Chronologically, the prefalcifer crura mainly occurred in the Early Jurassic rhynchonellid Lacunosellinae (Cirpinae and the falcifer crura mainly occurred in the Late Jurassic rhynchonellids) although this would not necessarily mean that subfalcifer crura-bearing genera have close mutual affinities or that the crural development reflects the evolutionary trend at the moment.

This subfamily differs from the Lacunosellinae by its small size, fine and numerous costellae, as well as having subfalcifer crura and a dorsal septum or ridge. It differs from the Davanirhynchiinae in having no distinct posterior smooth areas.

Rahouiarhynchia Tchoumatchenko, 1987, was originally described as having falcifer or radulifer crura. According to the only set of serial sections illustrated by Tchoumatchenko (1987:55, text-fig. 6), however, the crura are apparently of the subfalcifer type. This kind of crura is similar to falcifer in appearance, but the crural bases of subfalcifer crura are differentiated much later in ontogeny than those of the falcifer. Subfalcifer crura started at the anterior parts or the distal edges of the dorsal side of the hinge plates, and are fairly long in the posterior-anterior dimension. The falcifer crura, in contrast, begin much earlier, at the very posterior parts of the hinge plates where the real, definite hinge plates have not yet been

differentiated. The subfalcifer crura also are similar to calcarifer, both of them having high, vertical plate-like ends. Generally the calcarifer crura are shorter (posterior-anterior direction) and curve strongly in toward the ventral valve; the narrow crural bases have hammer-like heads. These two kinds of crura differ in origin and mode of formation.

Ptyctorhynchia Buckman, 1918, has been transferred to this subfamily in this paper. This genus resembles *Dzhangirhynchia* externally, and has subfalcifer crura inside. However, it has a well developed dorsal septum and variable septalium internally, and has short external smooth areas. These characters are similar to those of the Rhynchonellidae, especially the Ivanoviellinae.

Subfamily LACUNOSELLINAE Smirnova, 1936

Usually medium to large, with well developed falcifer crura; septum reduced, generally no septalium; dental plates short. Shell fully costate without smooth areas; costae usually strong and few, with occasional bifurcation or intercalation.

Generally, this subfamily is easy to distinguish, both internally and externally. The most important characters are the falcifer crura and reduced septum. Most of the known genera have no septalium in dorsal valve, excepting only *Dichotomosella* Tchoumatchenko, 1987, which has very short septalium. Externally the genera *Pamirorhynchia* and *Aidynkulirhynchia*, have finer multicostae and are somewhat similar in appearance to the Tetrarhynchiinae.

Family RHYNCHONELLIDAE Gray, 1848

Crura radulifer or its varieties; dorsal septum and septalium variably developed; septum generally not very prominent in dorsal valve and absent in ventral valve. No cardinal process, crura comparatively short. Anterior commissure rectimarginate to uniplicate, shell semicostate or fully costate, without spines.

This family constitutes the major part of Rhynchonellacea in the Jurassic and is one of the best studied families. Most genera of the family have the typical appearance of rhynchonellids as accepted by most paleontologists and they are generally easy to separate from forms in other families. Internally this family has the typical characters of Rhynchonellacea, but all the structures may vary considerably. Externally this family also varies greatly, from being almost smooth to fully costate, costae from fine to fairly strong, and shell shape from depressed, almost equally biconvex, to globose or cynocephalous.

Subfamily RHYNCHONELLINAE Gray, 1848

Crura radulifer; septum and septalium generally well developed; dental plates variable, no prominent median septum present in ventral valve. Shell strongly inequivalve, often subcynocephalous to cynocephalous in profile, with sharp fold

and uniplication; smooth areas well developed posteriorly, with but strong ribs anteriorly.

This subfamily is relatively primitive in internal characters for the family. Generally, most of the genera have a well developed V-shaped septalium and higher, longer dorsal septum. As it will be seen, these characters become gradually obsolescent or reduced in the other later and more advanced subfamilies of Rhynchonellidae. This subfamily mainly flourished in the Triassic to early Middle Jurassic, although some genera extend into the Late Jurassic or even Early Cretaceous, but these never constituted the major stock of this family.

Subfamily PIARORHYNCHIIINAE, new subfamily

DIAGNOSIS.—Crura radulifer; dorsal septum and septalium generally well developed; no ventral septum, dental plates present. Shell generally small, nearly equivalve, moderately biconvex to subglobose; without sharp uniplication; smooth areas well developed posteriorly, with a few strong costae anteriorly.

This new subfamily was originally called the *Piarorhynchia* Branch by Ager, Childs, and Pearson (1972) and was put in the subfamily Tetrarhynchiinae. This group is in fact much closer to the Rhynchonellinae in affinity rather than to the Tetrarhynchiinae. Externally, most genera in this subfamily have a smaller shell, well developed posterior smooth areas, and few strong costae anteriorly, such as *Cuneirhynchia*, *Scalpellirhynchia*, *Bihendulirhynchia*, *Pseudomonticlarella*, *Tropiorhynchia*, and *Piarorhynchia*. Internally, most of the genera have a well developed septalium and dorsal septum, some with clear callus or secondary thickenings. These characters are similar to those in the Rhynchonellinae. It is separated from the latter mainly by its shape, the lower fold, and evenly recurved dorsal valve instead of strong fold and uniplication, as well as markedly everted dorsal valve and cynocephalous profile. The general outline and equivalved shell of the subfamily suggest the Tetrarhynchiinae. The later subfamily, however, generally has a fully costate shell and no posterior smooth areas. Interiorly, the Tetrarhynchiinae has less developed septum and variable septalium in dorsal valve.

Characteristically, the Piarorhynchiinae are relatively primitive in the family Rhynchonellidae, but in general they occur later than Rhynchonellinae and have not been found in the Late Jurassic.

Subfamily IVANOVIELLINAE Makridin, 1964

Crura calcarifer; septum and septalium variably developed. Shell small, with variable length posterior smooth areas and early sulcate stage in ontogeny; generally subcynocephalous to cynocephalous in profile, with well developed uniplication and numerous fine costellae anteriorly.

This is a compact subfamily among the Jurassic rhynchonellids and is easy to distinguish from the others by its small

shells, distinct posterior smooth areas, fine costellae, and internal calcarifer crura. In contrast to members of this subfamily, *Lotharingella* and *Microrhynchia* are not cynocephalous in profile, and *Sharpirhynchia* and *Makridinirhynchia* have no recognizable smooth areas, all others generally are subcynocephalous in side view and possess smooth areas on the valves.

Its history shows that from the Pliensbachian to the Oxfordian the subfamily developed a consistent increase toward the norelliform stage through time. The earlier forms, especially the Early Jurassic and the early Middle Jurassic ones, usually have very short smooth areas and hardly recognizable sulcation of the dorsal umbo. Most of the Middle Jurassic forms have short, but clear smooth areas on valves and recognizable sulcation. The late Middle Jurassic and the Late Jurassic forms have clearly shown smooth areas and are sulcate. When tracing the sediments in which these forms occur, it is found that the earlier forms, especially those of the Aalenian to Bajocian, occur more often in marls and other kinds of nearshore sediments, associated with other shallowwater benthic organisms. In contrast, the later Jurassic forms are more often found in micrites and lutites that are followed by black shales. This might indicate that the subfamily Ivanoviellinae had shifted its living habitat from nearshore shallow-water environments to deeper ones through time. This suggestion is supported by other evidence: the corresponding changes in uniplication, costation, and shell-wall thickness. The earlier genera usually have stronger costae, thicker shells, and less uniplicate anterior commissures, features that are usually thought to be more adaptive to nearshore environments (Ager, 1965b, 1967b; Fursich and Hurst, 1974; Rudwick, 1965b). Possibly the increases of the smooth areas and sulcation are at least partly related to ecological adaption as well as to phylogenetic development.

Ager, Childs, and Pearson (1972) considered the ivanoviellins a branch of the subfamily Rhynchonellinae, indicating that it has a close relationship with that group. It is true that the Ivanoviellinae share some similarities with the Rhynchonellinae, especially the genera *Makridinirhynchia* and *Rhynchonelloidella* of the Ivanoviellinae, which show external characters similar to *Rudirhynchia* and *Rhynchonelloidea* of the Rhynchonellinae. However, the differences are fairly distinct; most of the genera in the Ivanoviellinae have more and finer costellae, short smooth areas, and calcarifer crura. The Rhynchonellinae have radulifer crura and stronger costae. Possibly the subfamily evolved from one genus of Rhynchonellinae in the Early Jurassic and developed in different directions.

Cardinirhynchia was erected by Buckman (1918) with the Bajocian species *Terebratula acuticosta* Zieten, 1830, as type-species, which is characterized by having a long, nearly straight hinge line and somewhat extended cardinal extremities. Seifert (1963) revised this genus based on the interiors of its type-species. According to his study, most species of the genus

have calcarifer crura and a well developed dorsal septum, showing a close relation to Ivanoviellinae. On the other hand, Ager (1965a) placed this genus into Cyclothyridinae mainly based on its large foramen, strong costae, and other exterior characters. Makridin (1964:193, fig. 64a,b) illustrated two sets of serial sections of *Cardinirhynchia roissica* Makridin from the Lower Callovian of Russia. One of the sets (Makridin, 1964:193, fig. 64b) shows clearly calcarifer crura, while the another (fig. 64a) has the crura somewhat suggestive of those in the Bathonian genus *Cryptorhynchia* as revealed in this paper. Makridin (1964:192) was so impressed by the shell shape of *Cardinirhynchia* that he based the new family Cardinirhynchidae on this genus. This family, however, was rejected by Ager, Childs, and Pearson (1972) and the genus was kept in the Cyclothyridinae. Kamyshan and Babanova (1973:57, 103), on the other hand, prefer to take this group as the subfamily Cardinirhynchiinae under Rhynchonellidae. The serial sections of *Cardinirhynchia planifrons* (Quenstedt) illustrated by them also show clearly calcarifer crura. To the present authors, it seems that this genus is more closely related to Ivanoviellinae, especially to *Sharpirhynchia* in having a transverse shell with a relatively long hinge line and calcarifer crura. Externally, many species of the genus resemble *Rhynchonelloidella* in having an everted dorsal valve and strongly uniplicate shell with high tongue, giving it a subcynocephalous contour in side view. These species usually do not possess smooth areas on valves and no sulcation in dorsal umbones, showing a primitive character of Ivanoviellinae. Therefore, we prefer to place this genus in the Ivanoviellinae, rather than to take it as a separate subfamily.

Subfamily TETRARHYNCHIINAE Ager, 1965

Crura radulifer; septum commonly reduced, either very short or as a ridge; septalium variable, generally not well developed or short. Shell uniplicate, with moderately developed fold, and covered with numerous costae, without smooth areas; beak not strong, deltidial plates scarcely strengthened.

This subfamily is mainly composed of "ordinary looking" forms and constitutes the major stock of the Rhynchonellidae. It seems that many genera in this subfamily are capable of variation both internally and externally, and are easily confused with some genera of the Cyclothyridinae and Piarorhynchiinae. Ager (1965a) mentioned that the foramen is not rimmed in this subfamily, but this seems not to be true. Many genera in this subfamily, when well preserved, can be seen to have rims, such as in *Cymatorhynchia*, *Daghanirhynchia*, *Goniorhynchia*, *Kallirhynchia*, *Lacunaerhynchia*, and *Robustirhynchia*, although rims are not as prominent as in the Cyclothyridinae. *Kallirhynchia* and *Sphenorhynchia*, which were previously placed in the Cyclothyridinae, have been proved to belong in the Tetrarhynchiinae without much doubt, while *Rhactorhynchia* and *Obsoletirhynchia* are not easy to place confidently into either the Tetrarhynchiinae or Cyclothyridinae. These two

genera have external characteristics similar to Cyclothyridinae, especially in having well developed rims around foramina, conjunct and strengthened deltidial plates, as well as strong costae, and sometimes an asymmetrical anterior commissure. Nevertheless, they have been revealed to have radulifer crura and some other internal structures that are close to those in Tetrarhynchiinae. Here these two genera are placed in the Tetrarhynchiinae mainly on the basis of their interior characters, but we expect further research, especially the internal structures of their type-species, to test this arrangement.

Subfamily INDORHYNCHIINAE Ovtsharenko, 1975

EMENDED DIAGNOSIS.—Shell small to medium, fully multicostate; no norelliform stage, fold and sinus weak; costae not strong, occasionally dichotomous. Septum reduced, septalium generally absent, septalial plates present; septoidium may exist; crura basically calcarifer, with variations similar to canalifer and to arcuifer(?) crura.

This subfamily was created by Ovtsharenko (1975:123) in coordination with the subfamily Ivanoviellinae under the family Ivanoviellidae Makridin, 1964 (there Ovtsharenko promoted the subfamily to a family rank). The subfamily Indorhynchiinae was defined as: "medium-sized, often asymmetric shells, covered with frequent, more or less conspicuously dichotomizing costellae. Plicae are weakly expressed in relief on valves. Crura from calcarifer to nearly arcuifer" (Ovtsharenko, 1975:123). Beside the nominal genus *Indorhynchia*, Ovtsharenko also included *Kutchirhynchia* Buckman, 1918, but with doubt. However, the Pamirian specimens identified as *Kutchirhynchia kutchiensis* (Kitchin) by Ovtsharenko (1975), judging from his illustration and serial sections, are not the same as the Indian one, while similar to his genus *Indorhynchia* (Ovtsharenko, 1975) and *Tanggularella* erected by Shi (1990).

Ovtsharenko (1975) did not comment further on his new subfamily. In the comparison, he mentioned that the new subfamily is distinguished from the Ivanoviellinae primarily by the asymmetrical, faintly expressed plication, usually dichotomizing costae, and the less distinct calcarifer or nearly arcuifer crura. He did not make it clear if this subfamily has a norelliform stage. If these forms had a norelliform stage, then they should definitely be put in the subfamily Ivanoviellinae. According to the illustration and description of Ovtsharenko (1975), combined with a study on more than 1,000 specimens of eight species of the other two genera in this subfamily from the North Qinghai-Tibetan Plateau by Shi (1990) and Shi and Yang (1991), it has been proved that all of these forms have neither sulcation at the dorsal umbone nor posterior smooth areas on the valves. In more than 20 sectioned specimens of the eight species, though not as typical as those in *Rhynchonelloidella* and *Thurmannella*, the crura are basically of the calcarifer type, in which the secondary lamella of each crus is longer than the primary lamella and with a wide angle between them,

giving the crura a similar appearance to canalifer crura in transverse section. Arcuifer crura have not been observed in any of the sectioned specimens. Judging from the serial sections figured by Ovtsharenko (1975:125–129, fig. 1–5), the “arcuifer” crura might result from breakage to the crural ends or misunderstanding.

This subfamily, as emended here, differs from the Ivanoviellinae in having no norelliform stage, no strongly uniplicate shell, and no everted dorsal valve, but having feeble fold and sinus. Internally, this subfamily is characterized by having a reduced septum and crura that are not as unequivocal as those in Ivanoviellinae, although both of them are calcarifer. Externally, this subfamily resembles Cyclothyridinae in having no norelliform stage, while the latter often has a rimmed, larger foramen and stronger ribs. Internally, most of the genera in the subfamily Cyclothyridinae have canalifer crura, although they also have the septum reduced.

The Indorhynchiinae seem to reside morphologically between the Ivanoviellinae and the Cyclothyridinae, but are closer to the former.

Subfamily CYCLOTHYRIDINAE Makridin, 1955

Crura canalifer; septum usually reduced or short, septalium generally not well developed or absent, occasionally possessing septoidium. Shell multicostae, without smooth areas, costae commonly strong. Beak comparatively massive, with large and clearly rimmed foramen, deltidial plates well conjunct and often strengthened. Anterior commissure sometimes asymmetrical.

This subfamily is also very important among the Mesozoic rhynchonellids, especially from the Middle Jurassic to Cretaceous, and some members are not easy to distinguish definitely from the Tetrarhynchiinae. Although the canalifer crura have been regarded as one of the best criteria for this subfamily, several genera that have been put in this subfamily do have radulifer crura. It is difficult at this moment to give the subfamily a very strict definition or to put a rigid boundary between the two subfamilies. Nevertheless they are generally discernible and belong to the same family. Further detailed study of the internal structures may provide new insights to the topic, but there will still be a problem of how the researchers recognize the objective things.

Subfamily STRIRHYNCHIINAE Kamyshan, 1968

EMENDED DIAGNOSIS.—Crura radulifer; septum usually reduced and septalium generally absent. Shell with capillae posteriorly passing into short strong costae anteriorly or with dichotomizing fine capillae on the whole shell. Beak generally small and incurved, deltidial plates narrow.

This subfamily, called the *Rimirhynchia* Branch by Ager, Childs, and Pearson (1972), seems to have constituted a distinct and tightly knit group in the Mesozoic Rhynchonellidae

through the period of Late Triassic to Middle Jurassic. Unlike the Cyclothyridinae, in which this group was previously placed, all the genera of this subfamily, except *Parvirhynchia* Buckman, 1918, have characteristically fine capillae passing posteriorly into short strong costae anteriorly, or have dichotomizing capillae on the whole shell, as in *Strirhynchia* Buckman, 1918. These genera usually have a small, incurved beak, small foramen, and narrow deltidial plates with or without rims, except *Capillirhynchia* Buckman, 1918, in which the beak is strong, the foramen large, and the ribs clear. Internally they have radulifer instead of canalifer crura as in the Cyclothyridinae, although several genera have not yet been studied with proper attention to internal structures. *Parvirhynchia* is placed in the subfamily doubtfully. This genus has a few strong ribs on the shell, while the capillae are feeble. Instead of passing into strong costae anteriorly, the capillae are displayed on the ribs. This might indicate that this genus did not have the early stage in which the shell had no costae, but only fine capillae in its ontogeny. According to the research of Almeras and Lathuiliere (1984), the capillae on the shell of *Parvirhynchia* are not always present and constant, capillae on some specimens of the type-species *Parvirhynchia parvula* (Deslongchamps) are barely visible.

Maxillirhynchia Buckman, 1918, which was placed in the subfamily Monticlarellinae Childs, 1969, by Ager, Childs, and Pearson (1972), has the same external characters as those in the Strirhynchiinae, but its interiors are not properly known. Dagis (1965) recorded two species of the genus from the Triassic of Siberia that were revealed to have arcuifer crura. The type-species of the genus is from the Pliensbachian to Toarcian of England, which shows clearly an early sulcate stage in the ontogeny. For this reason, this genus was put in the superfamily Dimerellacea Buckman, 1918, previously. Dagis' species, however, does not coincide with the English species in character and seems not congeneric with the English species.

Family ACANTHOTHYRIDIDAE Schuchert, 1913, new status

DIAGNOSIS.—Spinose Mesozoic rhynchonellids; crura variable, usually radulifer crura or its varieties; cardinal process present or absent.

This family was erected by Schuchert (1913) as a subfamily; here it is elevated to family rank. Although only a few genera have been recorded in this group, all of them have peculiar spinose shells, making them so distinctive from other rhynchonellid groups that it would be unsatisfactory to place them in any other family. Ager (1965a) mentioned that this group is doubtful to be placed in the family Rhynchonellidae. Later, Ager, Childs, and Pearson (1972) further stated that as no rhynchonellid with any trace of spinosity is known from the Lower Jurassic, it is very difficult to suggest an ancestry for these distinctive forms. They thought, however, this group may have a close relation with the Cyclothyridinae of the family

Rhynchonellidae. Whether to keep this peculiar group as a subfamily under the Rhynchonellidae or to promote it to a family rank again is a matter of viewpoint, but the distinctiveness of the group is obvious. The species known in this group are quite peculiar; some have a cardinal process and no hinge plates in the dorsal valve, while some have no dental plates in the ventral valve. These features might indicate that this group is actually a specialized group in the Rhynchonellida. The present authors, therefore, prefer to treat it as a separate family.

The origin of the spines on the shell in this family is not known, but it can be certain that they are not the same as those in the Productidina. Unlike the spines in Productidina, which are hollow, the external spines of this family are all solid, showing that they are totally different from those of Productidina in the mode of forming. The function of the spines in this family has not been definitely ascertained. Buckman and Walker (1889) and Rudwick (1965a) suggested that they were possibly sensory, for warning, in contrast to the largely stabilizing function of spines in the Productidina (Grant, 1966, 1968).

This family can be divided naturally into two subfamilies on the basis of crural types, which seem to be the most reliable taxonomic criteria for subdivision of Mesozoic rhynchonellids.

Subfamily ACANTHOTHYRIDINAE Schuchert, 1913

EMENDED DIAGNOSIS.—Spinose rhynchonellids with radulifer crura, shell ornamented with coarse costae and fewer, but stronger spines. Dental plates and septum present; septalium generally present; no cardinal process; deltidial plates usually well developed; beak strongly incurved.

This subfamily is internally similar to the Rhynchonellidae, having all the normal internal structures. At present, the only genus that can be placed confidently in this subfamily is *Acanthothiris* d'Orbigny, 1850. *Acanthothyropsis* is externally similar to this genus, but its interior structures are closer to Acanthorhynchiinae. This subfamily differs from the following one mainly in having radulifer, instead of calcarifer crura. Externally this subfamily has fewer but stronger spines and costae.

Subfamily ACANTHORHYNCHIINAE, new subfamily

DIAGNOSIS.—Spinose rhynchonellids with calcarifer to subfalcifer(?) crura; shell covered with numerous costellae and delicate, fine spines. Dental plates and hinge plates variable, often reduced or absent; septalium and septum usually reduced or absent; cardinal process (?) may exist in some species.

This subfamily is peculiar in that the internal structures are all variable. Although the septum and septalium are generally reduced or absent, some species do have them. In most of the genera, the crura are calcarifer, but in a few species the crura are somewhat similar to prefalcifer or subfalcifer in appearance. The dental plates and hinge plates are absent in *Acanthorhyn-*

chia and *Echinirhynchia*, while present in *Acanthothyropsis* and *Paraacanthothyris*. According to the description of Childs (1969) the cardinal process may exist in some species of *Acanthorhynchia* and *Echinirhynchia*. These structures, however, are somewhat suspicious; they are not the same as the normal cardinal process in shape. Externally, *Acanthorhynchia* and *Echinirhynchia* are ornamented with fine costellae and numerous delicate spines, while in *Acanthothyropsis* and *Paraacanthothyris* the costellae and spines are fewer, as in *Acanthothiris*. Deltidial plates are reduced in this subfamily and the beak is straight to suberect.

Family ERYMNARIIDAE Cooper, 1959

Rhynchonellids having septifer crura, no cardinal process.

This family was erected by Cooper (1959:17, 64) based on his new genus *Erymnaria* of the Eocene. Although at that time Cooper included only the single genus in this family, he noted that rhynchonellids with septifer crura also occurred in the Mesozoic. He especially mentioned the Jurassic genus *Septocrurella* Wisniewska, 1932 (Cooper, 1959:64). Ager, Childs, and Pearson (1972) suggested that this family should also be extended to include the Mesozoic forms, and created the subfamily Septocrurellinae to include Triassic and Jurassic genera with septifer crura. Study of those Mesozoic forms leads us to conclude that these genera can be grouped into two subfamilies based on their internal structures, in addition to the Eocene subfamily Erymnariinae Cooper, 1959.

Subfamily ERYMNARIINAE Cooper, 1959

EMENDED DIAGNOSIS.—Cenozoic rhynchonellids having septifer crura; lateral septa well separated from the socket fulcral plates and sitting directly on dorsal floor. Shell smooth or irregularly costate around margins.

Only the Eocene genus, *Erymnaria* Cooper, 1959, has been recognized for the subfamily. Owing to the erection of two new subfamilies for the Mesozoic forms, it necessitates the recognition of the subfamily Erymnariinae for the original Tertiary members.

Subfamily CRYPTORHYNCHIINAE, new subfamily

DIAGNOSIS.—Mesozoic rhynchonellids having septifer crura; lateral septa totally or partly fused with socket fulcral plates. Shell small, with numerous fine costellae and no smooth areas.

Only 3 genera are now included in this subfamily. They generally have a clearly developed median septum in the dorsal valve and the lateral septa are fused with the socket fulcral plates. In *Cryptorhynchia* the lateral septa are totally fused with the fulcral plates, giving the impression that the crura arise directly from the socket fulcral plates. Lateral septa in the dorsal valve of *Crurirhynchia*, however, are only partly fused

with the fulcral plates, so that the lateral septa can still be recognized at anterior. The present authors agree with the suggestion by Ager, Childs, and Pearson (1972) that the subfamily Septocrurellinae originated from *Crurirhynchia* in the Triassic period, and developed through the Jurassic as a companion subfamily with the Cryptorhynchiinae.

Subfamily SEPTOCRURELLINAE Ager, Childs,
and Pearson, 1972

EMENDED DIAGNOSIS.—Mesozoic rhynchonellids having septifer crura; lateral septa in dorsal valve fully developed and separated from socket fulcral plates, meeting valve floor vertically. Shell small, either with a few strong ribs or partially costate.

Ager, Childs, and Pearson (1972) did not give a clear definition for this subfamily. They included four genera in this subfamily: *Caucasella*, *Crurirhynchia*, *Cryptorhynchia*, and *Septocrurella*. This study shows that *Cryptorhynchia* has a very different interior from *Septocrurella*. A new subfamily has been founded, therefore, based on this genus. Beside *Septocrurella* and *Caucasella* mentioned by Ager, Childs, and Pearson (1972), perhaps another two genera, *Gnathorhynchia* Buckman, 1918, and *Omolonella* Moisseev, 1936, also should be transferred into this subfamily. Both of them have long posterior smooth areas and septifer crura in the dorsal valves. These two genera were separately placed in the family Norellidae by Ager, 1959, and in the Rhynchonellidae Gray, 1848, by Ager, Childs, and Pearson (1972); their interiors are not yet very well known. The Late Triassic genus *Dierisma* Jin, Sun, and Ye, 1979, from Qinghai, China should also be placed in this subfamily; it has the same internal structures as *Septocrurella* Wisniewska, 1932.

Family SEPTIRHYNCHIIDAE Muir-Wood
and Cooper, 1951

Usually large, pentameroid in appearance; cardinal process in dorsal valve and prominent septum in ventral valve; crura radulifer to cilifer, dorsal septum fairly long.

Only one genus has been recorded for this family so far. *Septirhynchia* Muir-Wood, 1935, is distinctive both externally and internally. It is regarded as one of the characteristic Jurassic brachiopods of the Ethiopian Province in the Tethyan Realm (Muir-Wood and Cooper, 1951).

This genus has been recently studied and complemented by Mancenido and Walley (1979) and Feldman (1987). Mancenido and Walley suggested that this family should be lowered to the level of subfamily within the family Rhynchonellidae. According to them, the cardinal process and ventral septum often occurred in the adults of the genus, while in juvenile specimens the cardinal process and ventral septum may be absent. The crura are radulifer and curve strongly inward ventrally. On the other hand, Feldman (1987), based on

silicified specimens from the Callovian of Sinai, stated that the crura of the genus are of the cilifer type. In this paper, this group is maintained as a family.

The pentameroid shell-shape, thick shell-wall, and the strong secondary thickenings in posterior cavities as well as strong ribs and obsolescent foramen in the adults of *Septirhynchia* suggest that the individuals of the genus might have lived in a nearshore environment in shallow and rough water, and that they might have lain directly on the substrate as adults. The well developed and prominent ventral valve septum, rarely seen in Mesozoic rhynchonellids, may have served some function in this life habit.

Systematic Descriptions of Selected Rhynchonellid
Genera and Species

In all tables of measurements and meristics in this section, L = length of ventral valve (mm); W = width of shell (mm); T = thickness of shell (mm); A = apical angle in degrees; N = number of costae on each valve; F = number of costae on fold; S = number of costae in sulcus. Number refers to the specimen number, specimen repositories are, USNM = National Museum of Natural History, Smithsonian Institution; D, H, Y = collections from the Department of Geology, China University of Geosciences, Beijing.

On the serial sections, the numeral at the lower right of each section shows the distance (in mm) from the section to the anterior margin of the shell.

Superfamily RHYNCHONELLACEA Gray, 1848

Family WELLERELLIDAE Likharev, 1956

Subfamily CIRPINAE Ager, 1965

Prionorhynchia Buckman, 1918

Prionorhynchia Buckman, 1918:62.

TYPE-SPECIES.—*Terebratula serrata* Sowerby, 1825:168.

Prionorhynchia belemnica (Quenstedt, 1858),
new combination

FIGURE 14; PLATE 13: FIGURES 19–21, PLATE 16: FIGURES 8–10

Terebratula belemnica Quenstedt, 1858:73, pl. 8: fig. 15; 1871:43, pl. 37: figs. 33–36.

Rhynchonella belemnica (Quenstedt).—Haas and Petri, 1882:164, pl. 1: figs. 1–6, pl. 2: figs. 25–27 [not pl. 1: figs. 9, 10].—Rollier, 1918:83.

?*Squamirhynchia belemnica* (Quenstedt).—Buckman, 1918:64.—Muir-Wood, 1926:184.

Squamirhynchia belemnica (Quenstedt).—Ager, 1967:144–145.

TYPE.—*Lectotype*: Quenstedt, 1871, pl. 37: figs. 33–36; designated by Ager 1967:144; from the Lower Sinemurian of Germany.

MATERIAL STUDIED.—More than 50 well-preserved specimens from the Lower Lias of Germany and Switzerland.

EMENDED DIAGNOSIS.—Shell medium, subtrigonal, and slightly depressed; valves almost equal in convexity and depth; anterior commissure uniplicate, with short tongue. Beak short, suberect; no interareas, planareas well developed; deltidial plates conjunct, but not doubled. Shell with coarse subangular ribs. Dental plates short; septum reduced, no septalium; hinge plates nearly horizontal, well separated; crura prefalcifer.

AGE AND DISTRIBUTION.—Lower Lias; Germany and Switzerland.

DESCRIPTION.—Shell medium size, subtrigonal to subpentagonal in outline, slightly depressed and flattened; almost equally biconvex or dorsal valve slightly more convex than ventral one. Lateral commissure oblique ventrally; anterior commissure uniplicate; tongue lower and broad, rectangular in shape.

Beak short, substraight to suberect; foramen small, subcircular, hypothyriddid to mesothyriddid; deltidial plates conjunct, without rims; beak ridges blunt, interareas absent, planareas well developed and clearly shown.

Ventral valve moderately convex posteriorly and tending to be flattened anteriorly; sulcus variably developed, generally wide and well defined, with flat bottom, occurring at posterior third of valve and turning over towards dorsal valve at frontal margin more or less sharply, forming front flattened area.

Dorsal valve slightly more convex than ventral one, flattened anteriorly; fold lower and broad, occurring at posterior $\frac{1}{3}$ of valve and well separated from slopes.

Shell with few strong, subangular ribs on each valve, numbering 9–13, with 3–6 on fold and 2–5 in sulcus; no bifurcation and smooth areas; growth lines feeble, visible only at anterior margin.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 31055a	18.0	21.0	13.0	98	10	4	3
USNM 31055b	18.4	21.0	13.2	96	13	5	4
USNM 75857a	21.9	24.7	15.4	103	10	4	3
USNM 75857b	19.9	22.2	13.9	98	9	4	3
USNM 75857c	20.8	24.0	14.5	96	11	4	3
USNM 429114	19.5	22.1	12.0	91	12	6	5
USNM 429115	20.0	22.6	13.2	96	12	4	3
USNM 429116	23.5	25.4	15.2	103	12	4	3
USNM 429117	24.2	27.0	15.4	103	11	4	3
USNM 429118	21.0	24.0	14.8	104	11	4	3
USNM 429119	21.4	21.2	13.7	90	10	4	3

INTERIOR.—No secondary thickenings present in either valve. No pedicle collar; dental plates very short, arising from ventral floor far from hinge zone; deltidial plates conjunct, but not doubled and strengthened; delthyrium wide; lateral cavities short; teeth short, nodular-shaped, held tightly in sockets.

Dorsal septum reduced into ridge, running about $\frac{1}{4}$ of valve

length; septalium absent, septalial plates short; hinge plates broad, well separated and slightly inclined ventrally; inner socket ridges low, but well demarcated from hinge plates; crural bases poorly formed, rising from inner margins of hinge plates and close to each other; crura prefalcifer, about $\frac{1}{4}$ as long as dorsal valve and only slightly incurved ventrally, without any specialized distal ends.

REMARKS.—This is a poorly known species both in interiors and exteriors. Externally it is close to *Cirpa*, especially in having well developed planareas and lateral and frontal flattened areas. However, its interiors are quite different from those in *Cirpa*, which has doubled deltidial plates and united hinge plates. The species is also similar to some species of *Squamirhynchia* into which Buckman (1918) placed this species with doubt. Ager (1967) thought that this species might be synonymous with *Squamirhynchia squamiplex* (Quenstedt), the type-species of the genus. The present study, however, shows that this species is quite different from that type-species internally and they can not even be put in the same genus. *Squamirhynchia squamiplex*, according to the serial sections illustrated by Ager (1967:143, text-fig. 90), has doubled deltidial plates and fused hinge plates anteriorly, as well as strongly incurved crura with specialized distal ends. Externally, *Squamirhynchia* has no planareas and its costae show early branching.

Prionorhynchia serrata (Sowerby) shares the same interior structures with the present species; both of them have reduced dorsal septum, no septalium, no doubled deltidial plates, and no united hinge plates. Externally, these two species all have well developed planareas, short beak, strong ribs, and slightly depressed shell. Therefore, it is more suitable to transfer this species into *Prionorhynchia* rather than to keep it in *Squamirhynchia*. Although this species shares superficial similarity with *Mediterranirhynchia* Sucic-Protic, 1969, in some aspects, the latter has well developed and widely V-shaped septalium, as well as a high septum in the dorsal valve (Sucic-Protic, 1969:53–56, pl. 36).

Family BASILIOLIDAE Cooper, 1959

Subfamily DZHANGIRHYNCHIIINAE Ovtsharenko, 1983

Bradfordirhynchia, new genus

Cryptorhynchia Buckman, 1918:66 [in part].

TYPE-SPECIES.—*Cryptorhynchia bradfordensis* Buckman, 1918:228.

DIAGNOSIS.—Shell small, subtrigonal to transverse; gently biconvex to feebly subcyncephalous. Beak suberect, foramen hypothyriddid; deltidial plates conjunct, with clear rims around foramen. Shell covered with numerous costae and fine elegant growth lines; fold and sinus variable. Septum reduced, septalium short or absent, crural bases well formed and long; crura subfalcifer.

FIGURE 14.—Serial sections of *Prionorhynchia belemnitica* (Quenstedt); topotype, USNM 75857b, L 19.9, W 22.2, T 13.9, A 98; from the Lower Lias, Hirschberg, Hindelang, Germany.

AGE AND DISTRIBUTION.—Upper Bathonian; England and France.

REMARKS.—The new genus is externally similar to *Cryptorhynchia*, to which the type-species was previously referred, in having well developed fine growth lines and the same general shell shape. However, the present study shows that their interiors are quite different. *Cryptorhynchia pulcherrima* (Kitchin), type-species of the genus, has septifer crura and conspicuous growth lines, that may become lamellae. These may cross the costae to produce a reticulate ornament. Some are strong enough to appear spine-like at their intersections. *Rahouiarhynchia* Tchoumatchenko, 1987, resembles the new genus in having the same kind of crura, but differs from the new genus in having no dorsal septum and its related structures. Exteriously it has a very short, obtuse beak and almost equally biconvex subglobose shell. *Dzhangirhynchia* Ovtsharenko, 1983, is close to the new genus externally, but internally it also lacks a dorsal septum and the related structures. Furthermore, the crural bases in *Dzhangirhynchia* are differentiated much earlier in ontogeny than in the new genus.

***Bradfordirhynchia bradfordensis* (Buckman, 1918),
new combination**

FIGURE 15; PLATE 2: FIGURES 1–4, PLATE 16: FIGURES 1, 2, 17, 18

Cryptorhynchia avonensis Buckman, 1918:228, pl. 19: fig. 6.

Cryptorhynchia bradfordensis Buckman, 1918:228, pl. 19: figs. 4, 5.

Cryptorhynchia vauhani Buckman, 1918:228, pl. 19: fig. 7.

"*Rhynchonella*" *bradfordensis bradfordensis* (Buckman).—Laurin, 1984a:404, pl. 3: fig. 18.

"*Rhynchonella*" *bradfordensis ecardensis* Laurin, 1984a:404, pl. 3: fig. 14, ?fig. 15 [in part].

TYPE.—*Holotype*: Buckman, 1918, pl. 19: fig. 4; from the Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England.

MATERIAL STUDIED.—10 well-preserved specimens from the Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire and 1 from Langton, Dorset, England; 3 from Upper Bathonian, Ranville, France.

DIAGNOSIS.—Shell small, subtrigonal, and depressed; anterior commissure rectimarginate to low uniplicate. Shell covered with 14–18 subangular ribs. Septum reduced to long low ridge; crura subfalcifer, relatively narrow.

AGE AND DISTRIBUTION.—Late Bathonian; England and France.

DESCRIPTION.—Shell small, depressed; subtrigonal to slightly flabelliform in outline; gently biconvex, with dorsal valve slightly more convex than ventral one. Lateral commissure sloping ventrally; anterior commissure rectimarginate to lower uniplicate; with short and broadly arched tongue.

Beak relatively long, substraight to suberect, with wide basis; foramen small, suboval, hypothyridid, slightly rimmed; deltidial plates wide, conjunct; beak ridges subangular, short;

well defined interareas narrow and slightly concave, with fine transverse growth lines.

Ventral valve moderately convex at posterior, tending to be flattened anteriorly; sinus developed variably, generally broad and shallow, occurring at anterior half to third of valve, distinctly bounded.

Dorsal valve slightly more convex than ventral one, with greatest convexity at anterior part; fold lower, only slightly raised over flanks at anterior part.

Shell bearing coarse subangular costae, separated by wider and deeper intertroughs, on each valve numbering 14–18, with 3–5 on fold and 2–4 in sinus; growth lines well developed, dense, regular.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 104765a	13	14.2	9	94	18	5	4
USNM 104765b	11.6	13.6	6.8	96	15	3	2
USNM 104765c	11.2	12.4	8.8	95	16	4	3
USNM 104765d	11.6	11.7	7.7	87	16	4	3
USNM 429127	13.8	15.7	7.9	101	19	6	5
USNM 429128	13.9	15.4	8.5	91	17	–	
USNM 429129	14.1	14.9	8.7	84	18	–	
USNM 429130	12.0	14.0	7.5	100	17	4	3
USNM 429131	12.4	14.1	8.0	101	16	3	2
USNM 429132	11.8	13.0	7.4	93	16	3	2
USNM 429133	11.7	13.2	7.5	94	16	4	3
USNM 429134	11.0	12.0	7.3	96	14	4	3

INTERIOR.—Shell comparatively thick; no secondary thickenings in either valve. No pedicle collar observed in sectioned specimens; deltidial plates conjunct; delthyrium wide and well developed; lateral cavities short and narrow; dental plates reaching hinge zone, diverging slightly toward ventral floor; teeth short, mallet-like, with expanded ends and crenulations; accessory dental cavities and denticulars present.

Dorsal septalium short, narrow, incomplete; septum reduced into a stout ridge running about a third of valve length; hinge plates narrow and thick, strongly tapering anteriorly; subhorizontal posteriorly and becoming inclined ventrally forward; inner socket ridges low, but well differentiated. Crural bases blade-like, given off dorsally from inner margins of hinge plates and fairly long; crura subfalcifer, about $\frac{1}{3}$ as long as dorsal valve, protruding forward almost along commissure plane, relatively narrow (dorsal–ventral direction) and shaped like reverse parentheses in transverse section.

REMARKS.—This species was hitherto not known internally. Buckman (1918) erected three new species, which were all from the same locality and horizon, and put them in *Cryptorhynchia*. These species differ only slightly in shape. It seems better to regard them as variation in a population. Laurin (1984a) split this species into two subspecies, "*Rhynchonella*" *bradfordensis bradfordensis* (Buckman) from England and "*Rhynchonella*" *bradfordensis ecardensis* Laurin from France.

FIGURE 15.—Serial sections of *Bradfordirhynchia bradfordensis* (Buckman); topotype, USNM 104765d, L 11.6, W 11.7, T 7.7, A 87; from the Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England.

The present study shows that the two subspecies differ both externally and internally, constituting separate species.

***Bradfordirhynchia ecardensis* (Laurin, 1984),
new status**

FIGURES 16–19; PLATE 2: FIGURES 5–14

"*Rhynchonella*" *bradfordensis ecardensis* Laurin, 1984a:404, text-figs. 174–178, pl. 3: figs. 11–13, 16, 17 [in part, not 14, 15].

TYPE.—*Holotype*: Laurin, 1984a: pl. 3: fig. 11? [not

designated in figure]; from the Upper Bathonian, Amfreville, Calvados, France.

MATERIAL STUDIED.—62 well-preserved specimens from the Upper Bathonian, Ranville and Amfreville, Calvados, France.

DESCRIPTION.—Shell small to medium, subtrigonal to subpentagonal in outline, with shell wider than long; shell unequally biconvex, dorsal valve much more convex than ventral one and adequately everted anteriorly, making shell more or less subcynocephalous in profile. Lateral commissure oblique ventrally at about 15 to 25 degrees; anterior commis-

FIGURE 16.—Serial sections of *Bradfordirhynchia ecardensis* (Laurin); Morphotype I, USNM 429141, L 14.8, W 17.4, T 9.6, A 108; (Upper Bathonian) Langueville, Calvados, France.

sure well uniplicate; tongue long, highly arched or subtrapezoidal in shape.

Beak usually short, acute, suberect; foramen subcircular, auriculate, hypothyridid; deltidial plates conjunct; beak ridges subangular; interareas narrow and slightly concave, with fine transverse growth lines.

Ventral valve moderately convex posteriorly and tending to

be flattened anteriorly; sinus broad and deep, with rounded bottom, occurring at posterior $\frac{1}{3}$ to $\frac{1}{2}$ of valve, distinct from flanks.

Dorsal valve moderately convex at umbonal region and slightly everted anteriorly; fold well developed, elevated above flanks at anterior and with clear borders from slopes.

Ribs coarse and subangular, separated by narrower intervals;

FIGURE 17.—Serial sections of *Bradfordirhynchia ecardensis* (Laurin); Morphotype I, USNM 429145, L 14.7, W 17.2, T 12.1, A 102; (Upper Bathonian) Langueville, Calvados, France.

on each valve numbering 16–21, with 4–6 on fold and 3–5 in sinus; growth lines fine and regularly spayed, becoming more obvious or even feebly imbricated near anterior margin. At gerontic stage, frontal margin thickened and bearing concentric lamellae.

INTERIOR.—Shell thick, no noticeable secondary thickenings in either valve. No pedicle collar observed in sectioned specimens; deltidial plates well conjunct and crumpled inside; delthyrium wide, trapezoidal in shape, lateral cavities narrow and short; dental plates just arriving at hinge zone, subparallel or slightly divergent to ventral floor; teeth short, massive, mallet-like, with expanded ends and crenulations; accessory dental cavities and denticulars present.

Septum reduced to ridge in dorsal valve, running about $\frac{1}{3}$ to $\frac{1}{2}$ of valve length; narrow, deep, and incomplete short

septalium either present or absent (among the four sectioned specimens, two have the septalium short and incomplete, one has no septalium at all, and the other has a narrow and short V-shaped septalium that is only about 0.4 mm long); hinge plates wider than in *B. bradfordensis*, almost horizontal or slightly inclined ventrally only at distal parts and tapering forward; inner socket ridge low, but well demarcated from hinge plates; crural bases well formed, given off dorsally from inner margins of hinge plates at anterior parts, relatively short; crura subfalcifer, much wider than in *B. bradfordensis* (ventral-dorsal direction), about $\frac{1}{3}$ as long as dorsal valve, diverging forward widely and reverse parentheses-shaped or vertical plate-like in sections.

REMARKS.—This species was originally considered by Laurin (1984a) a geographic subspecies of “*Rhynchonella*”

FIGURE 18.—Serial sections of *Bradfordirhynchia ecardensis* (Laurin); Morphotype II, USNM 429135, L 18.0, W 18.2, T 14.5, A 90; (Upper Bathonian) Langueville, Calvados, France.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 30908	15.2	17.0	10.4	97	19	5	4
USNM 30965a	14.3	14.7	9.0	92	18	5	4
USNM 30965b	13.5	14.2	9.5	91	19	5	4
USNM 92005a	14.2	15.5	9.3	96	16	4	3
USNM 104682a	17.4	19.0	10.7	103	22	6	5
USNM 104682b	17.3	18.0	11.1	95	19	6	5
USNM 104682c	16.3	17.7	10.2	99	18	5	4
USNM 104687a	16.4	16.4	13.7	88	20	5	4
USNM 104687b	16.1	16.9	13.5	97	21	4	3
USNM 429135	18.0	18.2	14.5	90	18	4	3
USNM 429136	17.4	19.0	15.5	90	16	4	5
USNM 429137	15.3	16.0	15.7	90	19	5	4
USNM 429138	14.6	17.3	9.5	103	19	5	4
USNM 429139	15.9	17.8	11.8	99	20	6	5
USNM 429140	16.5	18.1	9.7	97	20	5	4
USNM 429142	17.9	20.3	11.7	108	22	5	4
USNM 429143	17.5	18.4	11.9	101	18	6	5
USNM 429144	17.3	20.5	13.5	102	19	4	3

bradfordensis, but here it is regarded as a separate species. It differs from *B. bradfordensis* (Buckman) in having a much more convex and everted dorsal valve, more elevated fold, deeper and broader sinus, stronger ribs, strongly uniplicate anterior commissure with high tongue, as well as much more conspicuous concentric lines that become imbricated at anterior and have clearly thickened margins at gerontic stage. Interiorly, *B. ecardensis* has wider crura (ventral–dorsal direction) and broader hinge plates as well as shorter crural bases.

Ptyctorhynchia Buckman, 1918

Ptyctorhynchia Buckman, 1918:47.—Ager, 1965a:H618.

TYPE-SPECIES.—*Rhynchonella pentaptycha* Buckman, 1910:103.

DIAGNOSIS.—Shell small, subglobose, and uniplicate, with low and wide fold; costae few, relatively strong; beak small,

FIGURE 19.—Serial sections of *Bradfordirhynchia ecardensis* (Laurin); Morphotype II, USNM 104687c, L 17.0, W 17.4, T 11.7, A 93; (Upper Bathonian) Ranville, Calvados, France.

suberect; foramen hypothyridid and slightly rimmed. Septum well developed; septalium present or absent; crura subfalcifer.

AGE AND DISTRIBUTION.—Aalenian to Bajocian(?); England and China.

REMARKS.—This genus is poorly known. Since it was established by Buckman (1918), no further description has been made, and its interiors have remained unknown. The present research shows that the genus has a well developed septum and subfalcifer crura. The English specimen has a wide and well developed V-shaped septalium while many of the Chinese specimens have no septalium.

Ager (1965a) put the genus into the subfamily Cyclothyridinae Makridin, 1955, largely on the basis of its few and strong costae and its rimmed foramen. Ager, Childs, and Pearson (1972) transferred it to the subfamily Tetrarhynchiinae Ager, 1965, under the *Piarorhynchia* branch, without further comment. The present study shows that this genus is close to

Dzhangirhynchia internally and undoubtedly needs transfer to the subfamily Dzhangirhynchiinae.

***Ptyctorhynchia pentaptycha* (Buckman, 1910)**

FIGURES 20, 21; PLATE 1: FIGURES 1–3

Rhynchonella pentaptycha Buckman, 1910:103, pl. 12: figs. 19, 20.

Ptyctorhynchia pentaptycha (Buckman).—Buckman, 1918:47, pl. 18: figs. 17–19.

TYPE.—*Holotype*: Buckman, 1910, pl. 12: figs. 19, 20; from the Aalenian, Chideock Quarry Hill, Dorset, England.

MATERIAL STUDIED.—4 specimens from the Inferior Oolite (lower part, Aalenian), Chideock Quarry Hill and 3 from the Lower Inferior Oolite, Bridport, Dorset, England; 9 specimens from the Aalenian or Lower Bajocian of North Tibet, China.

DESCRIPTION.—Shell small, subcircular in outline, subglobose to globose in profile; almost equally biconvex or dorsal

FIGURE 20.—Serial sections of *Ptyctorhynchia pentaptycha* (Buckman); topotype, USNM 429120, L 11.9, W 10.8, T 8.1, A 87, from the Lower Inferior Oolite (Aalenian), Chideock Quarry Hill, Dorset, England.

valve slightly more convex than ventral one. Lateral commissure oblique ventrally at about 20 degrees; anterior commissure broadly uniplicate; with wide and low tongue.

Beak short, suberect; foramen small, subcircular, hypothyridid, with slight rims; deltidial plates low, disjunct; beak ridges subangular, defining narrow, slightly concave interareas.

Ventral valve convex evenly; sinus very shallow or only existing as wide depression along middle portion at anterior half of valve.

Dorsal valve gibbous at umbonal region and tending to be flattened anteriorly; fold wide and low, only slightly above slopes at anterior.

Costae coarse, round crested, becoming stronger anteriorly, separated by narrower intervals; on each valve numbering 12-17, with 5-6 on fold and 4-6 in sinus; growth lines fine but clear; smooth areas generally very short, absent in some specimens.

INTERIOR.—No secondary thickenings present in either valve. Pedicle collar and deltidial plates not seen in sectioned specimens; delthyrium wide, trapezoidal in shape; lateral

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 429120	11.9	10.8	8.1	87	17	6	5
USNM 429121	11.7	11.2	8.2	91	15	6	6
USNM 429122	11.2	10.5	9.1	98	13	6	5
USNM 429123	10.6	10.4	8.2	97	17	7	6
USNM 429124	11.3	11.4	9.0	97	19	8	7
USNM 429125	11.3	10.7	8.2	96	16	6	5
USNM 429126	10.0	9.9	7.5	98	11	4	3
D 123491	13.3	12.0	9.0	82	11	4	3
D 123492	13.4	12.3	9.1	80	13	5	4
D 123493	14.7	13.2	9.5	86	14	5	4
D 123494	13.2	12.1	9.0	76	12	4	3
D 123499	12.1	11.0	8.7	78	11	4	3

cavities short, semicircular; dental plates short, divergent to ventral floor in umbonal cavity, becoming parallel anteriorly and raising from ventral floor before reaching hinge zone; teeth short, mallet-like, with expanded ends and crenulations.

Dorsal septum high and delicate, supporting wide and V-shaped septalium at posterior part, running about 1/3 of

FIGURE 21.—Serial sections of *Ptyctorhynchia* aff. *pentaptycha* (Buckman); D123494, L 13.2, W 12.1, T 9.0, A 76; from the lower part of the Sewa Formation (Aalenian to Lower Bajocian), Dogai Coring, North Tibet, China.

ventral valve length; hinge plates broad, declined dorsally at posterior part and becoming horizontal anteriorly; crural bases well formed, given off dorsally from inner margins of hinge plates; crura subfalcifer, about $\frac{1}{4}$ as long as dorsal valve, only slightly incurved ventrally, appearing as vertical plate in section.

REMARKS.—This is the only species so far recorded in the genus. Closely related forms have recently been found in Tibet by Shi. The Chinese specimens are coincident with the English ones externally, except that they are narrower in shape and less strongly uniplicate, with shorter smooth areas. Among three sectioned Chinese specimens, two have no septalium and the third has a very short one. The septum in each of the three specimens is slightly lower. The septalium proves to be a variable structure in some rhynchonellids, as will be seen in the following several genera, so we do not regard it as a valuable criterion for the recognition of genera.

Family RHYNCHONELLIDAE Gray, 1848

Subfamily RHYNCHONELLINAE Gray, 1848

Costirhynchia Buckman, 1918

Costirhynchia Buckman, 1918:39.—Ager, 1965a:H610.—Ovtsharenko, 1983:13.

TYPE-SPECIES.—*Costirhynchia costigera* Buckman, 1918:39.

DIAGNOSIS.—Shell small, globose, and coarsely ribbed; beak very short, suberect to incurved; fold and sinus well developed; with a few ribs starting near umbo, short smooth regions present. Shell thick, septum high and long, hinge plates narrow and poorly differentiated; crura radulifer; dental plates short; a very short and lower septal ridge may exist in ventral valve.

AGE AND DISTRIBUTION.—Aalenian to Early Bajocian; England and Pamirs (USSR).

REMARKS.—This genus has not been properly studied yet. So far, only three species have been recognized for the genus, and their distributions, both spatial and temporal, are not quite clear. No investigations of the internal structures of the two English species have been made previously. The Russian species, *Costirhynchia martiros* Ovtsharenko (Ovtsharenko, 1983:13, text-fig. 3, pl. 1: fig. 4–8) from the Bajocian of Pamirs, is close to *C. costigera* Buckman externally, but internally it has well formed crural bases and a reduced septum, so is not quite coincident with those in the type-species revealed herein. The foregoing completed diagnosis of the genus is, therefore, mainly based on the type-species.

Costirhynchia costigera Buckman, 1918

FIGURE 22; PLATE 1: FIGURES 4–6

Rhynchonella subdecorata Davidson.—Davidson, 1851–1852, appendix:21, pl. A: figs. 24, 26 [only].

Costirhynchia costigera Buckman, 1918:39, pl. 18: fig. 20.

TYPE.—*Holotype*: Buckman, 1918, pl. 18: fig. 20; from the Inferior Oolite (Pea Grit, Aalenian), Crickley Hill, Gloucestershire, England.

MATERIAL STUDIED.—10 specimens from the Inferior Oolite (Pea Grit, Aalenian), with 4 from Crickley Hill and 6 from Leckhampton Hill, Gloucestershire, England.

DESCRIPTION.—Shell small, globose; oval to subtrigonal in outline; unequally biconvex, dorsal valve much more convex than ventral one. Lateral commissure deflected ventrally; anterior commissure uniplicate, with narrow and high linguiform extension.

Beak short and small, suberect to incurved, almost contacting dorsal umbone; foramen very small or minute, pin-hole to slit-like, hypothyriddid to submesothyriddid; deltidial plates small and narrow, disjunct to just conjunct; beak ridges obtuse; interareas not developed.

Ventral valve moderately convex; sinus deep and narrow, occurring at posterior $\frac{1}{3}$ of valve and turning over toward dorsal valve more or less sharply at anterior margin.

Dorsal valve highly convex, highest convexity at anterior $\frac{1}{3}$ of valve, but reverted anteriorly; fold narrow, occurring at anterior third of valve and well elevated above slopes.

Ribs few, strong, subangular, starting near umbonal regions thus leaving very short smooth region on each valve; each valve with 10–13 ribs, 2 or 3 on fold and 1 or 2 in sinus; growth lines feeble and fine.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 88709a	12.6	12.4	10.3	96	11	2	1
USNM 88709b	11.0	10.6	8.7	93	15	3	2
USNM 88709c	11.1	9.6	8.7	88	12	2	1
USNM 88709d	10.4	10.3	8.9	95	10	2	1
USNM 123711a	10.6	10.3	10.5	98	9	2	1
USNM 123711b	11.2	8.9	9.3	85	10	2	1
USNM 123711c	9.9	8.9	8.8	93	11	2	1
USNM 123711d	9.7	8.8	7.3	91	11	3	2

INTERIOR.—Shell thick, secondary thickenings present in apical cavity of each valve. Delthyrium narrow and high; lateral cavities very small and short; dental plates short, convergent to ventral floor; teeth stout, nodular-shaped, with expanded ends and crenulations; short and low septum present in ventral valve.

Dorsal septum strong, high and fairly long; septalium absent; septalial plates very short; hinge plates not well differentiated, very narrow and thick; no clearly demarcated inner socket ridges; crural bases poorly formed; crura radulifer, about $\frac{1}{4}$ as long as dorsal valve, rising from inner margins of hinge plates, slightly divergent forward and incurved ventrally.

Rhynchonelloidea Buckman, 1918

Rhynchonelloidea Buckman, 1918:38.

FIGURE 22.—Serial sections of *Costirhynchia costigera* Buckman; topotype, USNM 88709e, L 10.5, W 10.3, T 8.9, A 95; from the Inferior Oolite (Pea Grit, Aalenian), Crickley Hill, Cheltenham, Gloucestershire, England.

TYPE-SPECIES.—*Rhynchonella ruthenensis* Reynes, 1868:107.

REMARKS.—This is an important genus in the early Middle Jurassic. Its type-species *Rhynchonelloidea ruthenensis* (Reynes) has been studied internally by Muir-Wood (1936) and Almeras (1979a, b). However, this species is far less known than *Rhynchonelloidea subangulata* (Davidson). Ager (1965a) put this genus into the subfamily Rhynchonellinae. Later he (Ager, Childs, and Pearson, 1972) transferred it into the subfamily Ivanoviellinae because of its similarity to the genus *Rhynchonelloidella* Muir-Wood. Ager, Childs, and Pearson (1972) thought that these two genera were closely related in affinity and *Rhynchonelloidella* might have originated from this genus. Indeed, *Rhynchonelloidea* resembles that genus closely in exterior aspect, but they are quite different internally, especially by having different types of crura. This might indicate that they actually had originated from different lineages and evolved in different directions.

***Rhynchonelloidea angulata* (Sowerby, 1825),
new combination**

FIGURE 23; PLATE 1: FIGURES 13–17

Terebratula angulata Sowerby, 1825:166, Tab. 502: fig. 4.—Davidson, 1851–1852:92, pl. 17: fig. 13; 1878:207.

Kallirhynchia angulata (Sowerby).—Buckman, 1918:32.

Rhynchonella angulata (Sowerby).—Röhlér, 1918:156.—Almeras, 1964:53.

TYPE.—*Holotype*: Sowerby, 1825, Tab. 502: fig. 4; refigured by Davidson, 1851–1852, pl. 17: fig. 13; from the Inferior Oolite (lower part, Aalenian), Cleeve Hill, Cheltenham, Gloucestershire, England.

MATERIAL STUDIED.—33 well-preserved specimens from the Inferior Oolite (Pea Grit, Aalenian), Crickley Hill, Cheltenham, Gloucestershire, England.

DESCRIPTION.—Shell small to medium, transversely subpentagonal to elliptical in outline and subglobose in profile; valves almost equal in convexity and depth or dorsal valve slightly more convex than ventral one. Lateral commissure moderately oblique toward ventral side; anterior commissure widely uniplicate; linguiform extension low to medium in height, trapezoidal in shape.

Beak short, pointed to suberect, with broad base; foramen small, subcircular, hypothyriddid, with slight rims; deltidial plates short, disjunct to just conjunct; beak ridges subangular; interareas small, generally not developed.

Ventral valve moderately convex; sinus well developed, broad and moderately deep, with rounded bottom, beginning at posterior third of valve.

Dorsal valve slightly more convex than ventral one, with maximum convexity at anterior, but never everted anteriorly,

shell subglobose in profile; fold broad and low, starting at anterior third and elevated well above flanks.

Costae numerous, coarse, subangular, on each valve numbering 18–22, with 4–6 on fold and 3–5 in sinus; no distinct smooth areas recognizable; growth lines fine, becoming conspicuous or even feebly lamellose at anterior margin.

INTERIOR.—Slight secondary thickenings present only in apical cavities. Pedicle collar not seen; delthyrium wide; lateral cavities small; dental plates short, slightly divergent to ventral floor; teeth short, massive, with expanded ends and crenulations; accessory dental cavities and denticulars present.

Dorsal septum strong but short, reduced into ridge forward; septalium absent; septalial plates short, pendant; hinge plates

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 104764a	14.1	20.7	12.5	125	23	6	5
USNM 429155	16.8	19.1	11.3	107	21	5	4
USNM 429156	15.5	18.3	11.2	106	20	5	4
USNM 429157	14.7	17.6	11.1	116	20	5	4
USNM 429158	16.2	19.0	9.8	98	19	6	5
USNM 429159	15.3	17.7	9.9	105	21	5	4
USNM 429160	14.4	16.5	10.4	100	18	4	3
USNM 429161	15.2	18.0	10.0	102	16	4	3
USNM 429162	16.0	21.3	13.1	112	20	6	5
USNM 429163	15.6	19.2	12.2	110	18	5	4
USNM 429164	12.2	14.0	8.4	106	21	6	5

FIGURE 23.—Serial sections of *Rhynchonelloidea angulata* (Sowerby); USNM 429155, L 16.8, W 19.1, T 11.3, A 107; from the Inferior Oolite (Pea Grit, Aalenian), Crickley Hill, Cheltenham, Gloucestershire, England.

broad, almost horizontal; inner socket ridges very low; crural bases short but well formed; crura radulifer, about 1/3 as long as dorsal valve, only slightly incurved ventrally, without specified distal ends.

REMARKS.—This is a barely known species both externally and internally. The species name has been used only rarely in the literature since it was proposed, although some specimens described previously under other names were similar to this species. Sowerby (1825:166) presented only two poor views of the holotype, but he stated that the species is “transversely oblong; gibbous, largely plaited, front elevated with 6 plaits, of which the lateral ones are the largest; beak slightly protruded, plaits 20, sharp.” Davidson (1851–1852) reillustrated the holotype and gave a relatively complete diagnosis. He compared this species with *Kallirhynchia concinna* (Sowerby), but also pointed out its differences from that species. Buckman (1918) placed this species into *Kallirhynchia*, following Sowerby’s suggestion, and regarded it as a synonym of *Rhynchonella acutiplicata* Brown. The present study shows that this species is more closely related to *Rhynchonelloidea subangulata* both in morphology and chronology than to *Kallirhynchia concinna* (Sowerby). This species is similar to *Rhynchonella acutiplicata* Brown externally, but differs internally (see discussion of *Sharpirhynchia acutiplicata* (Brown)).

This species is easily confused with *Rhynchonelloidea subangulata* (Davidson) as they both occur in the same horizon and look alike in external morphology. Generally *Rhynchonelloidea subangulata* is less transverse, and its dorsal valve is strongly everted anteriorly, with high and subtrigonal tongue. While *Rhynchonelloidea angulata* usually has lower fold and shallower sinus, its linguiform extension is much lower, but wider.

Rhynchonelloidea subangulata (Davidson, 1877)

FIGURE 24; PLATE 1: FIGURES 7–12

Rhynchonella subangulata Davidson, 1877:83, pl. 4: figs. 11, 12; 1878:208, pl. 29: figs. 14–16.—Buckman, 1882:36.—Upton, 1905:82, pl. 3: fig. 10.—Buckman, 1906:209.
Rhynchonelloidea subangulata (Davidson).—Buckman, 1918:38.—Almeras, 1979a:6–21, text-figs. 2–8, pl. 1: figs. 1–11.—Almeras and Peybernes, 1979:55–60, text-figs. 15, 16, pl. 2: figs. 10–12.
Rhynchonella (*Rhynchonelloidea*) *subangulata* Davidson.—Roche, 1939:265.

TYPE.—*Lectotype*: Davidson, 1877, pl. 4: fig. 12; designated by Almeras, 1979a:6; from the Lower Inferior Oolite (Paving Bed, Aalenian), Bradford Abbas, Dorset, England.

MATERIAL STUDIED.—More than 30 well-preserved specimens from the Inferior Oolite (Pea Grit, Aalenian), Crickley Hill, Leckhampton Hill, Painswick, and Stroud, Gloucestershire, England.

DESCRIPTION.—Shell small, strongly uniplicate; subtrigonal to subpentagonal in outline, some specimens transverse; dorsal valve markedly everted anteriorly, giving shell subcynocephalous to cynocephalous profile. Lateral commissure

oblique ventrally at 20–30 degrees to vertical; anterior commissure uniplicate; linguiform extension fairly high, subtrapezoidal, truncated.
Beak acute, suberect to substraight; foramen hypothyriddid, small and subcircular, with slight rims; deltidial plates short, disjunct to just conjunct; beak ridges subangular; interareas small, slightly concave.

Ventral valve moderately convex at posterior, tending to be flattened anteriorly; sinus well marked, wide and deep, occurring at posterior 1/3 to 1/2 of valve and turning over toward dorsal valve sharply at anterior margin.
Dorsal valve much more convex than ventral one, everted anteriorly; fold prominent, elevated over flanks markedly at anterior 1/2 of valve, making valve trilobate in appearance.

Costae angular, coarse, on each valve numbering 13–20, 3–5 on fold and 2–4 in sinus; smooth areas very short or absent; growth lines feeble, becoming obvious near anterior commissure.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 88740a	12.3	14.3	12.2	97	18	4	3
USNM 88740b	13.2	14.8	8.7	94	19	5	4
USNM 88740c	10.2	13.0	11.7	99	14	4	3
USNM 89075a	13.2	13.2	12.5	90	21	4	3
USNM 312350a	13.5	14.4	13.3	90	19	4	3
USNM 312350b	12.5	13.7	9.8	91	18	5	4
USNM 429146	18.8	23.0	14.7	107	17	5	4
USNM 429147	14.7	18.3	14.3	106	18	5	4
USNM 429148	14.0	16.7	12.9	109	20	5	4
USNM 429149	13.5	17.1	13.0	110	19	5	4
USNM 429150	14.4	18.9	13.5	110	18	4	3
USNM 429151	15.5	17.6	14.0	94	17	4	3
USNM 429152	17.2	18.5	13.2	98	22	5	4

INTERIOR.—Secondary thickenings only existing at posterior of apical cavities. Short pedicle collar present; dental plates short, subparallel, and relatively thick, rising from ventral floor before reaching hinge zone; delthyrium and lateral cavities well developed; teeth short, massive and mallet-like, with expanded ends and crenulations; accessory dental cavities and denticulars present.

Dorsal septum well developed, reduced into ridge after hinge zone, which is stout and fairly long, running about 1/2 of valve length; no septalium observed in two sectioned and one excavated specimen; septalial plates short, pendant; hinge plates broad, almost horizontal; inner socket ridges low and narrow, but clearly differentiated; crural bases short, well formed; crura radulifer, about 1/3 of dorsal valve length, incurved ventrally forward and appearing as vertical plates in section at distal ends.

REMARKS.—Almeras (1979a, b) illustrated three sets of serial sections of the species, all from France. One specimen (1979a:15, text-fig. 8) shows strong secondary thickenings in

FIGURE 24.—Serial sections of *Rhynchonelloidea subangulata* (Davidson); topotype, USNM 429154, L 15.2, W 18.2, T 15.2, A 108; from the Inferior Oolite (Pea Grit, Aalenian), Crickley Hill, Cheltenham, England.

both valves and has well developed, V-shaped septalium and narrow hinge plates. Of the other two (Almeras and Peybernes, 1979:57–58, text-figs. 15, 16), one shows no sign of a septalium and the other has a very short incomplete septalium, but both have wide hinge plates and radulifer crura with incurved ends. All of these specimens are surely the same species and quite similar to the English ones. This indicates that the septalium is variable within this species. It generally exists in juvenile individuals but tends to disappear from adults.

Rhynchonelloidea subangulata (Davidson) is one of the earliest species described in the genus. Internally, it is in close accord with the type-species *Rhynchonelloidea ruthenensis* (Reynes) (Muir-Wood, 1936; Almeras, 1979b), but differs slightly in external characters. *Rhynchonelloidea ruthenensis* has clearly developed posterior smooth areas on both valves and possesses fewer, but much stronger ribs than in *Rhynchonelloidea subangulata*. As far as its exterior characters are concerned, *Rhynchonelloidea subangulata* seems more similar to some species of *Rhynchonelloidea*, but their interiors are quite different. We do not think that this genus is closely related to *Rhynchonelloidea*, although they are in the same family.

Subfamily IVANOVIELLINAE Makridin, 1964

Lotharingella Laurin, 1984

Lotharingella Laurin, 1984a:368.

TYPE-SPECIES.—*Lotharingella woevrica* Laurin, 1984a:368.

Lotharingella leedsi (Davidson, 1878)

FIGURE 25; PLATE 3: FIGURES 19–21

Rhynchonella leedsi Davidson, 1878:216, pl. 28: fig. 17.—Rollier, 1918:168.
Burmishynchia leedsi (Davidson).—Buckman, 1918:49.—Douglas and Arkell, 1932:154, pl. 10: fig. 6.
Burmishynchia fusca Douglas and Arkell, 1932:155, pl. 10: fig. 7. [New synonymy.]
Rhynchonelloidea inflata Douglas and Arkell, 1932:156, pl. 10: fig. 8. [New synonymy.]
Lotharingella leedsi (Davidson).—Laurin, 1984a:370, pl. 3: figs. 8–10.

TYPE.—*Holotype*: Davidson, 1878, pl. 28: fig. 17; from the Cornbrash (upper part, Lower Callovian), Scarborough, Yorkshire, England.

MATERIAL STUDIED.—10 well-preserved specimens from the Cornbrash (Lower Callovian), Peterborough, Cambridgeshire, England.

EMENDED DIAGNOSIS.—Shell small, subcircular, globose, and nearly equivalve; fold and sinus feeble; tongue low and short; beak short, acute, suberect to incurved. Posterior smooth areas present, dorsal umbo sulcated; shell covered with many fine subrounded costellae anteriorly and fine growth lines. No septalium and septalial plates; septum reduced; crura calcarifer.

AGE AND DISTRIBUTION.—Early Callovian; England and ?France.

DESCRIPTION.—Shell small, subcircular or slightly transverse in outline, subglobose to globose in profile; valves nearly equal in convexity and depth or dorsal valve more convex than opposite one in adults. Lateral commissures oblique ventrally at about 10 to 20 degrees; anterior commissure moderately uniplicate; linguiform extension short and low, arched variably.

Beak short, acute, with incurved tip almost touching dorsal umbo in adult; foramen small, circular, hypothyriddid; deltidial plates disjunct to just conjunct, with slight rims around foramen; beak ridges angular, defining small and slightly concave interareas, fine transverse lines visible on interareas.

Ventral valve moderately convex, subcarinate posteriorly to about 1/4 of valve length; sinus starting at posterior 1/2 of valve, shallow and broad, may be slight depression of anterior.

Dorsal valve swollen, evenly recurved both longitudinally and transversely, with greatest convexity at middle of valve and flattened anteriorly; umbonal region sulcated variably, in some specimens sulcation quite distinct, running about 1/4 of valve length; fold feeble, only slightly raised over slopes at anterior margin, usually occurring at anterior 1/3 to 1/4 of valve.

Shell with clear but variable posterior smooth areas on both valves, ranging from 1/6 to 1/2 as long as valve; costellae fine, subrounded, on each valve numbering 20–26; growth lines fine, but clearly shown in troughs between costellae.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 429166	13.9	14.9	11.7	107	25	7	6
USNM 429167	14.1	14.8	10.6	98	20	6	4
USNM 429168	11.7	13.0	11.1	105	21	5	4
USNM 429169	16.0	16.5	15.2	104	24	6	5
USNM 429170	12.2	13.0	10.3	94	22	6	4
USNM 429171	12.7	12.5	10.3	90	22	6	5

INTERIOR.—No secondary thickenings in either valve. Short pedicle collar in ventral valve; delthyrium wide; lateral cavities very short and narrow; dental plates short, only about 1/5 of valve length and diverging toward ventral floor; teeth short, massive, with expanded ends and crenulations; accessory dental cavities and denticles present.

No septalium of septalial plates in dorsal valve; septum reduced to low but long ridge, extending beyond crura; hinge plates narrow, declined dorsally; inner socket ridges relatively high and strong; crural bases not well formed, comparatively narrow; crura calcarifer, very short, about 1/4 as long as dorsal valve, incurved ventrally forward and slightly furrowed on dorsal sides; crura with primary lamellae strongly extended toward dorsal floor and short, comma-shaped heads, showing distinctive shape in sections at distal ends.

REMARKS.—This species was not properly known. Davidson (1878) illustrated three views of the holotype, but he did not make it very clear in his description if the species possesses posterior smooth areas and sulcation at the dorsal umbo.

Nevertheless, he mentioned in the observation that "In full-grown examples the ribs become obsolete on the umbone" (Davidson, 1878:216). On the other hand, Douglas and Arkell (1932:155) thought that Davidson's diagnosis was valueless, because no specimens housed in the Natural History Museum, London, agreed with the holotype of the species as figured by Davidson. Meanwhile, they created two new species, *Burmihynchia fusca* and *Rhynchonelloidea inflata*. The former is quite similar to the supposed holotype of *Rhynchonella leedsi* illustrated by Davidson, except its having slightly coarser and less numerous costellae. In our opinion, *Burmihynchia fusca* is a synonym of *Rhynchonella leedsi*, although the holotype of the latter has been questioned. *Rhynchonelloidea inflata* Douglas and Arkell should also be regarded as a synonym of *R. leedsi*.

The only difference is that the former has a more swollen dorsal valve, more distinct sulcation on the dorsal umbo, and slightly more obvious subcarination on the ventral umbo (Plate 3: Figure 21).

Laurin (1984a, pl. 3: figs. 8–10) illustrated three French specimens that were identified as *Lotharingella leedsi* (Davidson). These French specimens, however, have much stronger but fewer ribs and slightly everted dorsal valve as well as a higher linguiform extension. The sulcation on dorsal umbone and subcarination on ventral umbone are not developed and the posterior smooth areas are much shorter than those in the English specimens. It seems to us that these French specimens are closer to *L. woevrica* Laurin (Plate 3: Figure 29) than to *L. leedsi* (Davidson).

FIGURE 25.—Serial sections of *Lotharingella leedsi* (Davidson); topotype, USNM 429167, L 14.1, W 14.8, T 10.6, A 98; from the Cornbrash (Lower Callovian), Peterborough, Cambridgeshire, England.

FIGURE 26.—Serial sections of *Rhynchonelloidella alemanica* (Rollier); topotype, USNM 123762d, L 15.1, W 16.0, T 11.9, A 107; (Upper Bathonian) Villey, Lorraine, France.

Regarding the interior of *L. leedsi* (Davidson), the genus *Lotharingella* is surely a close relative of *Thurmannella* and *Rhynchonelloidella*. Both morphologically and chronologically, it lies between *Rhynchonelloidella* and *Thurmannella*.

Rhynchonelloidella Muir-Wood, 1936

Rhynchonelloidella Muir-Wood, 1936:49.

TYPE-SPECIES.—*Rhynchonella varians* var. *smithi* Davidson, 1878:213.

Rhynchonelloidella alemanica (Rollier, 1911)

FIGURES 26–28; PLATE 3: FIGURES 1–6, 14, 15

Rhynchonella varians Schlotheim.—Haas and Petri, 1882:229, pl. 6: figs. 11–13, pl. 7: fig. 23.

Rhynchonella alemanica Rollier, 1911:12; 1918:151.

Cyclothyris varians (Schlotheim).—Leidhold, 1921:353, pl. 5: fig. 1.

Not *Ivanoviella alemanica* (Rollier).—Makridin, 1955:83; 1964, pl. 5, figs. 3–6.

Rhynchonelloidella alemanica (Rollier).—Laurin, 1984a:361, pl. 1: figs. 1–6, 7–10.

TYPE.—*Lectotype*: Haas and Petri, 1882, pl. 6: fig. 3;

designated by Laurin, 1984a:361; from the Upper Bathonian, Lorraine, France.

MATERIAL STUDIED.—Tens of well-preserved specimens from the Upper Bathonian, France; hundreds of specimens from the Varians Beds of Germany and Switzerland.

DESCRIPTION.—Shell small, subtrigonal to slightly subpentagonal in outline, with wide hinge line; inequivalve, almost plano-convex; dorsal valve markedly everted anteriorly, giving shell subcynocephalous to cynocephalus profile. Lateral commissures deflected ventrally at 15 to 30 degrees; anterior commissure highly uniplicate; linguiform extension high and narrow, top truncated.

Beak short, pointed, substraight to suberect; foramen large, oval in shape, hypothyridid, with well developed rim; deltidial plates wide, disjunct to just conjunct; beak ridges angular, extending laterally; interareas well defined and slightly concave with fine growth lines.

Ventral valve gently convex at posterior and flattened anteriorly; sulcus well developed, deep and narrow, with flat bottom, occurring at about posterior $\frac{1}{3}$ of valve, abruptly separated from slopes and turning over towards dorsal valve sharply at frontal margin, resulting in high linguiform extension.

Dorsal valve moderately convex at umbonal region, but less

FIGURE 27.— Serial sections of *Rhynchonelloidella alemanica* (Rollier); USNM 429176, L 14.7, W 16.4, T 11.8, A 99; from the Varians Beds (Upper Bathonian to Lower Callovian), Leisberg, alte Fabrick, Switzerland.

tumid than in *Rhynchonelloidella smithi*; norelliform stage feebly recognizable, sulcation short or even absent; fold eminent, narrow and well elevated over slopes with steep flanks, occurring at about posterior $\frac{1}{3}$ to $\frac{1}{2}$ of valve and making valve trilobate anteriorly. In some specimens, umbonal region more or less depressed, smooth area generally short or absent.

Costae numerous, subangular, on each valve numbering 19–26, with 4–6 on fold and 3–5 in sinus; growth lines feeble, only visible at anterior margin. At gerontic stage, shell thickened markedly along margins and frontal margin somewhat truncated, reminiscent of *Goniorhynchia boueti* (Davidson).

INTERIOR.—Secondary thickenings in apical cavities of both

FIGURE 28.—Serial sections of *Rhynchonelloidella alemanica* (Rollier); USNM 429177, L 14.6, W 15.6, T 10.2, A 107; from the Varians Beds (Upper Bathonian to Lower Callovian), Leisberg, alte Fabrick, Switzerland.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 75917a	13.6	14.3	11.8	102	21	5	4
USNM 106207a	14.7	15.0	11.5	105	22	6	5
USNM 123762a	12.5	13.7	11.0	107	20	4	3
USNM 123762b	13.0	14.7	11.2	106	22	5	4
USNM 123762c	12.1	13.2	9.7	107	21	5	4
USNM 123768a	14.0	15.8	12.2	103	25	5	4
USNM 123768b	14.2	15.1	10.3	95	22	5	4
USNM 429173	14.7	15.8	12.1	105	23	6	5
USNM 429174	13.1	14.4	11.9	99	20	4	3
USNM 429175	13.9	14.5	9.6	100	22	5	4
USNM 429176	14.7	16.4	11.8	99	24	6	5
USNM 429177	14.6	15.6	10.2	107	25	7	6
USNM 429178	14.0	16.1	11.4	100	21	5	4

valves. No pedicle collar observed in sectioned specimens; delthyrium wide, trapezoidal to rectangular in shape; lateral cavities narrow and short; dental plates thick and long, beyond hinge zone and divergent to ventral floor, or subparallel; teeth fairly strong, massive and mallet-like, held tightly in sockets; accessory denticulars and dental cavities present.

Septalium variably developed, generally short and V-shaped; septum low and massive, only supporting septalium at very posterior part and most part of it existing as a median ridge, running about 1/3 or more of dorsal valve length; hinge plates relatively thick and broad, almost horizontal or slightly inclined ventrally at anterior parts; inner socket ridges well developed, but not strong; crural bases narrow, well formed and given off dorsally from inner margins of hinge plates; crura thick, about

$\frac{1}{4}$ to $\frac{1}{3}$ dorsal valve length, calcarifer, incurved ventrally at anterior parts.

REMARKS.—*Rhynchonelloidella alemanica* (Rollier) is a well-known species in France, Germany, and Switzerland, and was selected as the type-species of *Ivanoviella* by Makridin (1955:83). Ager, Childs, and Pearson (1972:193) thought that the specimens figured by Makridin (1964) as *Ivanoviella alemanica* (Rollier) from the Russian Platform in fact might not be conspecific with the topotype materials. Laurin (1984a), on the other hand, tried to make the specimens illustrated by Makridin as a separate species, *Ivanoviella alemanica* Makridin, 1955, from *Rhynchonella alemanica* Rollier, 1911. On this basis he (Laurin, 1984a) reserved the genus *Ivanoviella* with doubt, but transferred the species *Rhynchonella alemanica* Rollier, 1911, into the genus *Rhynchonelloidella*. The present study shows that *Rhynchonella alemanica* Rollier, 1911, belongs to the genus *Rhynchonelloidella*, both its interiors and exteriors are generally coincident with *Rhynchonelloidella smithi* (Davidson). Comparing the specimens of *Ivanoviella alemanica* (Rollier) figured by Makridin (1964:140, text-figs. 42a,b, pl. 5: figs. 3–6) with the present specimens, it has been noticed that externally the Russian specimens usually have more pronounced smooth areas and fewer, but stronger ribs.

The interiors of the Russian specimen are basically the same as those of the present ones, although the former (Makridin, 1964:140, text-fig. 42b) has a less stout septum. We judge that the Russian specimens, which were improperly placed by Makridin in *Ivanoviella alemanica* (Rollier), and that they are not conspecific with the French and Swiss materials, although they certainly belong to the same genus. *Ivanoviella*, therefore, should be at least regarded as partially synonymous with *Rhynchonelloidella*. The several other species that were put into *Ivanoviella* by Makridin, such as *I. steinbesii* (Quenstedt) (Makridin, 1964:137, pl. 4: figs. 14, 15) and *I. personata* (Buch) (Makridin, 1964:138, pl. 4: figs. 16, 17, pl. 5: figs. 1, 2), show clear differences from most species of *Rhynchonelloidella* both externally and internally, and can hardly be put into the same genus.

Here we must face the difficult decision whether to retain or abandon the genus *Ivanoviella* Makridin. First, *Ivanoviella* was based on a Russian species that was mistakenly identified as the European species; secondly, the European species has proved to belong to the earlier named genus *Rhynchonelloidella*; and thirdly, the Russian species also belongs to *Rhynchonelloidella*, although some other species in *Ivanoviella* are probably not congeneric with *Rhynchonelloidella*. It seems clear to us

FIGURE 29.—Serial sections of *Rhynchonelloidella smithi* (Davidson); topotype, USNM 75628d, L 13.9, W 15.6, T 10.6, A 104; from the Fuller's Earth Rock (Bathonian), near Bath, Somerset, England.

that *Ivanoviella* can not be reserved as a separate genus any longer, unless the Russian species *Ivanoviella alemanica* Makridin, 1955, can be demonstrated not to belong to *Rhynchonelloidella*.

***Rhynchonelloidella smithi* (Davidson, 1878)**

FIGURES 29-31; PLATE 3: FIGURES 7-11

Rhynchonella varians (Schlotheim).—Davidson, 1851-1852:13, pl. 17: fig. 15 [in part].

Rhynchonella varians var. *smithi* Walker MS.—Davidson, 1878:213, pl. 28: figs. 1, 2 [in part].

Rhynchonella smithi Walker.—Richardson and Walker, 1907:431.

Rhynchonella smithi (Davidson).—Buckman, 1918:38, pl. 18: fig. 8.

Rhynchonella media (Sowerby).—Rollier, 1918:150 [in part].

Rhynchonelloidella smithi (Davidson).—Muir-Wood, 1936:5, pl. 1: fig. 10.

Rhynchonelloidella smithi var. *crassa* Muir-Wood, 1936:58, pl. 1: fig. 12.

TYPE.—*Lectotype*: Davidson, 1878, pl. 28: fig. 1; designated by Muir-Wood, 1936:55; from the Fuller's Earth Rock, near Bath, Somerset, England.

MATERIAL STUDIED.—35 well-preserved specimens from the Fuller's Earth Rock (Bathonian) of Bath, Weymouth, Bruton, Wiltshire, Gloucester, and Lamyat Beacon, England.

DESCRIPTION.—Shell small, subtrigonal to subpentagonal in outline and subcynocephalous in profile; shell slightly wider than long. Lateral commissures oblique ventrally at about 15 to

FIGURE 30.—Serial sections of *Rhynchonelloidella smithi* (Davidson); topotype, USNM 104786a, L 13.1, W 16.8, T 12.5, A 107; from the Fuller's Earth Rock (Bathonian), near Bath, Somerset, England.

25 degrees; anterior commissure strongly uniplicate; linguiform extension well developed, usually high and widely U-shaped.

Beak short, substraight to erect; foramen small, circular, hypothyridid; deltidial plates narrow, disjunct to just conjunct, without clear rims around foramen; beak ridges subangular to obtuse; interareas not developed.

Ventral valve gently convex at posterior, tending to be flattened anteriorly; sulcus well developed, broad and relatively shallow, with rounded bottom, occurring at posterior 1/3 of valve.

Dorsal valve much more convex than ventral one and moderately everted anteriorly; posterior smooth areas very short or even absent; fold wide, with rounded top, occurring at posterior 1/2 of valve and well elevated above flanks.

Shell covered with many fine subangular costae, on each valve numbering 22–32, with 6–9 on fold and 5–8 in sinus. In gerontic stage, shell thickened along frontal margins, feeble growth lines visible.

INTERIOR.—Secondary thickenings in apical cavities of both valves may obscure posterior structures. Pedicle collar either very short or absent; delthyrium wide and trapezoidal to rectangular in shape; lateral cavities small and short; dental plates thick, subparallel to slightly convergent to ventral floor, relatively long, beyond hinge zone; teeth strong, massive, mallet-like, with expanded ends and crenulations; accessory

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 75628a	14.7	14.7	10.7	103	26	6	5
USNM 75628b	14.5	15.9	10.0	105	25	7	6
USNM 75628c	13.1	14.9	9.3	102	24	6	5
USNM 75630a	15.8	18.0	12.7	108	31	9	8
USNM 75630b	13.8	16.5	9.8	107	23	7	6
USNM 77473a	12.5	15.3	9.2	102	24	7	6
USNM 77473b	13.7	14.4	8.7	92	23	6	5
USNM 104786a	13.1	16.8	12.5	107	26	7	6
USNM 104786b	13.7	14.5	9.6	96	25	7	6
USNM 104786c	14.1	14.5	11.8	92	24	6	5
USNM 104786d	12.0	14.2	8.1	100	22	6	5

denticulars and dental cavities well developed.

Dorsal septum stout, supporting septalium only in posterior part and rapidly reduced into ridge forward, running about 1/3 to 1/2 of valve length; septalium present or absent. In 3 sectioned specimens, one having well developed, V-shaped septalium; one having no septalium at all and third one with very short, incomplete septalium. Hinge plates generally thick, developed variably; in one sectioned specimen (Figure 29, USNM 75628d, topotype) hinge plates narrower, concave ventrally, inner socket ridges prominent, high and strong; in two others (Figure 31, USNM 75623a; Figure 30, USNM 104786a, topotypes) hinge plates broader, almost horizontal, inner socket

FIGURE 31.—Serial sections of *Rhynchonelloidella smithi* (Davidson); topotype, USNM 75623a, L 13.5, W 14.6, T 11.3, A 105; from the Fuller's Earth Rock (Bathonian), Lamyat Beacon, England. (The crura in this specimen were broken off, short septalium present.)

ridges much lower and less eminent, but well demarcated from hinge plates. Crural bases usually narrow, not very well formed; crura calcarifer; posterior parts showing trigonal shape in sections and anterior parts incurved ventrally; primary lamellae long; secondary lamellae short, existing as comma-like heads; hinge plates strongly tapering forward in one sectioned specimen, fairly long, but in two others not tapering.

REMARKS.—So far, only one set of serial sections of the species has been published, which was made by Muir-Wood in 1936. In her illustration (Muir-Wood, 1936:56, text-fig. 15) the shell was thickened posteriorly, a deep and V-shaped septalium exists with a low and long septum, the hinge plates are broad and nearly horizontal, the inner socket ridges are well shown, the crura are calcarifer, and the crural bases are fairly narrow. Comparing the serial sections provided by Muir-Wood with ours, it seems clear that the interiors of the species also vary, especially the septalium, hinge plates, inner socket ridges, and pedicle collar, though all these specimens have the same crura, septum, and exteriors.

A point to consider here is that the term "calcarifer crura" was originally proposed by Muir-Wood (1934:526) based on the crura in *Kallirhynchia yaxleyensis* (Davidson). Unfortunately she defined this kind of crura on longitudinal sections of the species, in which the real shape of the crura is not easy to interpret. On the other hand, the transverse serial sections of *Kallirhynchia yaxleyensis* (Davidson) illustrated by Muir-Wood at the same time (Muir-Wood, 1934:535, fig. 2) were incomplete, failing to show the anterior parts of the crura. Therefore, what the calcarifer crura are really like in transverse section was not known until 1936. At that time Muir-Wood described the calcarifer crura once again in *Rhynchonelloidella smithi* and several other species of the genus as well as in *Kallirhynchia platiloba* Muir-Wood (Muir-Wood, 1936: p. 41, text-fig. 11, p. 51, text-fig. 14, p. 56, text-fig. 15, p. 63, text-fig. 17). This time she illustrated several sets of transverse sections in which the calcarifer crura were very well shown. Ager (1965a:H599, figs. 478-5, 479-2) reillustrated the calcarifer crura and commented on their definition. This definition has been accepted widely by most brachiopodologists.

The present study has shown that the crura of *Kallirhynchia yaxleyensis* (Davidson) actually are not calcarifer, but radulifer as understood by most brachiopodologists. In order to avoid further confusion, the calcarifer crura have to be defined on the basis of those in *Rhynchonelloidella*, not in *Kallirhynchia*, although Muir-Wood originally defined them in *Kallirhynchia yaxleyensis* (Davidson). *Kallirhynchia platiloba* Muir-Wood, with its calcarifer crura, should be transferred into *Rhynchonelloidella*.

Sharpirhynchia, new genus

TYPE-SPECIES.—*Kallirhynchia sharpi* Muir-Wood, 1938:74.

DIAGNOSIS.—Shell small, depressed to moderately bicon-

vex; subtrigonal to transverse in outline; no clearly marked norelliform stage; beak suberect, foramen rimmed, hypothyridid; anterior commissure uniplicate, fold low; shell with numerous fine costae and conspicuous, elegant, dense concentric lines. No septalium or related structures in dorsal valve, septum reduced, crura calcarifer.

AGE AND DISTRIBUTION.—Late Bajocian to Early Bathonian; England and France.

REMARKS.—As a form closely related to *Rhynchonelloidella*, the new genus *Sharpirhynchia* is separated from the former by the absence of a norelliform stage and by having a depressed and transverse shell, less elevated fold, and reverted, rather than anteriorly everted, dorsal valve. The outer surface of the new genus has well-developed, fine and dense concentric lines, and has no clear smooth areas and no sulcation. Internally it has no septalium and septalial plates, the reduced septum is less stout than in *Rhynchonelloidella*, and the crura are not as distinctive as those in *Rhynchonelloidella*, although they are also of the calcarifer type.

It is advisable to separate *Sharpirhynchia* from *Rhynchonelloidella* because it is more primitive than *Rhynchonelloidella* in phylogeny, with characters between *Rhynchonelloidea* and *Rhynchonelloidella*. It might be possible that *Sharpirhynchia* was evolved from the *Rudirhynchia*-*Rhynchonelloidea* group of the subfamily Rhynchonelliinae as a earlier form of the Ivanoviellinae and led to *Rhynchonelloidella* in the late Bajocian to early Bathonian.

The type-species of the new genus was originally considered a species of *Kallirhynchia* and was compared with *Kallirhynchia yaxleyensis* (Davidson). The present study shows that *Sharpirhynchia sharpi* actually has no direct relation with *Kallirhynchia*. Its interior and exterior features are quite different from the type-species of that genus. *Kallirhynchia yaxleyensis* (Davidson) has well developed septalial plates, radulifer crura, and a stronger septum. Externally, *Kallirhynchia* does not have the same micro-ornament as *Sharpirhynchia*, nor clear rims around the foramen.

Sharpirhynchia acutiplicata (Brown, 1849), new combination

FIGURE 32; PLATE 2: FIGURES 18, 20-23

Terebratula acuti-plicata Brown, 1849:138, pl. 55: figs. 98, 99.

Kallirhynchia acutiplicata (Brown).—Buckman, 1918:31, pl. 15: figs. 3, 4.—Muir-Wood, 1938:75.

Kallirhynchia distendens Buckman, 1918:223, pl. 15: figs. 1, 2. [New synonymy.]

TYPE.—*Holotype*: Brown, 1849, pl. 55: figs. 98, 99, said to be from the Inferior Oolite, Bilsdale and Cheltenham, England (Brown, 1849:138). Muir-Wood (1938:75) mentioned that it was from the Upper *Trigonia* Grit.

MATERIAL STUDIED.—17 well-preserved specimens from the Inferior Oolite (Upper *Trigonia* Grit, Upper Bajocian) of Painswick, Birdlip Hill, and Tuffley Quarry, Cheltenham,

FIGURE 32.— Serial sections of *Sharpirhynchia acutiplicata* (Brown); USNM 89082d, L 16.3, W 20.2, T 11.8, A 107; from the Inferior Oolite (Upper *Trigonia* Grit, Upper Bajocian), Buckholt Wood, Cranham near Painswick, England.

Gloucestershire, England; 3 specimens from the Upper Bajocian, Lorraine and Ranville, Calvados, France.

EMENDED DIAGNOSIS.—Shell small, transversely elliptical in adults; shell depressed, fold slightly raised, sinus shallow and broad; beak short, suberect; costae numerous, subangular, growth lines fine and elegant, closely spaced. No septalium or septalial plates; septum reduced into ridge, crura calcarifer.

AGE AND DISTRIBUTION.—Late Bajocian; England and France.

DESCRIPTION.—Shell small, subtrigonal in youth, becoming laterally extended in adult; shell depressed, unequally biconvex, dorsal valve slightly more convex than ventral one. Lateral commissures sloping ventrally at 10–15 degrees; anterior commissure broadly uniplicate; with short, low, trapezoidal tongue.

Beak short, suberect; foramen small, circular, hypothyridid, rims slight; eltidial plates low and narrow, disjunct to just

conjunct; beak ridges subangular, defining small interareas.

Ventral valve convex gently; sinus shallow and broad, in posterior $\frac{1}{3}$ to $\frac{1}{2}$ of valve, expanding rapidly forward.

Dorsal valve recurved evenly; fold low, only slightly raised above slopes at anterior $\frac{1}{3}$, clearly demarcated from side regions.

Shell ornamented with 20–26 subangular costae on each valve, with 5–6 on fold and 4–5 in sinus; growth lines fine and elegant, but less conspicuous than in *Sharpirhynchia sharpi* (Muir-Wood).

INTERIOR.—No secondary thickenings present in either valve. No pedicle collar observed in sectioned specimen; deltidial plates disjunct; delthyrium wide, lateral cavities narrow; dental plates slightly divergent to ventral floor, long, beyond hinge zone; teeth short, massive, with expanded ends and crenulations; accessory denticulars and dental cavities present.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 75590a	16.0	20.3	12.3	110	25	7	5
USNM 75590b	14.8	18.3	11.3	102	23	6	5
USNM 75590c	14.1	17.2	10.1	113	26	6	5
USNM 89082a	16.3	20.8	11.8	108	25	6	5
USNM 89082b	13.2	16.1	7.4	104	22	5	4
USNM 89082c	14.5	19.6	9.5	121	22	6	5
USNM 104687a	16.3	20.4	10.0	108	21	5	4
USNM 123758a	10.5	18.4	11.1	100	30	7	6
USNM 429203	14.6	18.2	11.2	106	24	6	5
USNM 429204	13.7	16.4	10.3	106	25	6	4
USNM 429205	13.4	15.7	9.3	108	22	6	5

No septalium or septalial plates in dorsal valve; septum short, supporting hinge plates only at posteriormost cavity and rapidly reduced into ridge forward; hinge plates narrow, subhorizontal and tapering anteriorly; inner socket ridges low, but well demarcated from hinge plates; crural bases narrow, well formed, arising dorsally from inner margins of hinge plates; crura calcarifer, about 1/4 as long as dorsal valve length, slightly curved toward ventral valve at distal ends, with hammer-like heads.

REMARKS.—This is a barely known species. Brown (1849:132) defined it as: “transversely elongated, somewhat pocket-like; gibbous; beak little produced, but small, and slightly curved; front elevated, with six plaits.” This definition is not enough to distinguish it from other species, nevertheless, he provided two good views of the holotype. His figures show that the shell is transverse and slightly depressed, with broad and low fold as well as shallow sinus. Buckman (1918) figured another two specimens of the species, which also show the transverse and slightly depressed shell and a long septum, as well as massive teeth inside. At the same time, Buckman (1918:223, pl. 15: figs. 1, 2) also erected the species *Kallirhynchia distendens*, which was from the same horizon and locality as *Terebratula acuti-plicata* Brown, and shares similar characteristics. The only differences were said to be that the former was more depressed and broader than the latter. The present study shows that these two species are morphologically transitional, without an abrupt boundary between them. The present authors, therefore, prefer to combine them as one species.

This species is close to *Sharpirhynchia sharpi* (Muir-Wood) in general aspects, but the latter has much more conspicuous concentric lines and a narrower, more elevated fold, as well as a longer acute beak and bigger foramen that is rimmed clearly. *Rhynchonelloidea angulata* (Sowerby) is also similar to *S. acutiplicata* (Brown) in exteriors, but the former generally has a more raised fold, more swollen dorsal valve, and stronger ribs. Internally, *R. angulata* (Sowerby) has radulifer crura. We suggest that *R. angulata* (Sowerby) might be the direct ancestor of *S. acutiplicata* (Brown), and that *Sharpirhynchia* led to *Rhynchonelloidella* via one branch, to *Bradfordirhynchia* via

another branch. This is especially plausible when their internal structures and micro-ornaments are compared.

Sharpirhynchia sharpi (Muir-Wood, 1938),
new combination

FIGURE 33; PLATE 2: FIGURES 15–17, 19

Kallirhynchia sharpi Muir-Wood, 1938:74, fig. 15.

TYPE.—*Holotype*: Muir-Wood, 1938:75, fig. 15-2; from the Great Oolite (Lower Bathonian), *sharpi* bed of Limekiln Quarry, Hopping Hill, near Northampton, England.

MATERIAL STUDIED.—46 well-preserved specimens from the base of the Great Oolite (Lower Bathonian), Cranford South Quarry, Kettering; Corby, Lincolnshire; Islip, Northamptonshire; Cranwell Village, St. Giles, Lincolnshire, England.

DESCRIPTION.—Shell small, subtrigonal to transverse or laterally elongate in adults; unequally biconvex, dorsal valve more convex than ventral one, subglobose in profile. Lateral commissures oblique ventrally; anterior commissure narrowly uniplicate; linguiform extension developed variably, generally low and U-shaped. No clear sulcation on dorsal umbone.

Beak relatively long, acute, and suberect, with slightly incurved tip in adult; foramen big, oval, hypothyriddid, with well developed rim; deltidial plates narrow, disjunct to just conjunct; beak ridges subangular; interareas small, but well defined and slightly concave, with fine and clear transverse lines.

Ventral valve moderately convex; sulcus shallow and wide, well separated from slopes and with rounded bottom, occurring at posterior 1/3 to 1/2 of valve.

Dorsal valve more convex than ventral one, with greatest convexity at anterior part, but recurved anteriorly; fold occurring at anterior 1/2 to 1/3 of valve, generally narrow and lower, with rounded top, moderately raised above slopes, giving valve trilobate appearance. Dorsal umbones rarely slightly sulcate or depressed.

Numerous fine subangular costae separated by deep intervals, on each valve numbering 20–26, with 4–7 on fold and 3–6 in sinus; shell also bearing innumerable fine, conspicuous growth lines, becoming feebly lamellose or imbricated toward anterior margin. Gerontic shells thickened along margins, some costae occasionally bifurcating. No smooth areas observed.

INTERIOR.—No secondary thickenings present in either valve, structures delicate. No pedicle collar observed in two sectioned specimens. Delthyrium wide, trapezoidal; lateral cavities narrow; dental plates long, beyond hinge zone, slightly divergent toward ventral floor at posterior parts and becoming parallel anteriorly; teeth short, very strong and massive, with expanded ends and crenulations; accessory denticulars and dental cavities present.

No septalium or septalial plates in dorsal valve; septum short, reduced anteriorly to form low ridge, running about 1/3 of valve length; hinge plates thick and narrow, tapering toward

FIGURE 33.— Serial sections of *Sharpirhynchia sharpi* (Muir-Wood); USNM 429196, L 13.3, W 15.1, T 9.6, A 96; from the base of the Great Oolite (*Kallirhynchia sharpi* bed, Bathonian), Cranford South Quarry, Kettering, England.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 106205a	13.4	13.9	9.2	93	27	6	5
USNM 128854a	12.7	15.4	9.6	109	24	5	4
USNM 250407a	15.4	16.7	11.3	94	22	5	4
USNM 429193	13.7	15.5	9.0	104	22	5	4
USNM 429194	13.3	13.8	8.7	96	26	6	5
USNM 429195	13.2	16.5	11.1	108	25	5	4
USNM 429197	13.2	16.1	10.1	105	24	6	5
USNM 429198	13.8	15.7	7.9	99	26	6	5
USNM 429199	14.6	17.0	10.5	101	28	7	6
USNM 429200	13.5	15.5	9.8	98	23	6	5
USNM 429201	13.7	14.8	8.1	102	25	5	4
USNM 429202	13.0	14.3	9.4	103	26	5	4

each other at posterior parts and becoming horizontal anteriorly; inner socket ridges lower but well demarcated from hinge plates; hinge plates tapering forward; crural bases narrow, but well formed, given off dorsally from inner margins of hinge plates; crura calcarifer, about 1/3 of dorsal valve length, posterior parts trigonal-shaped in sections and curved slightly ventrally at anterior parts, but not as distinctive as those in *Rhynchonelloidella*.

REMARKS.—Muir-Wood (1938:75) mentioned that the internal structures of the species were similar to those in *Kallirhynchia yaxleyensis* (Davidson), but she did not illustrate any sections of the species. She compared this species with *Rhynchonelloidella* and mentioned that smooth areas exist on the valves and that the dorsal valve is sulcate umbonally. Careful examination showed that umbonal sulcation is very feeble, visible in few specimens; smooth areas were not observed on any of the studied specimens. Perhaps they only exist in young stages and become obsolete in adults.

Thurmannella Leidhold, 1921

Thurmannella Leidhold, 1921:357.

TYPE-SPECIES.—*Terebratula obtrita* DeFrance, 1828:161 (= *T. thurmanni* Voltz in Thirria, 1833:172; Childs 1969:45).

Thurmannella acuticosta Childs, 1969

FIGURE 34; PLATE 3: FIGURES 22–28

Rhynchonella varians var. *thurmanni* (Voltz).—Davidson, 1878:215, pl. 28: figs. 14–16.

Thurmannella acuticosta Childs, 1969:51, text-fig. 20, pl. 5: figs. 10, 11.

TYPE.—*Holotype*: Davidson, 1878, pl. 28: fig. 16; refigured by Childs, 1969, pl. 5: fig. 10; from the Lower Calcareous Grit (Oxfordian), Filey Brigg, Yorkshire, England.

MATERIAL STUDIED.—6 well-preserved specimens from the Lower Calcareous Grit (Oxfordian), Scarborough and Waydale Snainton, Yorkshire, England; 7 specimens from the Lower

Oxfordian, Wagrion (Ardeunnes) and Villers-Sur-Mer, Calvados, France.

DESCRIPTION.—Shell small, inequivalve; subtrigonal to subpentagonal in outline, cynocephalous in profile; dorsal valve much more convex than ventral one and everted anteriorly. Lateral commissures deflected ventrally at 20–30 degrees; anterior commissure strongly uniplicate.

Beak short, suberect to incurved; foramen small, subcircular in shape, hypothyriddid; deltidial plates narrow, disjunct; beak ridges subangular; interareas very narrow, but well defined and slightly concave.

Ventral valve gently convex posteriorly and slightly flattened anteriorly; sinus well developed, wide and shallow, occurring at posterior 1/3 and turning over sharply toward dorsal valve at frontal margin, resulting in high and trapezoidal tongue.

Dorsal valve swollen, no sulcation on umbo; fold elevated, slopes curving down laterally, making valve somewhat trilobate.

Costae numerous, coarse, subangular, separated by deep intervals, on each valve numbering 18–23, with 4–7 on fold and 3–6 in sinus; posterior smooth areas short, only about 1/5 to 1/4 of valve length; growth lines feeble, visible on smooth areas and at anterior margin.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 64412a	16.0	17.5	14.5	104	18	5	4
USNM 64412b	14.2	15.3	14.5	100	19	5	4
USNM 64412c	13.9	15.3	13.7	102	20	7	6
USNM 88738a	13.5	14.3	10.8	102	20	5	4
USNM 88738b	13.3	12.8	11.8	95	21	5	4
USNM 88738c	12.8	13.9	10.8	107	22	5	4
USNM 88738d	12.3	13.7	12.1	106	21	6	5
USNM 88738e	13.2	13.5	12.8	94	18	6	5
USNM 256407a	11.5	12.4	10.8	104	19	6	5
USNM 429218	14.2	15.0	13.5	106	23	7	6
USNM 429219	15.3	15.6	13.7	107	20	5	4
USNM 429220	12.4	14.3	9.9	108	22	7	6
USNM 429221	12.9	14.0	12.3	104	22	7	6

INTERIOR.—Slight secondary thickening of apical cavities. No pedicle collar observed in sectioned specimen; delthyrium wide, almost rectangular; lateral cavities small; dental plates thick, subparallel, leaving ventral floor at hinge zone; teeth short, massive, nodular, with expanded ends and crenulations; accessory denticulars and dental cavities present.

Dorsal septum short and thick, reduced abruptly to ridge, existing as ridge for most of length; septalium absent; septalial plates long, pendant; hinge plates broad, subhorizontal; inner socket ridges well developed, thick; crural bases narrow, well formed, given off dorsally from inner margins of hinge plates; crura calcarifer, about 1/3 as long as dorsal valve, initial parts comma-like in sections and slightly incurved toward ventral

valve anteriorly, with expanded, hammer-like heads and long tails.

REMARKS.—The present specimens fall into two morphological groups. One of them is smaller, with longer beak and longer smooth areas. The dorsal valve is less tumid and the fold relatively short, less sharp (Plate 3: Figures 22–24). The other is generally larger and circular in shape, with very short and incurved beak almost touching the dorsal umbo. The posterior smooth areas are much shorter and the fold is very prominent. In this group, the shell is strongly folded, with much more tumid dorsal valve (Plate 3: Figures 25–28). These morphological variations might have resulted from adaption to different environments, and may be regarded as variation in different populations.

According to Childs' original definition, *Thurmannella acuticosta* Childs has shorter smooth areas and sharper ribs than *Thurmannella obtrita* (Defrance). The present study shows that the first point is true, but the second is not clearly resolved. Nevertheless, *Thurmannella obtrita* always has sharper beak ridges and clear interareas.

***Thurmannella obtrita* (Defrance, 1828)**

FIGURES 35, 36; PLATE 2: FIGURES 24–27, PLATE 15: FIGURES 17, 18

Terebratula thurmanni Voltz.—Quenstedt, 1868–1871:90, pl. 38: figs. 83–87.
Rhynchonella thurmanni (Voltz).—Haas and Petri, 1882:238, pl. 7: figs. 14–17.—Loriol, 1900:135, pl. 6: fig. 53; 1901:112, pl. 6: figs. 17, 19.—Rollier, 1918:154–156.

FIGURE 34.—Serial sections of *Thurmannella acuticosta* Child; topotype, USNM 88738a, L 13.5, W 14.3, T 10.8, A 102; from the Lower Calcareous Grit (Oxfordian), Waydale Snainton, Yorkshire, England.

FIGURE 35.—Serial sections of *Thurmannella obtrita* (Defrance); USNM 306011h, L 15.1, W 17.1, T 11.4, A 110; (Lower Oxfordian) Park on South side of Benoit, Besancon, France.

Rhynchonella obtrita (Defrance).—Deslongchamps, 1884:337, pl. 28: figs. 1-3.—Haas, 1889:12.

Rhynchonelloidea thurmanni (Voltz).—Buckman, 1918:38.

Septaliphoria (*Thurmannella*) *obtrita* (Defrance).—Leidhold, 1921:362, pl. 5: fig. 5, pl. 6: figs. 1-9.

Septaliphoria (*Thurmannella*) *thurmanni* (Voltz).—Leidhold, 1921:363, pl. 5: fig. 6, pl. 6: figs. 10-18.

?*Thurmannella thurmanni* (Voltz).—Makridin, 1964:135, pl. 6: fig. 53.

Thurmannella obtrita (Defrance).—Childs, 1969:46, text-fig. 19, pl. 5: figs. 7-9.

Thurmannella thurmanni (Voltz).—Kamyshan and Babanova, 1973:117, pl. XIV: fig. 13.

TYPE.—*Neotype*: Childs, 1969, pl. 5: fig. 8; from the Oxfordian (Terrain a Chailles), Fagny-Sur-Meuse (Meurthe et Moselle), France.

MATERIAL STUDIED.—Hundreds of well-preserved specimens from France, 7 from England, and 8 from Switzerland; all of them are from the Lower Oxfordian.

DESCRIPTION.—Shell small, with well developed norelli-form stage; variable in shape, from subtrigonal, subcircular to transversely elliptical; adult specimens generally transverse, inequivalve, dorsal valve much more convex than ventral one; subcynocephalous in profile. Lateral commissures deflected ventrally at 15-30 degrees; anterior commissure strongly uniplicate; tongue high and broad, rectangular or U-shaped.

Beak short and small, with fairly broad base, generally suberect to slightly incurved; foramen small, circular, hypothyriddid, with well developed rims; deltidial plates narrow, disjunct to just conjunct; beak ridges angular, extending laterally; hinge line wide; interareas narrow, but distinct.

Ventral valve gently convex posteriorly and flattened anteriorly; sulcus developed variably, generally shallow and broad, with flattened bottom, occurring at posterior $\frac{1}{3}$ to $\frac{1}{2}$

FIGURE 36.—Serial sections of *Thurmannella obtrita* (Defrance); USNM 306011j, L 12.7, W 15.0, T 18.0, A 110; (Lower Oxfordian) Benoit, Besoncon, France.

and turning over sharply toward dorsal valve at anterior margin, resulting in high tongue.

Dorsal valve clearly sulcate at umbonal region and everted anteriorly; fold distinct, broad and well elevated over slopes at anterior $\frac{1}{3}$, borders distinct from slopes.

Costae numerous, fine, subangular to sharp, on each valve numbering 16–26, with 5–9 on fold and 4–8 in sinus; all costae starting well forward of umbones, leaving distinct smooth areas on both valves, varying in length, from $\frac{1}{4}$ to $\frac{1}{2}$ valve length; growth lines feeble, visible only at anterior parts.

INTERIOR.—No secondary thickenings present in either valve. Pedicle collar short or absent; delthyrium and lateral cavities well developed; dental plates short, splitting from ventral floor before reaching hinge zone; teeth short, nodular in shape, with expanded ends and crenulations; accessory denticulars and dental cavities present.

No septalium observed in sectioned specimens and in excavated specimens; septalial plates very short or absent; septum reduced, only existing as ridge, running about $\frac{1}{3}$ to $\frac{1}{2}$ of valve length; hinge plates relatively broad, almost horizontal and tapering forward; inner socket ridges well developed, clearly demarcated from hinge plates; crural bases narrow, but well formed, given off dorsally from inner margins of hinge plates, increasing in width constantly forward; crura calcarifer, about $\frac{1}{4}$ as long as dorsal valve, relatively short compared with those in *Rhynchonelloidella*, with expanded hammer-like heads or short hooks; primary lamellae very long, vertically plate-like in sections.

OBSERVATIONS.—The numerous specimens at different growth stages allow development of the shell shape to be traced.

1. Juvenile specimens are depressed, almost circular. The ventral valve is slightly convex and the dorsal valve

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 31422a	14.8	18.3	13.2	113	24	8	7
USNM 75583a	13.0	14.0	9.6	110	20	7	6
USNM 75583b	14.0	14.2	10.6	106	22	6	5
USNM 123746a	14.9	18.6	13.2	114	24	7	6
USNM 123758a	14.5	16.1	13.7	112	21	7	6
USNM 123758b	11.6	12.5	10.2	103	17	6	5
USNM 306011a	13.5	15.9	12.1	116	23	7	6
USNM 306011b	13.2	16.9	13.3	116	24	8	7
USNM 306011c	14.9	17.7	11.4	117	23	7	6
USNM 306011d	14.0	16.7	11.9	117	23	9	8
USNM 375028a	16.7	18.5	14.0	107	19	5	4
USNM 375028b	12.8	16.1	11.7	114	24	7	6
USNM 375028c	13.6	15.5	12.6	108	20	6	5
USNM 375028d	12.3	14.	11.4	109	18	5	4
USNM 429212	14.0	16.2	13.2	116	23	9	8
USNM 429213	13.3	14.5	11.6	114	22	8	7
USNM 429214	13.7	14.4	11.8	116	22	9	8
USNM 429215	15.8	16.9	13.3	118	23	8	7
USNM 429216	15.8	18.8	13.2	118	23	8	7
USNM 429217	12.6	14.6	10.9	114	22	7	6

is almost planate, with anterior commissure rectimarginate. At this stage, no costae are developed, except at margins with faint signs of costation. The beak is straight and shallow, but clear sulcation exists at dorsal umbo.

2. As it grows, the anterior commissure becomes widely arched dorsally and feeble costae occur around the margins of the valves. At this stage, the umbonal sulcation is visible and the beak becomes substraight to suberect.

3. In the third stage, the shell becomes variably shaped: subtrigonal, subcircular, or subpentagonal, slightly wider than long. The dorsal valve becomes more convex than the opposite one, but generally no eversion occurs anteriorly. At this stage, the umbonal sulcation becomes gradually indistinct, often only recognizable as a obscure depression. Costae become well developed, smooth areas occupy about half of the valve length and anterior commissure is moderately uniplicate. Correspondingly, the fold is raised slightly above the slopes and the ventral valve tends to be flattened anteriorly.

4. At the adult stage, the shell has all the characteristics of the species. The dorsal valve is strongly convex and everted anteriorly, the anterior commissure becomes highly uniplicate and the fold is well elevated. The posterior smooth areas are reduced to 1/2 to 1/3 of the valve length and the umbonal furrow becomes very feeble.

5. At the gerontic stage, the beak becomes erect to slightly incurved and the shell is thickened along the front margins. The foramen becomes obsolete and the umbonal sulcation is hardly recognizable.

At all these stages, the beak ridges are always angular and the narrow interareas are clearly shown and slightly concave.

REMARKS.—One of the most important characteristics of *Thurmannella* as defined by Leidhold in 1921, was the existence of a septalium in the dorsal valve. Leidhold (1921) originally defined the term “septalium” based on the structures in *Septaliphoria* and *Thurmannella*. At that time he illustrated several specimens to show the septalium. In his illustrations, *Thurmannella* did show a well developed and V-shaped short septalium (Leidhold, 1921, pl. 5: figs. 5, 6). However, none of the present specimens was seen to have a septalium, either in sectioned specimens or by excavation. Childs also illustrated two sets of serial sections for the genus *Thurmannella* (1969:48, text-fig. 19, *Thurmannella obtrita*; 52, text-fig. 20, *Thurmannella acuticosta*), but neither possesses a septalium, but rather long septalial plates. Clearly, the septalium is also a variable structure in *Thurmannella*, even at the species level, so we do not regard the septalium as a key character for the genus.

Subfamily TETRARHYNCHIINAE Ager, 1965

Aalenirhynchia, new genus

TYPE-SPECIES.—*Rhynchonella subdecorata* Davidson, 1851–1852, appendix:21.

DIAGNOSIS.—Shell large, inequivalve, strongly uniplicate to subcynocephalous; beak very short, incurved, generally concealing foramen and deltidial plates; fold and sinus pronounced. Shell coarsely ribbed, no posterior smooth areas. Septum high, hinge plates very narrow; crura radulifer; septalium and septalial plates not developed; dental plates short.

AGE AND DISTRIBUTION.—Aalenian; Europe.

REMARKS.—The genus described here includes forms of Aalenian age that have large and strongly uniplicate shells, with many angular ribs, but no posterior smooth areas. The two species included in the genus have small beaks and tiny foramina. The new genus is externally distinct and easily distinguished from other contemporary forms.

In general characters, the new genus should be put in the subfamily Tetrarhynchiinae without much doubt, but it is similar to *Homoeorhynchia* and *Rhynchonelloidea* of the Rhynchonellinae, in having strong uniplication and cynocephalous profile, as well as a distinctive fold and sinus. The type-species of the two latter genera, however, are generally smaller and have but few strong ribs anteriorly after a long and pronounced smooth stage on each valve. Internally these genera have well-developed septalia and longer septa, although they also have radulifer crura.

The new genus resembles *Isjuminella* Makridin and *Cymatorhynchia* Buckman of the subfamily Tetrarhynchiinae in some aspects, especially in lacking posterior smooth areas and having many strong ribs. The species *Rhynchonella walkeri* Rollier, 1918, is somewhat similar to *Cymatorhynchia quadriplicata* (Zieten), to which Almeras (1966a) placed it as a subspecies, but its small, incurved beak and well elevated fold

and deep sinus indicate that it is more closely related to *Rhynchonella subdecorata* Davidson rather than to *Cymatorhynchia cymatophorina* Buckman. The type-species *Aalenirhynchia subdecorata*, as its name implies, is similar to *Isjuminella decorata* (Schlotheim) in exteriors. However, the latter has strong secondary thickenings and incurved crura that show vertical plate-like sections. Buckman (1918) put *Rhynchonella subdecorata* into *Quadratorhynchia* of Early Jurassic age and thought it might be related to *Quadratorhynchia quadrata* Buckman. Surely this species shares external similarity with *Quadratorhynchia quadrata*, but that genus has long dental plates that are close to each other, and a well developed pedicle collar that is supported by a septum, as well as a very short septum in the dorsal valve.

The Aalenian genus *Druganirhynchia* Tchoumatchenko, 1983, resembles the new genus in shape and other external features, but differences also are clear. Externally, *Druganirhynchia* has a small and subglobose shell, the dorsal valve is not everted, and the anterior commissure is not as high as in the new genus. Its beak is massive, the foramen and deltidial plates are not hidden, and the costae are finer and more numerous. Its fold and sinus are less developed than in the new genus. Internally, *Druganirhynchia* has strong secondary thickenings of both valves, the dorsal septum is not developed; it is either absent or exists just as a ridge. The hinge plates are very narrow, although the genus has radulifer crura and lacks a septalium. Although Tchoumatchenko (1983) placed *Druganirhynchia* in the subfamily Cyclothyridinae Makridin, 1955, the external and internal features that he described, however, leave little doubt that *Druganirhynchia* should be transferred to the Tetrarhynchiinae, and is closely related to the new genus.

Deltarhynchia Cooper (1989:29), from the Bathonian of Saudi Arabia, should be regarded as a direct descendant of the new genus, and is in close external accord with *Aalenirhynchia*, except that this new genus has a longer beak and better developed deltidial plates. Interiorly, the dental plates and dorsal septum in the Arabian genus are much longer than those in the new genus.

Possibly the new genus evolved from the *Tetrarhynchia-Quadratorhynchia* branch of Early Jurassic age, and led to *Deltarhynchia* and to the *Hopkinsirhynchia-Isjuminella* branch in different directions during the early Middle Jurassic.

Aalenirhynchia subdecorata (Davidson, 1853), new combination

FIGURE 37; PLATE 1: FIGURES 18, 19

Rhynchonella subdecorata Davidson, 1851–1852, appendix:21, pl. A: figs. 23–26; 1878:198, 201.—Greppin, 1900:176, pl. XIX: figs. 9, 10.—Rollier, 1918:147.—Charles, 1950:8, pl. 2: fig. 4a,b.

Rhynchonella tetraedra Sowerby.—Davidson, 1851–1852:95, pl. 18: fig. 10 [in part].

Quadratorhynchia subdecorata (Davidson).—Buckman, 1918:43, 40.—Almeras, 1964:37, 126.

Homoeorhynchia subdecorata (Davidson).—Ager, 1956:27.

TYPE.—*Holotype*: Davidson, 1851–1852, pl. 18: fig. 10; from the Inferior Oolite (lower part, Aalenian), near Cheltenham, Gloucestershire, England.

MATERIAL STUDIED.—3 well-preserved specimens from the Inferior Oolite (Pea Grit, Aalenian), Leckhampton Hill, Gloucestershire, England.

DESCRIPTION.—Shell medium to large, subtrigonal to subpentagonal in outline; shell with strong uniplication, more or less trilobate; inequivalve, unequally biconvex to almost convex-planate, dorsal valve everted anteriorly; triangular or subcynocephalous to cynocephalous in profile. Lateral commissure depressed ventrally at about 20–25 degrees; anterior commissure strongly uniplicate; linguiform extension high subtrapezoidal to trigonal in shape, with truncated termination.

Beak very small, short, incurved; almost touching dorsal umbo; foramen and deltidial plates hidden; beak ridges obtuse, defining very small and curved interareas.

Ventral valve slightly convex posteriorly, tending to be flattened or even slightly concave anteriorly; sinus distinct, broad and fairly deep, occurring at posterior third of valve and curved toward dorsal valve abruptly at anterior margin, resulting in a high triangular tongue.

Dorsal valve much more convex than ventral one, everted anteriorly; fold prominent, occurring at posterior third of valve and continuing to elevate anteriorly as flanks curve down.

Shell covered with subangular ribs, on each valve numbering 18–21, with 3–5 on fold and 2–4 in sinus; ribs on fold and in sinus stronger than those on slopes; growth lines feeble.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 123721a	19.5	27.5	21.4	108	21	6	5
USNM 123721b	20.3	26.5	22.1	114	19	3	2
USNM 123721c	21.5	24.4	20.1	108	18	5	4

INTERIOR.—Slightly secondary thickenings exist only in posterior cavities. Short pedicle collar present; deltidial plates disjunct; delthyrium well developed, rectangular in shape; lateral cavities short and narrow; dental plates parallel to each other, getting off ventral floor at hinge zone; teeth very short and small, with expanded ends and crenulations.

No septalium or septalial plates in dorsal valve; septum high at its posterior part but reduced into ridge beyond hinge zone, running about $\frac{1}{4}$ to $\frac{1}{3}$ of valve length; hinge plates narrow, declined dorsally at posterior and becoming subhorizontal anteriorly; inner socket ridges recognizable only at anterior parts; crural bases not well formed; crura radulifer, about $\frac{1}{3}$ length of dorsal valve, rising from inner margins of hinge plates and curved ventrally forward, appearing as vertical plates at distal ends in section.

REMARKS.—This is a rare species, so heretofore no attention was paid to its interior. Ager (1956:27) put it in *Homoeorhynchia* on the basis of its sharply folded shell and high subtrigonal

FIGURE 37.—Serial sections of *Aalenirhynchia subdecorata* (Davidson); USNM 123721b, L 20.3, W 26.5, T 22.1, A 114; from the Inferior Oolite (Pea Grit, Aalenian), Leckhampton Hill, Gloucestershire, England.

tongue. Certainly the species is externally similar to *Homoeorhynchia*, especially to *Homoeorhynchia meridionalis* (Deslongchamps), which is almost the same size as this species. However, *Homoeorhynchia meridionalis* has only a few strong ribs anteriorly after a long smooth stage. Internally, most properly known species of *Homoeorhynchia* have a long and high septum and well developed septalium in dorsal valve, though they also have radulifer crura (Almeras, 1979a, b; Shi, 1987b). *Rhynchonella subdecorata*, in contrast, has many costae, all of which originate at the very posterior parts of the umbonal regions, and no smooth areas left. Interiorly, this species has a short septum but no septalium.

Aalenirhynchia subdecorata (Davidson) resembles general aspects of *Rhynchonelloidea*, but is much bigger than most species of the that genus, and has a smaller beak and a tiny foramen. *Rhynchonelloidea ruthenensis* (Reynes), the type-species, has a few strong ribs and clear smooth areas on both valves.

Ager, Childs, and Pearson (1972) pointed out that this shell-shape occurs repeatedly in different genera, implying an adaption to similar environments. We agree with this point, but also emphasize that the smooth stage in early ontogeny does not reflect adaptation, but is genetic.

***Aalenirhynchia walkeri* (Rollier, 1918),
new combination**

PLATE 17: FIGURE 14

Rhynchonella subdecorata var.? Davidson, 1878:201, pl. 29: fig. 13.

Rhynchonella walkeri Rollier, 1918:148.

Cymatorhynchia quadriplicata var. *walkeri* (Rollier).—Almeras, 1966a:79.

TYPE.—*Lectotype*: Davidson, 1878, pl. 29: fig. 13; designated by Rollier, 1918:148; from the Inferior Oolite (Aalenian), near Cheltenham, Gloucestershire, England.

MATERIAL STUDIED.—1 perfect specimen from the Inferior Oolite (Pea Grit, Aalenian), Leckhampton Hill near Cheltenham, Gloucestershire, England.

DESCRIPTION.—Shell medium to large, subpentagonal in outline, subglobose in profile; dorsal valve much more convex than ventral one; anterior commissure strongly uniplicate; tongue high, trapezoidal in shape.

Beak very short and small, incurved, touching dorsal umbo; foramen and deltidial plates hidden; small planoareas present.

Ventral valve moderately convex posteriorly, slightly flattened anteriorly; sinus broad and deep, occurring at posterior $\frac{1}{3}$ of valve, with flattened bottom and distinct lateral borders.

Dorsal valve swollen, with greatest convexity at anterior $\frac{1}{3}$, but recurved anteriorly; fold broad, with rounded top and well elevated above slopes, starting at posterior $\frac{1}{3}$ of valve and making valve more or less trilobate.

Ribs strong, angular, on each valve numbering 19, with 5 on fold and 4 in sinus; growth lines feeble.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 429165	22.5	26.3	18.9	104	19	5	4

INTERIOR.—Not investigated.

REMARKS.—This is a barely known species. Davidson (1878) thought that it might be a variant of *Rhynchonella subdecorata* whose characters lay between *R. subdecorata* Davidson and *R. subtetrahedra* Davidson. Rollier (1918) took the specimen illustrated by Davidson (1878, pl. 29: fig. 13) as a new species and named it *R. walkeri*, while pointing out that the species was close to *R. quadriplicata* (Quenstedt). Almeras (1966a) adopted this idea and arranged it as a variant of *Cymatorhynchia quadriplicata* (Quenstedt), with a comment that *R. walkeri* was similar to his new species *Cymatorhynchia cymatophorinoides*. It is true that *R. walkeri* resembles *Cymatorhynchia quadriplicata* in some aspects, whereas the former has much stronger fold and ribs, as well as a very short, incurved beak that touches the dorsal umbo and conceals the foramen and deltidial plates. These characters are closer to those of *R. subdecorata* than those of *C. quadriplicata*. The present authors, therefore, place this species in the new genus despite the lack of certainty regarding internal features.

***Burmishynchia* Buckman, 1918**

Burmishynchia Buckman, 1915:76 [nomen nudum]; 1918:49.—Reed, 1927:256.—Muir-Wood, 1937:10–13 [in part].—Fischer, 1964:27 [in part].—Ager, 1965a:H612.—Rousselle, 1965a:37 [in part].—Proso-rovskaia, 1968:57.—Fischer, 1969:64 [in part].—Ager, Childs, and Pearson, 1972:199.—Laurin, 1974:396 [in part].—Jin, Sun and Ye, 1979:158.—Sun, 1981:199.—Dardeau and Laurin, 1982:475 [in part].—Laurin, 1983:158 [in part].—Ovtsharenko, 1983:25.—Laurin, 1984a:387 [in part].—Almeras, 1987:175 [in part].—Almeras and Moulán, 1988:276 [in part].—Cooper, 1989:15 [in part].—Sun, 1990:288.

?*Burmishynchia* Buckman.—Tokuyama, 1957:131.—Campbell, 1965:95.

Not *Burmishynchia* Buckman.—Muir-Wood, 1925:183.—Weir, 1929:37.—Díaz-Romero, 1931:13, 14.—Douglas and Arkell, 1932:154.—Stefanini, 1932:110.—Muir-Wood, 1935:90.—Hudson, 1958:421.—Rousselle, 1966:346.—Dubar, 1967:34.—Ching, Sun, and Rong, 1976:299.—Parnes, 1981:21.—Laurin, 1984b:433–440.

TYPE-SPECIES.—*Burmishynchia gutta* Buckman, 1918:156.

EMENDED DIAGNOSIS.—Shell small to medium; globose; beak nearly straight to incurved; foramen small, hypothyridid; deltidial plates disjunct to just conjunct; shell with numerous rounded costae, no posterior smooth areas; fold and sinus developed variably, anterior commissure rectimarginate to uniplicate. Dorsal septum present, crura radulifer; septalium variable.

AGE AND DISTRIBUTION.—Late Bajocian to Bathonian, ?Early Callovian; Asia, Africa, Europe, and ?Australia.

REMARKS.—*Burmishynchia* is one of the most important Middle Jurassic rhynchonellid genera and certainly is widespread in the Tethyan Realm. According to the literature, more

than 90 species have been reported in the genus from Asia, Europe, Africa, and Australia. However, since the erection of the genus by Buckman in 1918, its interior has not been studied properly, especially in the type-species, and the Burmese specimens were actually not known. Because *Burmishynchia* is an ordinary-looking rhynchonellid and shares many common characteristics with other contemporary genera, it is not easy to distinguish it from several other genera confidently without interiors, so, much confusion has arisen and many different kinds of rhynchonellids have been included in the genus. Another cause for this confusion is that Buckman (1918) erected too many species for the genus. Many of those species were based on trivial characters and some were based on poorly preserved specimens. In the light of present knowledge, many Buckman species are nothing more than variants within populations. On the other hand, Buckman over-emphasized the importance of muscle scars, dental plates, and shell shape in his classification. Actually the muscle scars might be useful for the subdivision of a subfamily or family, but at the generic level their utility was exaggerated.

As illustrated by the generic synonymy, the name *Burmishynchia* has been applied indiscriminately to species all over the world, many with no information on interiors and some simply recorded by name, without description or illustration. Examples are those from Sahara and Tunisia (Dubar, 1938, 1967), Somaliland (Stefanini, 1932; Muir-Wood, 1935), Kenya (Weir, 1925, 1929, 1930, 1938), Morocco (Rousselle, 1965a, 1973, 1976), Algeria (Rousselle, 1974; Almeras, 1984), Ethiopian (Cotteau, 1956), India (Sahni, 1936, 1939, 1940, 1958; Mitra and Ghosh, 1973; Gupta, 1975, 1978), Pakistan (Muir-Wood, 1937), Pamirs (Ovtsharenko, 1983), Middle Asia (Prozorovskaya, 1968, 1985; Ovtsharenko, 1963, 1969, 1975), Japan (Tokuyama, 1957, 1959), Egypt (Frag and Gatinaud, 1960, 1962; Abbate et al., 1974), Israel (Hudson, 1958; Parnes, 1981), Jordan (Muir-Wood, 1925), Saudi Arabia (Almeras, 1987; Cooper, 1989), Australia (Campbell, 1965), New Zealand (Trechmann, 1923; Allan, 1945; Marwick, 1945), as well as those recorded from Madagascar and Afghanistan. Some of these specimens are so different from the Burmese specimens that they can hardly be accepted as the same genus, although some are difficult to be proved uncongeneric.

We believe strongly that most species recorded from the south shore of the Tethys, especially those from the Middle East and Africa, do not belong to this genus, which developed mainly along the north shore of the Tethys, especially at the eastern end. Externally, those forms from the south shore of the Tethys usually have coarse ribs, strong beaks, and a typically rimmed foramen. They are not quite coincident with those from Burma. As far as the exteriors are concerned, it seems that the *Burmishynchia termierae* Rousselle–*Burmishynchia preathiensis* Rousselle group might belong to *Baeorhynchia* Cooper, 1989, and the *Burmishynchia wieri* (Diaz-Romero)–*Burmishynchia gregoryi* Weir group should be assigned to *Kutchirhynchia*, *B. subversabilis* Weir and its related forms

should be transferred to *Daghanirhynchia*, *B. moulani* Almeras to *Conarosia* Cooper, 1989, and *B. nazeri* Almeras to *Colpotoria* Cooper, 1989. The specimens described as *Burmishynchia* sp. by Parnes (1981:21, pl. 2: figs. 13–15) possibly belong to *Amydroptychus* Cooper, 1989, while the *B. sp.* “group” *hopkinsi* described by him (Parnes, 1981:21, pl. 2: figs. 16–18) might be a species of *Pycnorhynchia* Cooper, 1989. It is also possible that some other species recorded from the Middle East and Africa that are presently under *Burmishynchia* may actually belong to *Echyrosia* Cooper, 1989, or *Schizoria* Cooper, 1989.

Many species of the genus were reported from England and France, but most of their interiors were not properly studied until recently. Laurin (1984a, b) did good work on the internal structures of some species, concluding that *Burmishynchia leedsi*, *B. fusca*, *B. gremifera*, and related forms belong to his new genus *Lotharingella* rather than to *Burmishynchia*, and that most species from England that were described by Buckman (1918) under *Burmishynchia*, such as the *Burmishynchia ornithella*–*B. polystema*–*B. vagans*–*B. tumida* group, should be transferred into *Kallirhynchia*. On the other hand, Laurin has also included some quite distinct forms in this genus, such as *Rhynchonella decorata* Schlotheim and *Rhynchonella quadricristata* Rollier, which are fairly large, strongly ribbed, and have thick shells. Our study and close comparison with the work of Laurin (1984a, b) negates this inclusion. These forms are so different from the *B. gutta* group both internally and externally that they can hardly be regarded as related forms. *Rhynchonella obsoleta* Sowerby and *Rhynchonella rostrata* Sowerby are also species that are often recorded under *Burmishynchia*. The present study shows that they have a very reduced septum, cilifer crura in the dorsal valve, and therefore have been transferred into the new genus *Obsoletirhynchia*. It appears that the only European forms that are closely related to the *Burmishynchia gutta* group of Burma are those of the *Rhynchonella hopkinsi* Davidson–*Rhynchonella elegantula* Deslongchamps group. The present study shows that these forms differ both externally and internally from the eastern Tethyan ones. Therefore, *Burmishynchia* has been divided into two subgenera in this paper, *Burmishynchia* s.s. and *Hopkinsirhynchia*. These two subgenera are not only separable morphologically, but also geographically and chronologically.

Our research indicates that the septalium is variable in this genus, as well as in other genera of the subfamily, so we do not emphasize it as a diagnostic generic character.

Subgenus *Burmishynchia* (*Burmishynchia*) s. s. Buckman, 1918

TYPE-SPECIES.—*Burmishynchia gutta* Buckman, 1918:156.

EMENDED DIAGNOSIS.—Shell small to medium, suboval to subcircular; valves almost equal in convexity and depth, globose in profile; fold and sinus feeble, anterior commissure

straight or slightly uniplicate; beak short, suberect to incurved; foramen small, hypothyridd; beak ridges and interareas not developed; shell with numerous fine rounded costae. Dental plates long, subparallel; dorsal septum low, hinge plates broad, subhorizontal; crura radulifer, incurved ventrally; septalium present or absent.

AGE AND DISTRIBUTION.—Late Bajocian to Early Bathonian; Asia, Europe, ?Africa, and ?Australia.

REMARKS.—*Burmihynchia* (*Burmihynchia*) s.s. seems mainly distributed along the north shore of the Tethys where it flourished at its eastern end, especially in Burma, western Yunnan, northern Tibet, and southern Qinghai of China, as well as in the Pamirs and Central Asia. Interior features of most species from Burma were not properly known, but those of many species from China have been investigated thoroughly. Shi has systematically studied 9 species of the subgenus represented by hundreds of specimens from northern Tibet, western Yunnan, and southern Qinghai, China. Among the 28 sectioned specimens of these species, only four specimens have a well developed V-shaped septalium, three specimens have a short, incomplete septalium, and the other 21 specimens have no septalium at all. All these specimens have broad hinge plates, reduced septum, and strongly incurved radulifer crura. So far no other species of the subgenus from Burma have been studied with regard to interior structures except the one studied here. The sectioned specimen, from the Namyau Beds of North Shan States (*Burmihynchia gutta* Buckman, the type-species of the genus) has a well developed V-shaped septalium, which is 0.8 mm long, 1.1 mm deep, and is supported by a low septum. It also has well demarcated inner socket ridges, but the other characters are the same as those of the Chinese specimens.

Burmihynchia (*Burmihynchia*) *gutta* Buckman, 1918

FIGURES 38–41; PLATE 4: FIGURES 1, 2, PLATE 16: FIGURES 11–13

- Burmihynchia dattai* Buckman, 1918:152, pl. 3: figs. 7–11.
Burmihynchia globulus Buckman, 1918:157, pl. 5: fig. 1.
Burmihynchia gutta Buckman, 1918:166, pl. 4: figs. 5–8.
Burmihynchia guttula Buckman, 1918:155, pl. 4: fig. 4.
Burmihynchia pyriformis Buckman, 1918:157, pl. 4: figs. 11, 12.
Burmihynchia regularis Buckman, 1918:168, pl. 7: figs. 8, 9.
?Burmihynchia seengensis Buckman, 1918:161, pl. 6: figs. 2–6.
Burmihynchia senilis Buckman, 1918:158, pl. 4: figs. 9, 10.
Burmihynchia subglobosa Buckman, 1918:148, pl. 5: figs. 5, 6.
Burmihynchia nyairongensis Jin, Sun, and Ye, 1979:159, text-fig. 96, pl. 45: figs. 12–15.—Sun, 1981:199, pl. 5: figs. 1–8.
Burmihynchia quinqueplicata Jin, Sun, and Ye, 1979:161, pl. 45: figs. 1–11.—Sun, 1981:200, pl. 5: figs. 9–12.
Burmihynchia shanensis Buckman.—Jin, Sun, and Ye, 1979, pl. 44: figs. 12–15 [in part].
Septaliphoria compta Jin, Sun, and Ye, 1979:158, text-fig. 95, pl. 46: figs. 1–8.
Kallirhynchia nudata Buckman.—Ovtsharenko, 1983:25, pl. 1: figs. 11–13.

TYPE.—*Holotype*: Buckman, 1918, pl. 4: fig. 5; from the Namyau Beds, Northern Shan States, Burma.

MATERIAL STUDIED.—2 specimens from the Namyau Beds,

Northern Shan States, Burma; 53 specimens from the Matuo Formation (Lower Bathonian), North Tibet and South Qinghai, China.

EMENDED DIAGNOSIS.—Shell small, globose; oval to broadly obovate in outline; almost equally biconvex or dorsal valve slightly more convex than ventral one; foramen small, hypothyridd; deltidial plates disjunct; fold feeble, hardly recognizable; sinus existing only as depression at anterior part; anterior commissure nearly rectimarginate to moderately arched; each valve covered with 22–30 fine rounded costae; growth lines feeble.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 132444	17.7	16.5	13.5	81	26	6	5
USNM 429222	17.5	17.3	12.2	82	24	6	5
H 244324	20.6	17.1	15.2	72	26	5	4
H 244333	15.2	13.2	13.3	86	26	5	4
H 244610a	19.1	16.8	15.2	76	20	5	4
H 244610b	16.3	15.2	14.2	80	23	6	5
H 244641	17.2	17.0	15.0	82	27	7	6
Y 123602	17.0	15.8	13.0	84	–	–	–

The average dimensions of the other 47 Chinese specimens are: L 17.0 (13–19), W 16 (12–18), T 13.7 (12–17), A 89 (80–94), N 24 (22–28), F 6 (5–7), S 5 (4–7).

INTERIOR.—No noticeable secondary thickenings in either valve. No clear pedicle collar observed in sectioned specimens; delthyrium broad, well developed; lateral cavities narrow and short; dental plates short, generally splitting from ventral floor at hinge zone; divergent to floor posteriorly and tending to be subparallel anteriorly; teeth strong, massive, relatively short, with expanded ends and crenulations, held tightly in sockets; accessory denticulars and dental cavities present.

Dorsal septum short, supporting hinge plates or septalium only at posterior 1–1.5 mm of apical cavity, reduced into ridge forward rapidly and generally less than 1 mm in height. Septalium variable; well developed and V-shaped in topotype specimen (Figure 38), 0.8 mm long, 1.1 mm deep and supported by a low septum; in seven sectioned Chinese specimens, one of them with a short, V-shaped septalium, one possessing an incomplete, very short septalium, but other five specimens having no septalium. Hinge plates broad, subhorizontal posteriorly and becoming slightly declined dorsally at anterior; inner socket ridges low, well demarcated; crural bases very narrow, but clearly formed and subtrigonally shaped in cross section, given off dorsally from inner margins of hinge plates; crura radulifer, $\frac{1}{4}$ to $\frac{1}{3}$ as long as dorsal valve, with expanded and ventrally incurved distal ends, generally appearing parentheses-like in section. Burmese crura slightly shorter, CL/LD (crural length/dorsal valve length) being 0.25; 7 Chinese specimens with CL/LD of 0.24, 0.25, 0.28, 0.29, 0.29, 0.30, and 0.32.

FIGURE 38.—Serial sections of *Burmihynchia* (*Burmihynchia*) *gutta* Buckman; topotype, USNM 123602, L 17.0, W 15.8, T 13.0, A 84; from the Namyau Beds (Bathonian), Northern Shan State, Burma.

***Burmihynchia* (*Hopkinsirhynchia*), new subgenus**

TYPE-SPECIES.—*Rhynchonella hopkinsi* Davidson, 1851–1852:97.

DIAGNOSIS.—Shell small to medium, inequivalve, trilobate; subtrigonal to subpentagonal, beak long and massive; fold and sulcus well developed; anterior commissure uniplicate, with

high trapezoidal tongue; costae numerous, coarse; shell wall thick, secondarily thickened; septum stout, reduced; septalium generally present and V-shaped; hinge plates narrow and thick; crura radulifer, curved ventrally.

AGE AND DISTRIBUTION.—Middle Bathonian to Lower Callovian; England, France, Germany, Switzerland, Middle East, and Africa.

FIGURE 39.—Serial sections of *Burmihynchia* (*Burmihynchia*) *gutta* Buckman; H244324, L 20.6, W 17.1, T 15.2, A 72; from the Matuo Formation (Lower Bathonian), Nardigangre, Northern Tibet, China.

REMARKS.—This subgenus is externally distinct from *Burmihynchia* s.s.; in most species the fold and sulcus produce a trilobate shell. Generally the shell wall is thick and has coarsely subangular costae. Gerontic shells are thickened at the margins and are distinctly trilobate and strongly costate, as in *Burmihynchia turgida* Buckman and *Burmihynchia thierachensis* (Fischer), which are similar to the *Rhynchonella decorata* Schlotheim–*Rhynchonella quadricristata* Rollier group. At the

other extreme, however, as in *Rhynchonella elegantula* Deslongchamps and *Burmihynchia multiplicata* Laurin, the shell is closer to *Burmihynchia* s.s., although it also has well developed trilobation. It seems best here to regard it as a subgenus of *Burmihynchia* Buckman, even though we retain the suspicion that it may not be congeneric with *Burmihynchia* s.s. Morphologically this subgenus appears to lie between *Burmihynchia* s.s. and *Isjuminella*, but also resembles *Gonio-*

FIGURE 40.—Serial sections of *Burmihynchia* (*Burmihynchia*) *gutta* Buckman; H244641, L 17.2, W 17.0, T 15.0, A 82; from the Matuo Formation (Lower Bathonian), Northern Tibet, China.

rhynchia in having secondary thickenings in both valves, especially along the margins in the gerontic stage, as well as its clear trilobation.

Comparison of interiors reveals that *Burmihynchia* (*Hopkisirhynchia*) resembles *Isjuminella* in that both forms possess notable secondary thickenings, thick shells, stout septa, narrow hinge plates, and strongly curved but short crura.

***Burmihynchia* (*Hopkisirhynchia*) *hopkinsi*
(Davidson, 1852)**

FIGURE 42; PLATE 4: FIGURES 3–5, 16

Rhynchonella hopkinsi M'Coy, MS.—Davidson, 1851–1852:97, appendix:21, pl. A: figs. 20, 21. [Not Choffat, 1947, pl. 19: figs. 6–17.—Charles, 1950:6, pl. 7: fig. 10.]

?*Burmihynchia calculosa* Buckman, 1918:222, pl. 16: fig. 7.

Burmihynchia hopkinsi (Davidson).—Buckman, 1918:49, pl. 16: figs. 9, 10.

Burmihynchia restitula Buckman, 1918:222, pl. 16: fig. 11.

Rhynchonella hopkinsi M'Coy-Davidson.—Rollier, 1918:159.

Burmihynchia hopkinsi (Davidson).—Laurin, 1984a:388, pl. 7: figs. 5–9.

TYPE.—*Lectotype*: Davidson, 1854, pl. A: figs. 20, 21; refigured by Buckman, 1918, pl. 16: fig. 9; from the Great Oolite, Minchinhampton, Gloucestershire, England. (Rollier mentioned that the holotype specimen might be from France).

MATERIAL STUDIED.—8 well-preserved specimens from the Bathonian, Pas de Calais and Anney, France.

DESCRIPTION.—Shell medium, globose, inequivalve; sub-oval to subpentagonal in outline, strongly domed in anterior view; dorsal valve swollen and much more convex than ventral one. Lateral commissures oblique ventrally; anterior commissure highly uniplicate; linguiform extension wide and high, trapezoidal to rectangular in shape.

Beak long, massive, nearly straight at young stage and becoming strongly incurved at gerontic stage, almost touching dorsal umbo; foramen small, circular, hypothyriddid to sub-mesothyriddid; deltidial plates narrow, conjunct; beak ridges subangular to obtuse; interareas narrow, but well defined and concave.

Ventral valve adequately convex, recurved evenly; sinus

FIGURE 41.—Serial sections of *Burmira* (*Burmira*) *gutta* Buckman; Y132444, L 17.7, W 16.5, T 13.5, A 81; from the Matuo Formation (Lower Bathonian), south of Wenquan, Southern Qinghai, China.

well developed, starting at posterior $\frac{1}{3}$ of valve, generally shallow and broad, with rounded or flattened bottom, in some specimens fairly deep.

Dorsal valve inflated and domed, with greatest convexity at anterior part, but seldom everted anteriorly; fold well developed and wide, raised above slopes distinctly, starting at posterior $\frac{1}{3}$ to $\frac{1}{2}$ of valve, with rounded top, making valve more or less trilobate.

Costae numerous, coarse, subrounded to subangular, on each valve numbering 21–29, with 4–7 on fold and 3–6 in sinus; growth lines fine, distinct, conspicuous at anterior margins. At gerontic stage, shell thickened markedly along margins, sides becoming almost parallel in anterior view.

FIGURE 42 (facing page).—Serial sections of *Burmira* (*Hopkinsira*) *hopkinsi* (Davidson); USNM 429225, L 21.9, W 19.7, T 17.4, A 83; (Middle Bathonian) Ancy, France.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 32112a	20.2	17.5	18.2	89	30	6	5
USNM 75100	18.0	15.2	15.1	77	27	6	5
USNM 104676a	18.5	14.1	15.2	87	27	6	5
USNM 104676b	17.1	16.5	15.0	103	26	7	6
USNM 429223	22.2	21.5	19.9	90	22	4	4
USNM 429224	23.8	21.2	23.2	83	22	5	4
USNM 429225	21.9	19.7	17.4	83	26	6	5

INTERIOR.—Obvious secondary thickenings in umbonal cavities of both valves. Short pedicle collar present; delthyrium broad, rectangular in shape; lateral cavities wide, but short; dental plates subparallel, very short, splitting away ventral floor far from reaching hinge zone; teeth very strong, massive, mallet-like, with crenulations; accessory denticulars and dental cavities well shown.

Dorsal septum low and stout, reduced into ridge after hinge zone; septalium short, narrow and deep, V-shaped; hinge plates narrow, thick, and concave ventrally at posterior parts, becoming inclined ventrally forward; inner socket ridges very well developed, fairly high, which constitute troughs together with inclined hinge plates anteriorly; radulifer crural bases weak, rising from inner margins of hinge plates and markedly curved toward ventral valve at distal ends, about $\frac{1}{4}$ dorsal valve length.

REMARKS.—This species is well known in the Bathonian of England and France, but hitherto the interior was not properly studied. Ager, Childs, and Pearson (1972:199) mentioned that it is internally characterized by having a thick shell, clear secondary thickenings in both valves, and a massive septum reminiscent of *Goniorhynchia*. Juvenile specimens are narrower than adults, have finer costae, and are similar to *Burmishynchia* s.s. As it grew, the shell became broader and less costate, the fold became more elevated, making it more similar to *Isjuminella decorata* (Schlotheim) except the latter is much larger and has stronger ribs.

***Burmishynchia* (*Hopkinsirhynchia*) *elegantula*
(Deslongchamps, 1863)**

PLATE 4: FIGURES 12, 13

Rhynchonella elegantula (ex Bouchard MS) Deslongchamps, 1863:62, pl. 10: fig. 7.

Burmishynchia concinnoides (d'Orbigny).—Buckman, 1918:222, pl. 16: fig. 8.

Burmishynchia elegantula (Deslongchamps).—Buckman, 1918:49.

Rhynchonella elegantula (Bouchard) Deslongchamps.—Rollier, 1918:160.—Charles, 1950:3, pl. 1: fig. 3.

Rhynchonelloidella elegantula (Bouchard, Deslongchamps).—Fischer, 1969:69, text-fig. 8, pl. 7: figs. 5, 6.

Rhynchonella elegantula Deslongchamps.—Laurin, 1977:889–903, pl. 1.

Burmishynchia elegantula elegantula (Deslongchamps).—Laurin, 1984a:395, pl. 8: figs. 9–11.

?*Burmishynchia elegantula burgundiae* Laurin, 1984a:396, pl. 8: figs. 12–17.

TYPE.—*Neotype*: Laurin, 1984a, pl. 8: fig. 9; from the Upper Bathonian, Belle-et-Houlefort, Pas-de-Calais, France.

MATERIAL STUDIED.—15 well-preserved specimens from the Upper Bathonian of Marquise and Les Essalolis, Pas des Calais, France.

DESCRIPTION.—Shell small, outline subtrigonal, profile subglobose; valves unequally biconvex, dorsal valve much more convex than ventral one and slightly everted anteriorly in adult. Lateral commissures oblique ventrally; anterior commissure uniplicate; linguiform extension well developed, rectangular or U-shaped.

Beak acute, fairly long, and rostrate, with incurved tip; foramen small, oval, hypothyriddid, with or without slight rims; deltidial plates disjunct; beak ridges obtuse; interareas small, but well defined and concave.

Ventral valve adequately convex; sulcus well developed, generally shallow and wide with rounded bottom, starting at posterior $\frac{1}{3}$ of valve.

Dorsal valve more convex than ventral one, with greatest convexity at anterior part, less tumid than in *Hopkinsirhynchia hopkinsi* (Davidson); fold well elevated above slopes, occurring at posterior $\frac{1}{3}$ to $\frac{1}{2}$ of valve, relatively narrow and low, with rounded top and clear borders, making valve slightly trilobate. Gerontic shells markedly thickened along margins.

Costae numerous, fine, subrounded, on each valve numbering 22–30, with 4–7 on fold and 3–6 in sulcus; growth lines well developed, conspicuous near anterior margin.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 75584a	13.5	13.8	8.8	83	24	6	5
USNM 75584b	12.4	11.5	8.7	82	23	6	5
USNM 75584c	11.6	11.6	8.6	90	26	7	6
USNM 19886a	13.7	12.2	11.2	78	29	7	6
USNM 19886b	12.4	11.9	9.3	75	25	6	5
USNM 64441a	13.3	13.2	12.0	83	27	6	5
USNM 64441b	11.5	11.5	9.5	88	28	7	6
USNM 64441c	12.2	12.4	9.2	90	22	6	5
USNM 64441d	12.7	13.5	10.5	92	24	6	5
USNM 64441e	11.7	11.7	10.3	88	23	5	4

INTERIOR.—Not investigated.

REMARKS.—Fischer (1969:70, fig. 8) illustrated a set of serial sections of the species, showing clear secondary thickenings in the umbonal cavities and a very short pedicle collar. Dental plates are parallel to each other and the teeth are massive. The dorsal septalium is well developed and V-shaped, supported by a stronger septum. The hinge plates are narrow and the crura are radulifer, with ventrally curved distal ends. All these characteristics are similar to *B. hopkinsi* (Davidson), except the strong septum. Laurin illustrated two sets of serial sections of *Burmishynchia elegantula burgundiae* Laurin (1984a:264, fig. 171). One shows an incomplete septalium and the other has a well developed, V-shaped septalium, but both of them have narrow hinge plates and strongly incurved radulifer crura, as well as a relatively high septum.

Laurin (1984a) put the specimens illustrated by Fischer

(1969) as *Rhynchonelloidella elegantula* (Bouchard MS, Eudes-Deslongchamps) into his new species *Burmirhynchia proteiformis*. Compared with the specimens illustrated by Laurin (1984a, pl. 9: figs. 5–23), it has been found that Fischer’s specimens have finer and more numerous costae, the beak is much longer than that of *B. proteiformis* Laurin, while the dorsal valve is less tumid than in the latter. *Burmirhynchia* (*Hopkinsirhynchia*) *elegantula* differs from *Burmirhynchia* (*Hopkinsirhynchia*) *hopkinsi* in its much smaller shell, more and finer costae, and much longer beak.

Burmirhynchia (*Hopkinsirhynchia*) *latiscensis*
Laurin, 1974

PLATE 4: FIGURES 6–10, 14, 15, 17, PLATE 14: FIGURES 14, 15, 17,
PLATE 15: FIGURES 9–16

Burmirhynchia latiscensis Laurin, 1974:396–404, pl. 11: figs. A–D, 1–20; 1984a:399.

TYPE.—*Holotype*: Laurin, 1974, pl. 11: figs. A–D; from the Lower Callovian of Chatillon-sur-Seine, France.

MATERIAL STUDIED.—Thousands of silicified specimens, all etched out by acid with well-shown internal structures. All of them are from the Lower Callovian, Chatillon-Sur-Seine, France.

DESCRIPTION.—Shell small, generally subtrigonal to subpentagonal in outline, some of them suboval; subglobose to globose in profile, dorsal valve more convex than ventral one, with greatest convexity at anterior part, but rarely everted. Lateral commissures moderately oblique toward ventral side; anterior commissure uniplicate, with trapezoidal to rectangular tongue, relatively high.

Beak long, massive, suberect to erect; foramen bigger, subcircular, hypothyridid; deltidial plates short and small, disjunct; beak ridges subangular to obtuse; interareas well developed, slightly concave.

Ventral valve moderately convex and regularly curved; sulcus well developed, generally occurring at posterior 1/3 to 1/2 of valve, wide and shallow.

Dorsal valve swollen, but less tumid than in *B. (H.) hopkinsi* (Davidson); fold broad, well elevated above slopes, with rounded top and clear borders, occurring at posterior 1/3 to 1/2 and expanding rapidly forward.

Costae numbering on each valve 20–26, with 4–7 on fold and 3–6 in sulcus; growth lines fine, most obvious at front margins.

INTERIOR.—No secondary thickenings in juveniles; shell very thin; secondary thickenings becoming clear with growth; in adults, shell thickened markedly in both umbonal cavities; gerontic specimens usually strongly thickened posteriorly, callus hiding septum in dorsal valve. Pedicle collar short but clear; delthyrium broad, trapezoidal; lateral cavities well developed. Some specimens having low and short septal ridge, generally 1–3 mm in length; at gerontic stage, callus very thick, low septal ridge generally absorbed and pedicle collar

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 429226	17.1	16.0	12	89	22	7	6
USNM 429227	16.5	15.4	14	88	27	7	6
USNM 429228	16.1	14.2	13	86	24	6	4
USNM 429229	16.3	15.2	12	81	23	6	5
USNM 429230	15.0	14.1	12	82	22	5	4
USNM 429231	16.0	14.2	12	84	19	6	5
USNM 429232	17.3	17.1	14	89	20	6	5
USNM 429233	17.0	14.2	13	76	19	6	5
USNM 429234	17.1	17.1	15	86	20	5	4
USNM 429235	17.2	16.0	14	86	21	6	5
USNM 429236	17.1	15.5	13	88	22	6	5
USNM 429237	17.2	13.1	13	73	20	6	5
USNM 429238	16.4	13.5	12	73	24	7	6

also tending to be absorbed. Dental plates short, just reaching hinge zone, about 1/4 to 1/5 as long as ventral valve, subparallel; gerontic dental plates thickened and reduced, or even partly absorbed, leaving very short parts on ventral floor at apical cavity; teeth massive, short, with ends expanded and crenulate; accessory denticulars and dental cavities present; muscle scars large, long pear shaped.

Dorsal septum generally reduced into ridge or only supporting very short septalium in apical cavity when present; generally septal ridge very low, less than 1 mm in height and running about 1/3 to 1/2 valve length. Septalium variable, usually well developed in juvenile specimens, deep and wide, V-shaped; adult septalium tending to be obsolete and variable in shape; some very short and narrowly V-shaped, supported by low septum; others sitting directly on ventral floor and not supported by septum; in some other specimens septal ridge not inserting between septalial plates, but starting anterior to them; septalium absent from most gerontic specimens, callus at umbonal cavities quite distinct, septal ridge and septalial plates absorbed posteriorly, septal ridge visible only about 2 to 4 mm anterior to dorsal umbonal cavity. Hinge plates generally wide and subhorizontal in young specimens, subtriangular in outline and tapering forward; at adult and gerontic stages, hinge plates becoming thicker and narrower, slightly convex or inclined ventrally. Inner socket ridges lower, but well demarcated from hinge plates and suberect; sockets narrow, deep and long, crescent-shaped in ventral-view, with clear crenulations. Crural bases not well formed, very narrow, present only as thickened ridges along inner margins of hinge plates; crura radulifer, generally about 1/4 dorsal valve length, simple rod-like, curved ventrally forward, without any specified distal ends; dorsal muscle scars clearly shown, composed of four small parts, flanking sides of septal ridge.

OBSERVATIONS.—Young specimens generally are narrow, suboval in shape, with long, acute beak, both valves are less tumid and the fold is broad, low. As it grows, the shell increases in width much more rapidly than in length, so that the shell becomes subtrigonal or subpentagonal, with dorsal valve more convex than the ventral one. The beak becomes massive and the

fold becomes well elevated. Internally the most notable changes are that the secondary thickenings increase as it grows, the septalium becomes obsolete and the septum is gradually reduced, retrogressing from the posterior umbonal cavity toward anterior. The hinge plates thicken with growth and become narrower from junior to adult. The crura remain generally constant, only becoming more obviously curved with growth. The foramen usually is circular and proportionately larger in young specimen, becoming subcircular or oval and relatively smaller in adults. The deltidial plates are usually very narrow and disjunct in the young specimens, becoming wider and just conjunct in adult. This might indicate that as it grows the pedicle became gradually obsolete.

REMARKS.—This species is closely related to *Burmishynchia* (*Hopkinsirynchia*) *hopkinsi* (Davidson) and so is put in this subgenus. The species is externally similar to the contemporary forms *Rhynchonelloidella spathica* (Lamarck) and *Rhynchonelloidella socialis* (Phillips), but is internally quite different. Another French species *Burmishynchia multiplicata* Laurin (1984a:395, pl. 7: figs. 10, 11) from the Middle Bathonian, seems not much different from this species but occurs earlier in age, so is better regarded as a chronological subspecies of this species.

***Burmishynchia* (*Hopkinsirynchia*)? *oxoniensis*
Buckman, 1918**

FIGURE 43; PLATE 13: FIGURES 9–12

Rhynchonella concinna Sowerby.—Clerc, 1904:89, pl. 3: figs. 12, 14 [in part].
Rhynchonella obsoleta Sowerby.—Clerc, 1904:92, pl. 3: fig. 11 [in part].
 ?*Burmishynchia ornitheia* Buckman, 1918:221, pl. 17: fig. 8. [New synonymy.]
Burmishynchia oxoniensis Buckman, 1918:221, pl. 17: fig. 9.
 ?*Burmishynchia patula* Buckman, 1918:221, pl. 17: fig. 10. [New synonymy.]
 ?*Burmishynchia polystema* Buckman, 1918:221, pl. 17: fig. 11. [New synonymy.]
Kallirhynchia concinna (Sowerby).—Laurin, 1984a:381 [in part].

TYPE.—*Holotype*: Buckman, 1918, pl. 17: fig. 9; from the Middle Bathonian, Kidlington, Oxfordshire, England.

MATERIAL STUDIED.—8 well-preserved specimens from the Homomyenmergel and Ferrugineusschicht (Middle to Upper Bathonian), Liesberg Switzerland; 2 specimens from the Middle to Upper Bathonian, Woevre-Ebene, France.

DESCRIPTION.—Shell medium size, subpentagonal, profile subglobose, dorsal valve more convex than ventral one. Lateral commissures deflected ventrally at 15–25 degrees; anterior commissure uniplicate, with well developed and rectangular to U-shaped tongue.

Beak short, acute, erect to slightly incurved; foramen small, circular, hypothryidid; deltidial plates very small, disjunct to just conjunct; beak ridges obtuse; no interareas.

Ventral valve moderately convex; sulcus well developed, relatively narrow and deep, with flattened bottom and well defined borders from slopes, occurring at about mid-valve.

Dorsal valve regularly convex, greatest convexity at anterior

$\frac{1}{3}$ of valve, and reverted anteriorly; fold low, but elevated above slopes at anterior part, with rounded top and well defined borders.

Costae numerous, fine, subrounded to subangular, on each valve numbering 27–36, with 6–8 on fold and 5–7 in sinus; growth lines feeble, visible only at front.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 75871a	19.2	21.7	15.4	104	27	6	5
USNM 75871b	20.1	21.2	15.2	90	29	5	4
USNM 429250	19.5	20.5	14.2	96	30	6	5
USNM 429251	17.5	18.7	12.6	98	34	7	6
USNM 429252	18.7	19.7	14.1	96	30	6	5
USNM 429253	18.0	19.7	14.5	103	28	6	5
USNM 429254	19.5	21.6	16.3	102	35	8	7
USNM 429255	18.7	19.7	15.0	101	31	6	5

INTERIOR.—No noticeable secondary thickenings existing in either valve. Pedicle collar short; delthyrium wide; lateral cavities narrow and short; dental plates short, splitting from ventral floor far anterior to hinge zone; teeth relatively long, less massive, with expanded ends and crenulations; accessory denticulars and dental cavities present.

Dorsal septalium short, narrow, and V-shaped; septum short, supporting septalium only at umbonal cavity and reduced into ridge beyond hinge zone, running about $\frac{1}{3}$ valve length; hinge plates broad, subhorizontal posteriorly and inclined ventrally at anterior parts; inner socket ridges low, but recognizable; crural bases not well formed, subtrigonal in cross section; crura radulifer, very short, about $\frac{1}{5}$ as long as dorsal valve, without any specialized ends, arising from inner margins of hinge plates, curved only slightly toward ventral valve.

REMARKS.—The present specimens have basically the same characteristics as those illustrated by Buckman, except that the present specimens have a narrower and deeper sinus. Buckman's other three species, *B. ornitheia*, *B. patula*, and *B. polystema*, are all in close accord with *B. oxoniensis*, although they do have some slight differences, so it seems better to regard them as synonyms of *B. oxoniensis*. We chose the name *B. oxoniensis*, because the holotype of that species was well illustrated and it lies morphologically between *B. patula* and *B. polystema*.

The species is externally similar to *Kallirhynchia concinna* (Sowerby) in some aspects and was taken as a synonym of the latter by Laurin (1984a). Indeed, *Kallirhynchia* and *Burmishynchia* are closely related both interiorly and exteriorly. Compared with the type-species of the latter, *Kallirhynchia* generally has a shorter, more pointed beak and its dorsal valve is much more convex than the ventral one, which is more or less flattened anteriorly. Internally, *Kallirhynchia* generally lacks a septalium, the hinge plates are horizontal, and the septalial plates are long and pendant, although both genera have a

reduced septum, incurved radulifer crura, and wide hinge plates. We judge the interiors of this species to be closer to *Burmishynchia* (*Hopkinsirynchia*) *hopkinsi* than to those of *Kallirynchia yaxleyensis* (Davidson) hence our placement of this species in the subgenus *Hopkinsirynchia*.

Cymatorynchia Buckman, 1918

Cymatorynchia Buckman, 1918:53.

TYPE-SPECIES.—*Rhynchonella cymatophorina* Buckman, 1910:105.

AGE AND DISTRIBUTION.—Aalenian to Upper Bajocian; Europe, Africa, Arabia, India, Burma, China, and Tibet.

REMARKS.—*Cymatorynchia* is important in the early Middle Jurassic of the Tethyan Realm. Most of its species were

recorded from the Middle to Upper Bajocian, except *Cymatorynchia cymatophorina* Buckman, the type-species, which was reported from the Aalenian and is far less known than *Cymatorynchia quadriplicata* (Zieten). The genus is externally similar to *Kutchirynchia* Buckman, which Ager (1965a) thought might be synonymous with this genus. Generally, *Cymatorynchia* has stronger and fewer costae, a less tumid dorsal umbo, and a stronger beak. Internally, *Cymatorynchia* has a less massive septum and slightly incurved crura. There is little doubt that these two genera are closely related, and possibly *Cymatorynchia* had led to the *Kutchirynchia*–*Daghanirynchia*–*Somalirynchia* group that constituted a main lineage of the subfamily Tetrarhynchiinae in the Bathonian to Oxfordian on the south shore of Tethys.

Another Bajocian genus *Formosarynchia* Seifert, 1963 (type-species: *Formosarynchia formosa* Seifert), is fairly

FIGURE 43.—Serial sections of *Burmishynchia* (*Hopkinsirynchia*)? *oxonensis* Buckman; USNM 429254, L 19.5, W 21.6, T 16.3, A 102; from the Homomyenmergel (Bathonian), Liesberg, Switzerland.

close to *Cymatorhynchia* in general characters. Seifert (1963) did not compare these two genera at that time. Ager (1965a) mentioned that the major differences between them are that the posterior part of the dorsal valve of *Formosarhynchia* is less inflated and the shell contains a definite septalium. Almeras (1966a) made a thorough study of this genus including a detailed investigation of its internal structures. According to his study, *Cymatorhynchia* can also have a well developed septalium. Almeras (1966a) pointed out that one of the specimens on which the type-species *Formosarhynchia formosa* Seifert was based was illustrated by Quenstedt (1858) as one of the typical specimens of "*Terebratula*" *quadriplicata* Zieten. Therefore, he thought that these two genera are at least partly synonymous. On the basis of the species *Formosarhynchia pugnacea* (Quenstedt) and *Formosarhynchia subpugnacea* Seifert, however, he defined the genus in a more restrictive sense. Ager, Childs, and Pearson (1972:198) further stated that these two genera have basically the same characters and might therefore be inseparable. Nevertheless, *Formosarhynchia* generally is smaller, has less pronounced anterior plication, and finer costae. Considering the evolutionary relation of *Formosarhynchia* to *Burmishynchia*, Ager, Childs, and Pearson (1972) preserved the generic name *Formosarhynchia*. Almeras (1979b) considered *Formosarhynchia* as a subgenus of *Cymatorhynchia*. Here we treat them as separate genera, because they have some differences in the details of internal structures.

***Cymatorhynchia quadriplicata* (Zieten, 1830)**

PLATE 7: FIGURES 17–19, PLATE 8: FIGURES 8–13, PLATE 9: FIGURES 1–7, 11–17, PLATE 12: FIGURES 1, 2, 6, 7

Terebratula quadriplicata Zieten, 1830–1833:55, pl. 41: fig. 3.—Quenstedt, 1851:453, pl. 36: fig. 16; 1858:423, pl. 58: figs. 5–8; 1868–1871:81, pl. 38: fig. 42.

Rhynchonella quadriplicata (Zieten).—Davidson, 1851–1852, appendix:23, pl. A: fig. 22; 1878:201, pl. 29: figs. 1–3.—Rollier, 1918:148.—Arcelin and Roche, 1936:59, pl. 2: figs. 1–6, pl. 11: figs. 1, 4, 5, pl. 12: fig. 5, pl. 13: figs. 3, 4.—Roche, 1939:268, pl. 4: fig. 11.

Cymatorhynchia quadriplicata (Zieten).—Buckman, 1918:54.—Pevny, 1969:143, pl. 28: fig. 1a–c.—Fischer, 1980:140, pl. 58, figs. 1, 2.—Parnes, 1981:21, pl. 2: figs. 5–13.—Shi, 1987b:55, pl. III: fig. 12.

Cymatorhynchia quadriplicata (Zieten in Davidson).—Rousselle, 1965a:52, pl. 2: figs. 11, 12.

Cymatorhynchia quadriplicata (Zieten).—Almeras, 1966a:70–97; var. *quadriplicata*, p. 73, pl. F–G, pl. 2: figs. 5–8; var. *vergissonensis*, p. 79, pl. D–E, pl. 2: figs. 1–4; var. *lata*, p. 88, pl. I, pl. 4: figs. 6–8; var. *depressa*, p. 95; var. *trilobata*, p. 96.

TYPE.—*Holotype*: Zieten, 1830, pl. 41: fig. 3; from the Upper Bajocian, near Gosheim and Harras, Germany.

MATERIAL STUDIED.—Tens of silicified specimens completely etched out by acid, displaying good interiors, from the Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone et Loire, France.

DESCRIPTION.—Shell large, subpentagonal in outline; valves moderately biconvex, with dorsal valve more convex than ventral one. Lateral commissures oblique ventrally at 10–20

degrees; anterior commissure widely uniplicate; linguiform extension usually wide, trapezoidal to rectangular in shape.

Beak short, massive, suberect; foramen small to medium, subcircular, hypothyriddid; deltidial plates short, disjunct to just conjunct; beak ridges obtuse; interareas narrow, slightly concave.

Ventral valve moderately convex at posterior, slightly flattened anteriorly; sulcus well developed, generally broad and shallow, starting at posterior half of valve.

Dorsal valve evenly convex, not tumid, with greatest convexity at anterior third, but not everted; fold well elevated above slopes at anterior half of valve, generally broad, low, top flattened.

Shell ornamented with strong, subangular to sharp ribs, on each valve numbering 16–28, with 4–8 on fold and 3–7 in sulcus; growth lines generally feeble, visible at anterior parts.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 429256	24.3	23.5	18.1	90	20	5	4
USNM 429257	23.5	22.5	18.0	87	18	5	4
USNM 429258	31.2	34.0	21.1	108	28	8	8
USNM 429259	22.0	19.3	13.2	73	16	4	3
USNM 429260	34.0	34.2	24.0	85	35	8	7
USNM 429261	26.1	29.2	18.0	100	25	6	5
USNM 429262	28.0	27.2	21.1	85	22	5	4
USNM 429263	27.1	30.2	21.0	100	27	7	6
USNM 429264	28.2	32.3	19.1	101	26	5	4
USNM 429265	31.0	30.8	21.6	101	26	5	4
USNM 429266	29.0	31.3	18.7	97	24	6	5
USNM 429267	30.5	31.5	20.4	103	26	8	7

INTERIOR.—Generally no noticeable secondary thickenings existing in either valve, but slight callus recognizable at posterior part of delthyrium of some specimens. Very short pedicle collar often present; dental plates short, subparallel, just short of hinge zone; delthyrium wide; lateral cavities well developed; teeth short, massive, with expanded ends and crenulations, inserting deeply into sockets.

Dorsal septum well developed, generally high and blade-like, 1–2 mm in height, running $\frac{1}{4}$ to $\frac{1}{3}$ of dorsal valve. Septalium variable, generally present and short, V-shaped; among 34 examined specimens, 13 having no septalium, 19 having normal-shaped and septum-supporting septalium (of which, 14 have very short V-shaped septalium, 5 have wide and longer one), and 2 possessing septalium in which short septalial plates set on dorsal floor directly, with septum inserting between them. Hinge plates not very broad, triangular in ventral view; in some specimens, hinge plates strongly tapering anteriorly and in others, notched at their anterior margins; hinge plates generally subhorizontal, in some specimens inclined ventrally. Inner socket ridges low, but well demarcated from hinge plates; sockets deep, crescent in ventral view; crural bases very narrow, but recognizable, generally existing as thickened ridges along dorsal sides of inner margins of hinge

plates; crura radulifer, generally $1/5$ to $1/4$ as long as dorsal valve, divergent and incurved forward, distal ends in some specimens slightly expanded, with very feeble furrows on dorsal sides.

REMARKS.—This species is well known both internally and externally, and is widespread in the Middle to Upper Bajocian of the Tethys. It varies considerably in morphology, so that Almeras (1966a) split it into seven variants. After a careful comparison, it has been noticed that among these variants, 5 (except var. *densecosta* and var. *inflata*) have basically the same characteristics: dorsal valve less tumid than ventral valve, somewhat depressed shell, subpentagonal outline, and few but strong ribs. We therefore prefer to regard them as a single variable species, *C. quadriplicata* (Zieten). The varieties *densecosta* and *inflata* clearly differ from the other variants in having a subcircular shell, more inflated dorsal valve, finer and denser ribs, as well as a less developed fold and sinus. It seems better to combine them as a single species—*Cymatorhynchia densecosta* Almeras.

***Daghanirhynchia* Muir-Wood, 1935**

Daghanirhynchia Muir-Wood, 1935:82.—Hudson, 1958:420.—Ager, 1965a: H617.—Almeras, 1987:178.—Cooper, 1989:26. [Not Parnes, 1981:22.—Li and Gu, 1982:52.]

?*Daghanirhynchia* Muir-Wood.—Muir-Wood, 1937:13.—Sahni, 1939:14.

TYPE-SPECIES.—*Daghanirhynchia daghaniensis* Muir-Wood, 1935:82.

AGE AND DISTRIBUTION.—Bathonian to Callovian; from Saudi Arabia, Egypt, Israel, Kenya, Somaliland, Morocco, Tunisia, ?Ethiopia, ?India, and the Qomolongma area, South Tibet and has generally been regarded as a characteristic of the south shore of the Tethys Seaway.

REMARKS.—This genus was erected by Muir-Wood (1935) based on material from Somaliland, and has come to be regarded as one of the most important forms in the “Ethiopian” fauna. An important internal structure of the genus was said to be that its “divided hinge plates horizontal, reunited by thin lamella anteriorly in adults” (Muir-Wood, 1935:82). Muir-Wood (1935:83) also stated that “the thin lamella which reunited the divided hinge-plates in the adults appears to be characteristic of all species of *Daghanirhynchia*... This accessory plate is absent in young specimens of *Daghanirhynchia* spp.” However, she did not illustrate sections for other species that she had described, the only set of serial sections illustrated is that of *D. daghaniensis* (Muir-Wood, 1935:84, 85, figs. 5, 6). So far, no any other published sections of the genus show this kind of structure. The present authors have sectioned one specimen of *Daghanirhynchia daghaniensis* Muir-Wood, from the Callovian, at locality 227, Daghani section, Somaliland, the same locality and horizon as the holotype. It is figured here on Plate 10: Figure 7 and in Figure 44. The serial sections show that the species has no sign of this kind of reunited structure, and it is apparently an adult specimen.

Cooper sectioned many specimens of the genus from Saudi Arabia and illustrated two sets of serial sections (1989:26–28, figs. 13, 14), none of them shows structures similar to those shown by Muir-Wood. The senior author discussed this problem with Dr. Ellis Owen who worked on the Mesozoic brachiopods in the Natural History Museum, London. Owen said that he also sectioned several specimens of the genus from the Callovian of Somaliland, but none of them was found to possess this kind of reunited structure. As a final resort, Shi examined the original specimens described by Muir-Wood (1935), which are deposited in the Natural History Museum, London. The sections and specimen illustrated by Muir-Wood (1935:84, text-fig. 5, BMNH 86449) could not be found there, but Shi was able to find specimen BMNH 86448 figured by Muir-Wood (1935:85, text-fig. 6), which was cut off in the posterior part, with sectioned surface just at that position. Careful observation of that specimen under the microscope revealed that the reuniting structure in that specimen actually is not a real structure, but a fissure filled with secondary calcite, and it also is not shaped as regularly as that in Muir-Wood’s figure. *Burmishynchia? termierae preathiensis* and *Burmishynchia? termierae athiensis* described by Rousselle (1965a:43–49, pl. 2: figs. 1–8, pl. 3: figs. 1–13) from the Bathonian of Morocco, which should be transferred to *Daghanirhynchia* although they were not originally recognized as this genus, have internal structures similar to those of *Daghanirhynchia daghaniensis* as revealed here, and have no sign of an accessory plate uniting the hinge plates in the dorsal valve (Rousselle, 1965a: figs. 15, 16, 19). The same situation also occurs in *Rhynchonella tazerduensis* and *Rhynchonella dieffarae* described by Dubar (1967:38–41) from Tunisia, which, as mentioned by Cooper (1989:26), should be referred to *Daghanirhynchia*. All these facts lead to the strong impression that this accessory plate probably is not a real structure in the genus. If true, the genus should be emended.

After examining the many specimens of *Daghanirhynchia*, *Kutchirhynchia*, and *Somalirhynchia* housed in the Natural History Museum, London, and in the Museum of Natural History (Washington) we are sure that these three genera are closely related and they should be regarded as a single lineage in the evolution of the Tetrarhynchinae. Both chronologically and morphologically, *Daghanirhynchia* lies between *Kutchirhynchia* and *Somalirhynchia*. It is highly possible that the Bajocian genus *Cymatorhynchia* is the direct ancestor of *Kutchirhynchia* that led in turn to *Daghanirhynchia*.

***Daghanirhynchia daghaniensis* Muir-Wood, 1935**

FIGURE 44; PLATE 10: FIGURES 6–8, PLATE 16: FIGURES 14–16

Daghanirhynchia daghaniensis Muir-Wood, 1935:83, pl. 8: fig. 5.—Almeras, 1987:179, pl. 3, figs. 11–17.

Daghanirhynchia daghaniensis var. *elongata* Muir-Wood, 1935:85, pl. 8: fig. 6.

Daghanirhynchia daghaniensis var. *platiloba* Muir-Wood, 1935:86, pl. 8: fig. 4.

FIGURE 44.—Serial sections of *Daghanirhynchia daghaniensis* Muir-Wood; topotype, USNM 75666a, L 21.8, W 20.9, T 14.9, A 89; (Lower Callovian) Daghani section, 227, Somaliland.

TYPE.—*Holotype*: Muir-Wood, 1935, pl. 8: fig. 5; Callovian, Daghani section 227, Somaliland.

MATERIAL STUDIED.—10 well-preserved specimens from the Callovian, Daghani, Somaliland.

DESCRIPTION.—Shell medium size, subtrigonal to subpentagonal outline; subglobose, dorsal valve more convex than

ventral, Lateral commissures deflected ventrally at 10–25 degrees; anterior commissure strongly uniplicate; linguiform extension high, trapezoidal.

Beak long, massive, suberect; foramen large, subcircular to longitudinally elliptical in shape, hypothyridd, with or without slight rims; deltidial plates narrow, generally disjunct; beak

ridges obtuse; interareas small but distinct and slightly concave.

Ventral valve adequately convex posteriorly; sinus well developed, broad and deep, with flattened bottom, beginning at posterior 1/3 to 1/2.

Dorsal valve evenly convex, greatest convexity at midvalve to anterior 1/3; fold well raised over slopes, broad and pronounced, starting at posterior 1/3 to 1/2, with rounded top, making valve slightly trilobate.

Costae coarse, subangular, on each valve numbering 17–21, with 3–5 on fold and 2–4 in sinus; growth lines generally feeble and irregular, becoming conspicuous near anterior margin.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 75665a	21.0	21.5	13.5	85	19	5	4
USNM 75665b	21.5	20.2	14.1	80	18	4	3
USNM 75666a	21.8	20.9	14.9	89	19	5	4
USNM 75666b	23.5	20.8	15.2	82	21	4	3
USNM 75666c	18.8	17.8	10.0	79	18	3	2
USNM 75667	23.5	24.2	13.5	93	22	5	4
USNM 75668	18.5	19.0	11.3	88	18	5	4
USNM 75669	19.3	20.5	14.2	86	13	4	3
USNM 429281	19.3	20.2	14.2	88	21	6	5
USNM 429282	18.5	17.5	12.0	82	17	5	4

INTERIOR.—No secondary thickenings. No pedicle collar observed in ventral valve; delthyrium wide, trapezoidal; lateral cavities narrow; dental plates slightly divergent toward ventral valve floor and splitting away from floor just at hinge zone; teeth short, massive, rectangular in section, with crenulations.

Dorsal septum short, supporting hinge plates only at very posterior of apical cavity, reduced to ridge forward, extending for about 1/4 of valve length; septalium absent, septalial plates very short; hinge plates broad, well separated, slightly inclined or arched ventrally and tapering anteriorly; inner socket ridges low, but well demarcated from hinge plates; crural bases not well formed; crura radulifer, about 1/5 as long as dorsal valve, almost protruding along commissure plane and only slightly incurved ventrally at distal ends, arising from prolongations of hinge plates, relatively wide and somewhat similar to cilicifer at preliminary parts in section.

REMARKS.—The only serial sections of the species illustrated by Muir-Wood (1935) are incomplete, and do not show the distal ends of the crura, but Muir-Wood mentioned that the crura extend nearly horizontally, curving medially at their extremities. The present specimen shows interior features similar to those in Muir-Wood's sections, except there is no reuniting accessory plate and the hinge plates are slightly inclined or arched in the present specimen. The interiors of the Saudi Arabian specimens illustrated by Cooper (1989:27, 28, figs. 13, 14) are in close accord with those in the present specimen. The distal parts of the crura in the Saudi Arabian specimens, however, are slightly convergent and expanded.

Goniorhynchia Buckman, 1918

Goniorhynchia Buckman, 1918:52.—Aitken and McKerrow, 1948:19.—Mitra, 1958a:992; 1958b:228.—Ager, 1965a:H612.—Laurin, 1984a:273.

TYPE-SPECIES.—Rhynchonella boueti Davidson, 1852 (= Goniorhynchia goniaeae Buckman, 1918).

DIAGNOSIS.—Shell medium, subtrigonal to transversely subpentagonal, with strong uniplication and well-developed fold; shell trilobate; beak short, suberect, with small, circular, hypothyriddid to submesothyriddid foramen; shell strongly thickened and with numerous costae; septum reduced, no septalium; crura radulifer.

AGE AND DISTRIBUTION.—Upper Bathonian; England and France.

Goniorhynchia boueti (Davidson, 1852)

FIGURES 45, 46; PLATE 6: FIGURES 1–5

Rhynchonella boueti Davidson, 1852:254, pl. 13: figs. 4, 5.—Oppel, 1856–1858:500.—Davidson, 1878:179, pl. 26: figs. 15, 16.—Rollier, 1918:168.
Goniorhynchia boueti (Davidson).—Buckman, 1918:52.—Aitken and McKerrow, 1948:19, pls. 2, 3.—Mitra, 1958a:992–1006; 1958b:228, pl. 43.
Goniorhynchia contracta Buckman, 1918:229, pl. 18: fig. 23.
Goniorhynchia goniaeae Buckman, 1918:229, pl. 18: fig. 22.
Goniorhynchia boueti arenaemontis (Bigot).—Laurin, 1984a:375, text-figs. 132, 133, pl. 11: figs. 3, 4.
Goniorhynchia boueti boueti (Davidson).—Laurin, 1984a:373, text-figs. 129, 130, pl. 11: figs. 1, 2.
Goniorhynchia boueti goniaeae Buckman.—Laurin, 1984a:374, text-fig. 131.

TYPE.—Lectotype (here designated): Davidson, 1852, pl. 13: fig. 5; from the Upper Bathonian, Ranville, Caen, France.

MATERIAL STUDIED.—Hundreds of specimens from the boueti Bed and the Bradford Clay of England; 37 specimens from the Upper Bathonian of France.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 19893a	22.0	23.5	17.1	89	27	4	3
USNM 39213a	22.8	24.0	15.1	103	26	5	4
USNM 92005a	20.8	24.7	17.0	100	31	6	5
USNM 104687a	20.3	22.2	14.3	101	27	6	5
USNM 104687b	22.1	24.0	13.0	102	24	4	3
USNM 309601a	19.1	22.1	14.4	102	27	4	3
USNM 355632	19.2	21.3	16.0	98	31	6	5
USNM 429283	20.4	24.3	14.2	102	32	5	4
USNM 429284	21.5	27.0	14.3	104	36	8	7
USNM 429285	22.5	26.5	17.1	102	29	6	5
USNM 429286	24.3	26.5	17.2	102	35	7	6
USNM 429287	20.5	24.4	16.2	104	40	6	5
USNM 429289	20.1	22.0	14.5	99	35	7	6
USNM 429290	23.9	25.1	16.0	102	40	7	5
USNM 429291	20.3	22.1	12.4	93	38	7	6

INTERIOR.—Shell strongly thickened secondarily and with marked callus in both valves, obscuring interiors of apical

FIGURE 45.—Serial sections of *Gonioryhynchia boueti* (Davidson); USNM 429299a, L 21.0, W 24.8, T 13.3, A 93; from the base of the Forest Marble (Upper Bathonian), Dorset, England.

FIGURE 46.—Serial sections of *Goniorynchia boueti* (Davidson); USNM 429299b, L 22.9, W 23.2, T 15.5, A 96; from the base of the Forest Marble (Upper Bathonian), Herbury Promontory, 1 mile south of Langton Herring, Dorset, England.

cavities. Pedicle collar not determined because of strong secondary thickenings; delthyrium wide, trapezoidal; lateral cavities narrow and short; dental plates thick and long, arising from hinge zone, subparallel or convergent to ventral floor; teeth very strong, with expanded ends and crenulations, inserting into deeply sockets; accessory denticulars and dental cavities present.

Dorsal septum reduced to long and stout ridge, extending

about $\frac{1}{3}$ to $\frac{1}{2}$ valve length; septalium absent, septalial plates absent or short; hinge plates very thick, inclined or concave ventrally, close to each other; inner socket ridges low, well differentiated from hinge plates; crural bases not well formed; crura radulifer, about $\frac{1}{4}$ as long as dorsal valve, arising from inner margins of hinge plates and only incurved toward ventral valve slightly.

REMARKS.—This species is very abundant in the Upper

Bathonian of England and France, and varies considerably in morphology. Davidson (1852) defined this species mainly on specimens collected from Ranville, Caen, France. Later, Davidson (1878) illustrated several English specimens, which were slightly different in shape from those he had illustrated earlier. For this reason, Buckman (1918:52, 229), based on the English specimens, proposed the two further names, *G. goniaeae* and *G. contracta*, to split *G. boueti* into three species. Aitken and McKerrow (1948) and Mitra (1958b) respectively studied this species by detailed statistical analysis. Their analyses did not support the separation of the species, instead they thought that the species named by Buckman actually were only the variations within the population of *G. boueti* and that only the one species *G. boueti* existed. However, all the specimens they studied were from Dorset, England, and the French specimens were not taken into the consideration at that time. In fact the French specimens do differ somewhat from the English ones (Plate 6: Figures 1–5). Generally, the French specimens have the fold more elevated, stronger and fewer ribs, and are less transverse than the English specimens. Laurin (1984a) attempted to keep all these species as subspecies in *G. boueti*; we agree with him in preserving *G. boueti boueti* and *G. boueti goniaeae* as two separate subspecies, but regard *G. boueti arenaemontis* the same as *G. boueti boueti*.

Although this species is well known for its abundance in the Upper Bathonian and its peculiar shape, its interior was not properly studied until Laurin (1984a) first illustrated several sets of complete serial sections. Before then the only section published was that made by Mitra (1958a), in which the strong secondary thickenings and very thick shell can be seen. The strong secondary thickening is quite distinct for the genus and also the absence of the septalium and septalial plates as well as the stout and long septal ridge in the dorsal valve make it easy to be distinguished from other contemporary genera internally. These characters together with the shell shape, the well rimmed foramen, as well as their occurrence in clusters suggest that it lived in shallow water near to the shore.

Isjuminella Makridin, 1955

Isjuminella Makridin, 1955:85 [in part].—Drot and Fischer, 1966:53–61.—Fischer, 1969:67.—Ager, Childs, and Pearson, 1972:163, 200. [Not Makridin, 1960:254.—Ager, 1965a:H613.]

Burmihynchia Buckman.—Dardeau and Laurin, 1982:476 [in part].—Laurin, 1984a:387.

Sardorhynchia Ruggiero and Ungaro, 1983:228.

TYPE-SPECIES.—*Terebratulites decoratus* Schlotheim, 1820:264; redesignated by Drot and Fischer, 1966.

EMENDED DIAGNOSIS.—Shell large, strongly folded and highly uniplicate, with few very strong and sharp ribs, no posterior smooth areas; beak massive, incurved; foramen small, hypothrydid; shell thick, with marked secondary thickenings and callus in both valves; dental plates very short; septum reduced; hinge plates narrow; crura radulifer, incurved ventrally, very short.

AGE AND DISTRIBUTION.—Bathonian to Early Callovian; France, Germany, Italy, and England.

REMARKS.—There has been some controversy regarding the validity of this genus. Drot and Fischer (1966), Ager, Childs, and Pearson (1972) and Ruggiero and Ungaro (1983) all dealt with the intricate problem in some details, but much remains to be settled. Much as we may dislike to enter the fray, we must discuss the matter further.

The name *Isjuminella* was originally proposed by Makridin (1955) and its type-species was designated as *Rhynchonella decorata* Von Buch. Makridin (1960), however, changed the generic name to *Isjuminelina* and the type-species to *Rhynchonella pseudodecorata* Rollier, 1918, without explanation. Makridin (1964) further listed the "*Septaliphoria*" *decorata* described by himself in 1952 as the synonym of *Isjuminelina pseudodecorata* and put the genus *Isjuminelina* in his new subfamily Praecyclothyridinae. Ager (1965a) disposed of the genus *Isjuminella* because the binomen *Rhynchonella decorata* Von Buch never originally existed as such. Drot and Fischer (1966) sought to preserve this genus with *Terebratulites decoratus* Schlotheim as type-species and presented an emended diagnosis for this genus. Dardeau and Laurin (1982) and Laurin (1984a), however, did not accept this suggestion and put all the forms related to *Rhynchonella decorata* (Schlotheim) into *Burmihynchia* on the grounds of their similarities with *Burmihynchia hopkinsi* (Davidson) and *Burmihynchia turgida* Buckman. It was not proper for Makridin (1960) to abandon the name *Isjuminella* and to substitute *Isjuminelina*, or to designate *Rhynchonella pseudodecorata* as type-species and reject *Isjuminella* as a junior synonym. According to the International Rules of Zoological Nomenclature *Isjuminella* and *Isjuminelina* constitute two valid and named genera, and we have to accept them. Ager, Childs, and Pearson (1972:189) mentioned that these two genera named by Makridin were based on one Russian form wrongly identified as two different West European species, but the name *Isjuminella*, just like the genus *Isjuminelina*, is valid. Here it has been emended on the basis of *Terebratulites decoratus* Schlotheim as a genus separate from *Isjuminelina* Makridin, 1960.

This Bathonian genus is externally distinctive, easily distinguished from other genera. Internally it somewhat resembles *Goniorhynchia* in having strong secondary thickenings and narrow hinge plates in the absence of a septalium, but the two genera are quite different externally. The English species *Rhynchonella subdecorata* Davidson, as its name implies, is externally similar to *Isjuminella decorata* (Schlotheim) in some aspects, but their interiors are different. Since they also differ in some details of the exterior, they have been referred to the new genus *Aalenirhynchia*.

Isjuminella, *Aalenirhynchia*, and *Hopkinsirhynchia* are three closely related genera that share some common characteristics, such as strongly uniplicate shells, well developed folds and sinus, strong costae, and no smooth areas. Internally, *Isjuminella* has strongly secondary thickenings and callus, very

narrow hinge plates, and short crura. *Hopkinsirhynchia* has a very well developed septalium, while *Aalenirhynchia* has high septum and no conspicuous secondary thickenings. All three have radulifer crura.

Drot and Fischer (1966) emended *Isjuminella* on the basis of "*Terebratulites*" *decoratus* Schlotheim, but in the diagnosis presented by them the crura were wrongly defined as falcifer type. According to the serial sections illustrated by them and the present study on the topotypes, the crura of *Isjuminella decorata* (Schlotheim) are surely radulifer, in which the distal ends of the crura are strongly incurved toward the ventral valve, so that they appear as vertical plates.

Another genus must be mentioned here. Ruggiero and Ungaro (1983) founded the genus *Sardorhynchia*, based on the Bathonian to Callovian species *Sardorhynchia crassa* Ruggiero and Ungaro, 1983, from Sardin, Italy. This genus, as mentioned in their paper, is fairly close to *Isjuminella* in general characters. Ruggiero and Ungaro (1983) presented a detailed comment on *Isjuminella* and attempted to abandon the generic name *Isjuminella* and to replace it with *Sardorhynchia*. After a long discussion, they stated (1983:230)

The systematic situation of '*decorata*,' which was already confused, has consequently become even more inextricable. It is certain that the new genus (*Sardorhynchia*) has nothing to share with the Russian forms described by Makridin, nor with *Isjuminella* as it is considered by Ager, et al., 1972. On the other hand it appears to be very close to *Isjuminella* emended by Drot & Fischer [1966] and partially to *Burmishynchia decorata kiliani* Dardeau & Laurin [1972]...It [*Sardorhynchia*] differs from the diagnosis of *Isjuminella* as it was emended by Drot & Fischer for its jointed deltidial plates, the presence of a clear septalium, and crura of radulifer type, while, as far as septalium is concerned, Drot & Fischer themselves refer in the text to some 'cretes septaliales.' One should check whether in other less globose and less thick-shelled specimens of '*decorata*,' the septalium appears in its normal shape or as clear septalial plates. In the specimens studied by us the septalium actually appears more or less clear according to the thickness of the shell and the curvature of the brachial valve.

They further pointed out

In the progress of time one might perhaps attribute to the genus *Sardorhynchia* also the forms belonging to the group of '*Rhynchonella decorata*' (Schlotheim), but only after checking the following characters, possibly on topotypes: 1) deltidial plates, 2) the actual presence of septalium, 3) whether crura are really radulifer. In any case, the choice made by Drot & Fischer of the name *Isjuminella* does not seem to have been so happy because in its original definition this genus had been instituted on a species quite different from *Terebratulites decoratus* Schlotheim and even belonging to a different subfamily; moreover Makridin never intended to allude for this genus to the typical characters of the '*decorata*' of Schlotheim. Lastly, genus *Isjuminella* has been put in synonymy with *Isjumiellina* by the author himself. For this reason, even if further studies on the group of '*Rhynchonella decorata*' (Schlotheim) may point out such similarities with the form studied by us as to induce us to put them in the same genus, one should not use the name *Isjuminella*, but rather *Sardorhynchia*.

As can be seen, Ruggiero and Ungaro (1983) actually have made it clear that these two genera are related closely. In order to settle the intricate problem, we must answer the following two questions. Is the genus *Sardorhynchia* basically the same as *Isjuminella*? If the answer is positive, we should go to the

second question: shall we replace *Isjuminella* with *Sardorhynchia* or reserve the former?

For the first question, the answer is essentially positive. Exteriorly, both of these genera have large, strongly folded shells, with massive beak, strong ribs, and thick shell-wall. Interiorly, they all have markedly secondary thickenings and callus, reduced septum, narrow hinge plates, and radulifer crura. The only major difference is that *Sardorhynchia crassa* often has a septalium in the dorsal valve, while *Isjuminella decorata* has not been found with a septalium in adult specimens. As has been mentioned earlier in this paper, the septalium is a variable structure in the subfamily Tetrarhynchiinae, many genera or even species of it could be considerably variable in septalium. Generally in juvenile specimens of a particular species, the septalium is well developed, while in the adults it tends to be obsolescent. The same situation also occurs in the species within one genus. So far no definite and clear septalium has been found in the sectioned topotype adult specimens of *Isjuminella decorata* (Schlotheim), but in its subspecies, "*Burmishynchia*" *decorata kiliani* Dardeau and Laurin, the septalium can exist. On the other hand, Ruggiero and Ungaro illustrated four sets of serial sections of *Sardorhynchia crassa*, of which two specimens possess a septalium (1983:235-237, text-fig. 3 and text-fig. 5, which is a juvenile specimen) and the others (p. 234, text-fig. 2, p. 236, text-fig. 4) have no septalium at all. In their pl. 3, only figs. 1, 2, which were said to be taken from a juvenile specimen, show a septalium, while figs. 3-6, which were of adult specimens, have no septalium. Obviously, the septalium is also a variable structure in *Sardorhynchia crassa*, the type-species of the genus. At the generic level, therefore, *Sardorhynchia* and *Isjuminella* should be regarded as synonymous, while *Sardorhynchia crassa* and *Isjuminella decorata* certainly are two separate species.

The second question is really difficult to decide. In our opinion, although Makridin erected *Isjuminella* with a wrongly identified Russian specimen, the generic name *Isjuminella* is valid under the International Rules of Zoological Nomenclature and its type-species *Terebratulites decoratus* Schlotheim is a well known species. After all, Drot and Fischer (1966) has emended this genus and made it acceptable in definition, so here we prefer to preserve the generic name *Isjuminella*.

Isjuminella decorata (Schlotheim, 1820)

FIGURE 47; PLATE 1: FIGURES 20, 21, PLATE 6: FIGURE 13

Terebratulites decoratus Schlotheim, 1820:264.

Terebratula decorata (Schlotheim).—Von Buch, 1834:65, pl. 2: fig. 36.

Quadratirhynchia decorata (Schlotheim).—Buckman, 1918:4.

Rhynchonella decorata (Schlotheim).—Rollier, 1918:127.—Almeras, 1966b:292, pl. 17: fig. 4, pl. 19: figs. 4, 5.

Isjuminella decorata (Schlotheim).—Drot and Fischer, 1966:53, figs. 1-21.—Fischer, 1969:67.

Burmishynchia decorata decorata (Schlotheim).—Laurin, 1984a:391, pl. 4: figs. 1-8, pl. 5: figs. 1-14.

TYPE.—*Lectotype*: Von Buch, 1834, pl. 2: fig. 36; designated by Almeras 1966b, pl. 17: fig. 4; from the Bathonian, Poix-Terron (Ardennes), France.

MATERIAL STUDIED.—17 well-preserved specimens from the Bathonian of Ardennes, France; 3 specimens from Germany.

DESCRIPTION.—Shell large, globose in lateral view and strongly domed in anterior view; outline variable, generally subtrigonal to subpentagonal; dorsal valve strongly inflated, much more convex than ventral one. Lateral commissures deflected ventrally; anterior commissure strongly uniplicate, tongue high, trapezoidal or nearly subtrigonal in shape.

Beak short, massive, incurved and almost touching dorsal umbo; foramen small, usually concealed; beak ridges obtuse; small planoareas often present.

Ventral valve adequately convex, recurved strongly in longitudinal direction; sulcus well developed, broad and deep, occurring at posterior $\frac{1}{4}$ and turning over toward dorsal valve at anterior margin more or less sharply, resulting in high tongue.

Dorsal valve markedly inflated, with swollen umbo; greatest convexity located at anterior part, usually recurved anteriorly, in some specimens slightly everted; fold prominent, broad, and sharp, starting near umbo, making valve roof-like in anterior view.

Costae few, strong, angular, on each valve numbering 10–17, with 3–6 on fold and 2–5 in sinus; growth lines well developed, more conspicuous or weakly lamellose near anterior margins.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 31331a	30.7	30.1	29.5	92	14	4	3
USNM 31331b	27.3	36.0	30.2	103	14	4	3
USNM 31331c	32.5	31.1	28.9	93	14	4	3
USNM 75850a	27.4	26.0	23.2	90	15	5	4
USNM 75850b	31.5	27.0	29.0	78	15	5	3
USNM 75850c	36.3	36.1	29.5	94	15	5	4
USNM 92920a	28.8	31.0	29.2	97	12	3	2
USNM 92920b	22.4	29.1	24.6	100	10	3	2
USNM 429300	37.0	37.0	34.3	100	10	3	2
USNM 429301	26.2	25.0	25.3	93	14	4	3

INTERIOR.—Shell-wall thick, with strong secondary thickenings in both valves. Callus thick in ventral valve, obscuring structures at posterior cavity, pedicle collar not determined. Delthyrial chamber very short and small; lateral cavities almost not developed and full of callus; dental plates very short; teeth long, nodular in shape, with crenulations and inserting tightly into sockets; accessory denticulars and dental cavities present.

Dorsal septum reduced, only existing as stout ridge and running about $\frac{1}{3}$ to $\frac{1}{2}$ of valve length; no septalium and septalial plates; hinge plates narrow, inclined ventrally; inner socket ridges well developed, constituting shallow troughs

together with inclined hinge plates; crural bases not well formed; crura radulifer, very short, about $\frac{1}{5}$ as long as dorsal valve, only divergent slightly forward, arising from inner margins of hinge plates and incurved strongly toward ventral valve anteriorly.

REMARKS.—This is a very distinct species externally and has been studied quite well. Drot and Fischer (1966) illustrated a set of very good serial sections that show the internal structures to be in close accord with those of the present specimen, except the present one has more pronounced inner socket ridges. Drot and Fischer (1966) incorrectly described the crura of the species as of falcifer type, while in fact they are radulifer, with strongly incurved distal ends. On the other hand, Laurin (1984a:91, 92, fig. 53, 54) figured two sets of serial sections of the species from Rumigny, which show well developed and deep septalium. Nevertheless, they are externally similar to the present specimens. This shows that the septalium is variable in the species and can not be taken as a key structure for the genus.

***Kallirhynchia* Buckman, 1918**

Burmishynchia Buckman, 1918:49 [in part].

Kallirhynchia Buckman, 1918:31.—Douglas and Arkell, 1928:168; 1932:152.—Muir-Wood, 1934:534; 1936:34.—Ager, 1965a:H608.—Fischer, 1969:66 [in part].—Jin, Sun, and Ye, 1979:142 [in part].—Ovtsharenko, 1983:20.—Laurin, 1984a:381. [Not Wisniewska-Zelichowska, 1978:68.]

?*Kallirhynchia* Buckman.—Cooper, 1989:45.

TYPE-SPECIES.—*Rhynchonella concinna* var. *yaxleyensis* Davidson, 1878:206.

EMENDED DIAGNOSIS.—Shell medium, unequally bi-convex to almost convexo-planate; with well developed uniplication and rectangular tongue; fold and sulcus well defined; beak short, suberect; foramen hypothyriddid; deltidial plates disjunct to just conjunct; shell ornamented with many costae; septum short, reduced; septalium absent, septalial plates well developed; crura radulifer.

AGE AND DISTRIBUTION.—Bathonian to ?Early Callovian; Europe, India, Pakistan, China, Pamirs, ?Morocco, Algeria, and ?Japan.

REMARKS.—*Kallirhynchia* is a very important Bathonian rhynchonellid in the Tethys and, like *Burmishynchia*, it has been used widely and contains many nominate species. Buckman (1918), based on the exteriors and the muscle scars, grouped the species of the genus into 4 subgroups and 12 series, and included altogether 28 species in it. Buckman over emphasized some trivial characteristics of the exteriors just like in *Burmishynchia* and the groups as well as the series divided by him actually do not have much significance in the evolution as suggested by him. Buckman compared *Kallirhynchia* with *Burmishynchia* in details, mainly on the bases of exteriors and some interiors, such as muscle scars, dental plates, and septum. However, these characters were merely observed on the shell surface or in molds and often does not reflect the real characters

FIGURE 47.—Serial sections of *Isjuminella decorata* (Schlotheim); topotype, USNM 31331a, L 30.7, W 30.1, T 29.5, A 92; (Bathonian) Poix-Terron (Ardennes), France.

FIGURE 48.—Serial sections of *Kallirhynchia multicostata* Douglas and Arkell; USNM 429316, L 18.2, W 17.4, T 13.2, A 88; from the Lower Combrash (Upper Bathonian), Dorset, England.

of the interiors. Muir-Wood (1934), for the first time, studied the interior of specimens of the genus and defined its crura as calcarifer type based on the sections of *Kallirhynchia yaxleyensis* (Davidson). Unfortunately, she defined this kind of crura mainly on the longitudinal sections, while the transverse sections presented were incomplete, without showing the anterior parts. Therefore, for a long time the crura of

Kallirhynchia were not clear in transverse sections. The present study shows that the crura of the genus are in fact not calcarifer, but radulifer as accepted by most researchers. Laurin (1984a) sectioned several French specimens of the genus, which also show the same crura character as those in the present topotype materials. In order to avoid further confusion, the calcarifer crura have to be defined on the basis of those in *Rhynchonelloi-*

della smithi (Davidson), though Muir-Wood (1934) originally defined the calcarifer crura in *Kallirhynchia yaxleyensis* (Davidson).

The present study reveals that the internal structures of *Kallirhynchia* are quite close to those of *Burmishynchia*, and that both of them have reduced septum, wide hinge plates, and ventrally incurved radulifer crura. It seems to us that the only major internal difference is that *Burmishynchia* has a variably developed septalium, which has not been found in all the properly known species of *Kallirhynchia*. Besides, *Kallirhynchia* more often has longer, pendant septalial plates and a shorter septalium. These two genera are distinguishable mainly in their exterior characters.

Recently, four more new species of *Kallirhynchia* were depicted by Cooper (1989) from the Bathonian of Saudi Arabia. Externally, however, these species have a long and massive beak, as well as a clearly rimmed foramen, and less developed tongue. Interiorly, these species, as shown by *Kallirhynchia arabica* Cooper (1989:46, fig. 25), have much higher and longer septum, strongly tapering hinge plates, and the crura somewhat similar to cilifer. These characters are suggestive of *Obsoletirhynchia*, new genus (see discussion under that genus), and are more like *Obsoletirhynchia obsoleta* (Sowerby) than *Kallirhynchia yaxleyensis* (Davidson), although Cooper's species do share external similarity with the latter.

***Kallirhynchia multicostata* Douglas and Arkell, 1928**

FIGURE 48; PLATE 7: FIGURES 7-9

Kallirhynchia multicostata Douglas and Arkell, 1928:169, pl. 11: fig. 4.—Laurin, 1984a:386, pl. 13: figs. 16-21.
Kallirhynchia elegantissima Buckman.—Douglas and Arkell, 1928:170, pl. 11: fig. 5.

TYPE.—*Holotype*: Douglas and Arkell, 1928, pl. 11: fig. 4; from the Lower Cornbrash, Dorset, England.

MATERIAL STUDIED.—20 specimens from the Upper Bathonian of France; 4 specimens from the Lower Cornbrash (Upper Bathonian), Dorset, England.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 223474a	17.1	16.5	13.2	80	32	8	7
USNM 223474b	15.4	16.0	12.0	88	30	7	6
USNM 223474c	16.5	16.2	12.1	84	31	8	7
USNM 429317	16.2	15.8	14.6	95	32	7	6
USNM 429318	17.5	16.5	14.5	93	33	6	5
USNM 429319	16.5	15.0	13.8	80	32	8	7

INTERIOR.—Slight callus existing in apical cavity of dorsal valve. No pedicle collar observed in sectioned specimen; delthyrial chamber wide, trapezoidal in shape; lateral cavities narrow; dental plates long, beyond hinge zone, parallel to each

other; teeth short, with expanded ends and crenulations; accessory denticulars and dental cavities present.

Dorsal septum short, reduced into ridge forward; hinge plates narrow, subhorizontal; inner socket ridges well demarcated and high; crural bases not very well formed, fairly narrow; crura radulifer, about 1/4 as long as dorsal valve, arising from inner margins of hinge plates, relatively strong; posterior parts of crura subtrigonal shape in sections, anterior parts of crura incurved pronouncedly toward ventral valve, with distal ends parentheses-like in sections.

REMARKS.—Douglas and Arkell (1928:169) stated that the species is close to *Kallirhynchia yaxleyensis*, but smaller, narrower, and with finer and more numerous costae. Laurin (1984a:386) extended the species to include all the specimens illustrated by Douglas and Arkell in 1928, such as *K. yaxleyensis* (pl. 11: figs. 1, 3), *K. crassicosta* (pl. 11: fig. 2), and *K. exalta* (pl. 11: fig. 6). It appears to us that *K. multicostata* is rather similar to *K. yaxleyensis*, but can be reserved as a separate species from *K. yaxleyensis* on the basis of its original definition. Further extension to this species would make it inseparable from *K. yaxleyensis*.

***Kallirhynchia yaxleyensis* (Davidson, 1878)**

FIGURES 49-51; PLATE 7: FIGURES 1-6, PLATE 13: FIGURE 2

Rhynchonella concinna var. *yaxleyensis* Davidson, 1878:206, pl. 27: fig. 23.
Rhynchonella concinna Sowerby.—Szajnocha, 1879:225, pl. 6: figs. 10-13.
Kallirhynchia yaxleyensis (Davidson).—Buckman, 1918:31, pl. 15: fig. 23.—Douglas and Arkell, 1928:168, pl. 11: figs. 1, 3; 1932:154, pl. 10: fig. 10.—Muir-Wood, 1934:534, pl. 62: figs. 15-17.—Laurin, 1984a:384, pl. 13: figs. 6, 7.
?Kallirhynchia amoena Buckman, 1918:224, pl. 15: fig. 20.
Kallirhynchia crassicosta Buckman, 1918:224, pl. 15: fig. 22.—Douglas and Arkell, 1928:169, pl. 11: fig. 2.
Kallirhynchia exalta Buckman, 1918:224, pl. 15: fig. 21.—Douglas and Arkell, 1928:170, pl. 11: fig. 6.
Kallirhynchia globularis Buckman, 1918:224, pl. 15: fig. 18.
Rhynchonella polonica Rollier, 1918:159.
Rhynchonella yaxleyensis Davidson.—Rollier, 1918:162.
Kallirhynchia polonica (Rollier)—Gardet, 1947:54, pl. 2: figs. 7-9.

TYPE.—*Holotype*: Davidson, 1878, pl. 27: fig. 23; refigured by Muir-Wood, 1934, pl. 62: fig. 15; from the Lower Cornbrash, Yaxley, Peterborough, England.

MATERIAL STUDIED.—22 well-preserved specimens from the Lower Cornbrash (Upper Bathonian) of England; 6 from the Upper Bathonian of France.

DESCRIPTION.—Shell medium, inequivalve; roundly subtrigonal to subpentagonal in outline, globose in profile; dorsal valve inflated, much more convex than ventral one. Lateral commissures deflected ventrally at 15-25 degrees; anterior commissure uniplicate; with high, rectangular tongue. At gerontic stage shell thickened markedly along margins, with parallel sides and more or less rectangular both in anterior and dorsal views; some variants with front flattened and commissure barely visible.

Beak short, nearly straight to suberect; foramen small, subcircular, hypothyridd, becoming obsolescent or very small at gerontic stage; deltidial plates short, mostly disjunct, or just conjunct; beak ridges obtuse; interareas very small.

Ventral valve moderately convex at posterior, flattened anteriorly; sulcus shallow, but well defined and with flattened bottom, occurring at anterior 1/2 to 1/3 of valve, turning over toward dorsal valve at anterior margin abruptly, with two stronger border ribs to join with those on fold.

Dorsal valve somewhat tumid, with greatest convexity at anterior part or slightly subcyncephalous in lateral view; fold flat, well demarked from slopes, occurring at anterior 1/2 or 1/3, with two border ribs stronger than others.

Costae many and coarse, on each valve numbering 25–31, with 5–8 on fold and 4–7 in sinus; growth lines fine and irregular, becoming conspicuous at anterior parts.

INTERIOR.—Slight secondary thickenings and callus only existing in apical cavities. Short pedicle collar present; delthyrium wide, trapezoidal in shape; lateral cavities well developed; dental plates long, reaching hinge zone, subparallel; teeth short, very strong and massive, with expanded ends and crenulations; accessory denticulars and dental cavities present.

Dorsal septum short, reduced into ridge rapidly forward, running about 1/4 or less of valve length; no septalium, septalial plates long, pendant. Hinge plates relatively thick; in one of sectioned specimens (Figure 51, USNM 429304) subhorizontal and narrower, with very strong inner socket ridges; while in another (USNM 429306) wider and slightly convex ventrally, with lower inner socket ridges. Crural bases not very well formed, generally narrow; crura radulifer, relatively long, about 1/3 of valve length, with strongly incurved distal ends, appearing as parentheses or vertical plates in section.

REMARKS.—This species was originally created as a variant of *Rhynchonella concinna* by Davidson in 1878 and was later promoted to be a separate species. It is similar to the latter in general characters and easy to be confused. According to Davidson's original definition (1878:206), this species differs from *Kallirhynchia concinna* (Sowerby) "in very much thickened frontal portions of valves, each valve, as it approaches the serrated frontal margin, more or less suddenly or abruptly bent at nearly right angles, giving to the frontal view of the shell a broad, square, flattened character." However, these characteristics generally can be observed only in the gerontic specimens. In young specimens, they usually become incipient and indistinct, making the species not easy to be distinguished from *Kallirhynchia concinna* (Plate 7: Figures 12–16). On the other hand, the holotype of *Kallirhynchia*

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 39212	17.6	17.5	13.8	87	31	8	7
USNM 123765a	19.3	20.1	16.0	92	27	6	5
USNM 123765b	17.0	17.5	14.0	90	25	5	4
USNM 123765c	17.8	18.0	14.2	87	27	6	5
USNM 123768a	18.0	18.1	16.2	88	29	7	6
USNM 429303	21.0	23.1	18.5	102	30	6	5
USNM 429305	16.4	16.8	14.4	105	29	7	6
USNM 429306	16.8	15.8	12.4	80	28	7	6
USNM 429308	17.2	18.0	14.7	90	32	7	6
USNM 429309	18.8	18.5	16.3	95	28	7	6
USNM 429310	17.0	17.2	13.0	87	27	7	6
USNM 429311	18.4	18.4	16.5	97	25	5	4
USNM 429312	18.8	19.0	17.8	97	34	7	6

FIGURE 49.—Serial sections of *Kallirhynchia concinna* (Sowerby); USNM 104672e, L 18.8, W 17.4, T 16.2, A 93; (Upper Bathonian) Hidreguent, Pas de Calais, France. (The crura are broken off).

FIGURE 50.—Serial sections of *Kallirhynchia yaxleyensis* (Davidson); topotype, USNM 429307, L 16.7, W 15.5, T 11.8, A 86; from the Lower Cornbrash (Upper Bathonian), Yaxley, near Peterborough, Cambridgeshire, England.

FIGURE 51.—Serial sections of *Kallirhynchia yaxleyensis* (Davidson); topotype, USNM 429304, L 21.8, W 23.2, T 18.1, A 96; from the Lower Cornbrash (Upper Bathonian), Yaxley, near Peterborough, Cambridgeshire, England. (Distal ends of the crura were missing).

concinna (Sowerby) illustrated by Sowerby (1815:192, pl. 83: fig. 6) was not very clearly shown, with only a single antero-lateral view figured. This species has been recorded extensively, most of the later illustrations were young specimens. Buckman (1918) illustrated a plastic mold of the holotype, but Douglas and Arkell (1928, 1932) and Muir-Wood (1934) thought that it was a poor plastic cast. It appears to us that these two species are not clearly separable from each other, except that *K. concinna* often has a more elevated fold, more

tumid dorsal valve and more convex ventral valve, as well as less thickening at the gerontic stage. The interiors of *K. concinna* are similar to *K. yaxleyensis* (Davidson) (see Figure 49 and compare it with Figures 50, 51).

Kutchirhynchia Buckman, 1918

Kutchirhynchia Buckman, 1918:54.—Agrawal, 1956:134.—Rousselle, 1965a:37 [in part].—Ager, 1965a:H614.—Mitra and Ghosh, 1973:181.—

Laurin, 1984a:376 [in part].—Almeras, 1987:180.—Cooper, 1989:47.
Kallirhynchia Buckman.—Fischer, 1969:66 [in part].

TYPE-SPECIES.—*Rhynchonella concinna* var. *kutchiensis* Kitchin, 1900:48.

DIAGNOSIS.—Shell medium to large; roundly subpentagonal in outline; subglobose to globose in profile; dorsal valve more convex than ventral one; with well-developed fold and sulcus; beak short, suberect; Costae numerous, coarse; dental plates long; septum stout; septalium variable, generally present; crura radulifer, strongly curved toward ventral valve.

AGE AND DISTRIBUTION.—Bathonian to Early Callovian; India, China, Saudi Arabia, Middle East, Europe, and North Africa.

REMARKS.—This is an ordinary looking rhynchonellid of Bathonian age; several genera resemble it externally. Buckman (1918) included in it only the type-species and questionably *Rhynchonella morierei* Davidson. Ager, Childs, and Pearson (1972:200) pointed out that the genus is probably also well represented in Europe, although the name is little used. Laurin (1984a) transferred some European species, such as "*Rhynchonella*" *obsoleta* (Sowerby), "*Rhynchonella*" *morierei* Davidson and their related forms into this genus. The name has existed for a long time, but the internal features of the type-species have not been studied properly. Its relationship with other genera is still not quite clear although Mitra and Ghosh (1973) and Laurin (1984a) have revised it.

Mitra and Ghosh (1973) emended the genus on the basis of material from Kutch, India. They characterized the genus as having a short, deep septalium, short but stout septum, hinge plates that are initially fused, are ventrally convex, and become subhorizontal and straight with growth. The crura are pseudocalcarifer. Unfortunately, their sections are too rough, with such long intervals between sections that details of the internal structures can not be determined clearly, even though they gave a detailed description. Kitchin (1900, pl. 15: fig. 11a-f) presented sections that show a well developed and V-shaped septalium supported by a stout septum, subhorizontal hinge plates, and radulifer crura with curved distal ends.

We sectioned several specimens of *Kutchirhynchia* sp. (Figures 2, 3) from the Bathonian of Southern Qinghai, China, that are externally similar to *Kutchirhynchia kutchiensis* (Kitchin). The serial sections show that the species has a well developed and V-shaped septalium, stout septum, subhorizontal hinge plates, and strongly incurved radulifer crura whose distal ends appear in section as vertical plates.

Dr. Ellis Owen (The Natural History Museum, London) has sectioned several specimens of *Kutchirhynchia kutchiensis* (Kitchin) from Kutch. When Shi visited the Natural History Museum, London, in 1987, Owen kindly showed him these sections (BMNH 20004, BMNH 19977, BMNH 52574, BMNH 50081, and one unnumbered specimen). These specimens show that the species has a short septum that supports the septalium or hinge plates only at the posterior end and is reduced to a ridge farther forward, so that it is a ridge for most

its length. The species has a subhorizontal hinge plate, radulifer crura, and massive teeth. The septalium is variable; for example, the specimens labelled BMNH 50081, BMNH 52574, and the unnumbered specimens have a V-shaped septalium; specimen BMNH 20004 has no septalium at all; specimen BMNH 19977 has a very short and incomplete septalium.

Cooper (1989:47, fig. 26; pl. 11: figs. 27–36) depicted a species from the Bathonian of Saudi Arabia that is close to *Kutchirhynchia kutchiensis* (Kitchin) in exterior characters, except the massive beak and clear interareas. This species, however, shows a fairly high and long septum, but has a variable septalium. According to Laurin (1984a), the European species *Kutchirhynchia moreieri* (Davidson) (Plate 6: Figures 8, 12) and *Kutchirhynchia indonea* Buckman both have the septum reduced, strongly curved radulifer crura, and a variable but short septalium (Laurin, 1984a:241–246, figs. 158–162).

Based on all the information available, it seems that the interiors of *Kutchirhynchia* could be summarized as follows: short pedicle collar present; dental plates subparallel, relatively long, reaching hinge zone; teeth strong, massive, with expanded ends and crenulations; dorsal septum low and short, reduced forward into stout ridge; hinge plates subhorizontal; inner socket ridges low, well differentiated; crural bases not very well formed; crura radulifer, with incurved distal ends vertical plate-like in sections; septalium variable, generally present, short.

Kutchirhynchia kutchiensis (Kitchin, 1900)

PLATE 6: FIGURE 9

Rhynchonella concinna var. *kutchiensis* Kitchin, 1900:48, pl. 10: figs. 1–5, pl. 15: fig. 11.

Kutchirhynchia kutchiensis (Kitchin).—Buckman, 1918:54, pl. 17: fig. 17.—Agrawal, 1956:140, pl. 12: figs. 1–3.—Mitra and Ghosh, 1973:181–185, figs. 1, 4E–I.

TYPE.—*Lectotype* (here designated): Kitchin, 1900, pl. 10: fig. 1; from the Upper Beds of Putchum Group, Kutch, India.

MATERIAL STUDIED.—1 specimen from the base of Charee Group (Upper Bathonian), Jooria, Kutch, India.

DESCRIPTION.—Shell 27.5 mm long, 30.8 mm wide, and 18.7 mm thick, with an apical angle of 103 degrees; transversely subcircular to subpentagonal in outline, subglobose in profile; dorsal valve more convex than ventral one. Lateral commissures deflected ventrally at about 20 degrees; anterior commissure uniplicate; tongue broad, not very high, trapezoidal in shape.

Beak short and small, suberect; foramen small, circular, hypothyriddid; deltidial plates low, just conjunct; beak ridges obtuse; interareas very small or not developed.

Ventral valve moderately convex at posterior, slightly flattened anteriorly; sulcus well defined, shallow and broad, starting at posterior $\frac{1}{3}$ of valve, with flattened bottom.

Dorsal valve highly convex, recurved regularly, with greatest convexity at midvalve; fold broad and low, but well defined,

occurring at posterior $\frac{1}{2}$ of valve and slightly elevated above flanks at anterior $\frac{1}{3}$.

Shell ornamented with many subrounded costae, on each valve numbering 33, with 8 on fold and 7 in sinus; growth lines fine, becoming obvious near frontal margin.

INTERIOR.—Not investigated for lack of material. The dental plates are about $\frac{1}{4}$ as long as ventral valve on the shell surface, divergent anteriorly with an angle about 40 degrees between them; septum (or septal ridge) running about $\frac{1}{3}$ of dorsal valve.

Lacunaerhynchia Almeras, 1966

Lacunaerhynchia Almeras, 1966a:97.—Shi, 1986:130; 1987b:56, 57.

Septulirhynchia Almeras, 1966a:110.

Nyalamurhynchia Ching, Sun, and Rong, 1976:301.

TYPE-SPECIES.—*Lacunaerhynchia vergissonensis* Almeras, 1966a:98.

EMENDED DIAGNOSIS.—Shell small to medium; subtrigonal, subcircular to transverse in outlines; shell depressed, valves equally and gently biconvex. Lateral commissures straight, anterior commissure rectimarginate to gently arched. Beak nearly straight to suberect, foramen hypothyriddid, deltidial plates often conjunct, with or without rims; shell ornamented with many costae and feeble growth lines. Septum well developed; septalium V-shaped; crura radulifer.

AGE AND DISTRIBUTION.—Aalenian to Bajocian and ?Late Bathonian to Early Callovian; France, England, Poland, and China.

SPECIES INCLUDED.—The following species are included in the genus.

Lacunaerhynchia gautheri Almeras, 1966a, Middle Bajocian.

Lacunaerhynchia vergissonensis Almeras, 1966a, Middle Bajocian.

Nyalamurhynchia merifica Ching, Sun, and Rong, 1976, Middle to Upper Bajocian.

Rhynchonella buckmani Rollier, 1918, Aalenian.

Rhynchonella palma Szajnocha, 1879, ?Upper Bathonian to Lower Callovian.

Rhynchonella palmaeformis Arcelin and Roche, 1936, Middle to Upper Bajocian.

Septaliphoria lungchiangensis Ching, Sun, and Rong, 1976, Middle to Upper Bajocian.

Septulirhynchia davidi Almeras, 1966a, Middle Bajocian.

REMARKS.—Almeras (1966a) erected the genus *Lacunaerhynchia* to include two species at that time. He stated that the main characteristics of the genus were "the shell almost equally biconvex, subpentagonal to circular, depressed; lateral commissures straight, anterior commissure slightly uniplicate; septalium deep, crura radulifer, septum well developed." Ager, Childs, and Pearson (1972) pointed out that *Lacunaerhynchia* did not differ significantly from *Cymatorhynchia*, its two species described by Almeras (1966a) being previously regarded as variants of *Cymatorhynchia quadriplicata* (Zieten).

The only differences between *Lacunaerhynchia* and *Cymatorhynchia* are that the former has almost equally biconvex valves, rounded costae, and lower anterior uniplication. Indeed, these two genera are fairly close to each other and have basically the same interiors, and are separable only on the basis of their exterior characteristics. At the same time Almeras (1966a), however, created the genus *Septulirhynchia* and included in it only the species *Septulirhynchia davidi* Almeras. This species is very close to *Lacunaerhynchia vergissonensis* Almeras, except for having a slightly more depressed and transverse shell, and more delicate internal structures. We do not deem these differences sufficient to maintain such a genus and to separate it from the closely related and contemporaneous genus *Lacunaerhynchia*.

Ching, Sun, and Rong (1976) lacked the reference to Almeras (1966a), so erected another Late Bajocian genus *Nyalamurhynchia* that contained only the species *Nyalamurhynchia merifica* Ching, Sun, and Rong. This genus has the same interior features as *Lacunaerhynchia* and *Septulirhynchia*, namely; a well developed septum, V-shaped septalium, and radulifer crura. The only differences are that *Nyalamurhynchia* has a more depressed and transverse shell, and fewer but stronger ribs than *Lacunaerhynchia*. We consider it as a subjective synonym of *Lacunaerhynchia*, but its type-species *Nyalamurhynchia merifica* is a valid species, separate from *Lacunaerhynchia vergissonensis*.

Lacunaerhynchia buckmani (Rollier, 1918), new combination

PLATE 8: FIGURES 3–5

Rhynchonella palma Szajnocha.—Buckman, 1882:47.—Davidson, 1884:271, pl. 19: fig. 21.

Rhynchonella buckmani Rollier, 1918:165.

TYPE.—*Holotype*: Davidson, 1884, pl. 19: fig. 21; designated by Rollier, 1918:165; from the Aalenian, Bradford-on-Avon Abbas, Dorset, England.

MATERIAL STUDIED.—4 well-preserved specimens from the Inferior Oolite (lower part, Aalenian), Dundry Hill, Somerset, England.

DIAGNOSIS.—Shell medium, roundly subtrigonal; beak fairly long, massive, and nearly straight; foramen large, deltidial plates conjunct, with well developed rims around foramen; shell thickened along margins; concentric lines conspicuous; anterior commissure rectimarginate or slightly flexed.

AGE AND DISTRIBUTION.—Aalenian; England.

DESCRIPTION.—Shell medium size, roundly subtrigonal to subcircular in outline; shell depressed, almost equally biconvex, ventral valve slightly more convex than dorsal one. Lateral commissures straight or slightly oblique toward ventral side; anterior commissure rectimarginate or slightly folded; fold and sulcus absent. Gerontic shells markedly thickened at margins.

Beak strong, rather long, with broad base; foramen large, subcircular to suboval, hypothyriddid to submesothyriddid; deltidial plates high, conjunct, clearly separating foramen from hinge line, with clear rims around foramen; beak ridges subangular to obtuse; interareas well developed, large and slightly concave.

Ventral valve moderately convex posteriorly and slightly flattened anteriorly; no recognizable sinus present.

Dorsal valve gently convex, umbonal region more or less flattened; no fold recognizable.

Costae coarse, rounded, on each valve numbering 26–33; growth lines well developed, becoming more conspicuous or even lamellose near anterior margin.

Measurements and counts.

Number	L	W	T	A	N
USNM 104773a	23.1	24.4	12.1	99	28
USNM 104773b	22.8	23.3	12.0	94	27
USNM 104773c	15.0	14.2	6.1	85	28
USNM 429280	21.0	22.5	12.0	101	33

INTERIOR.—Not investigated (specimens lacking).

REMARKS.—This species was not properly known and has not been studied internally yet for lack of material. Externally, it is in close accord with *Lacunaerhynchia palmaeformis* in many respects. The main differences between them are that *Lacunaerhynchia buckmani* has a much stronger beak and firmly conjunct deltidial plates, as well as conspicuous growth lines and a thickened shell. Young specimens are almost circular in outline, with a very long, almost straight beak with angular beak ridges that define high, distinct interareas. The foramen of juveniles is proportionately large, the dorsal valve is almost plane and ribs are flat. There seems little question that this species should be put in *Lacunaerhynchia*, but its conjunct deltidial plates and clearly rimmed foramen are reminiscent of *Rhactorhynchia subtetrahedra* (Davidson), though the differences from that species are also obvious. Compared with the present specimens, it seems that the specimen illustrated by Davidson (1884, pl. 19: fig. 21) is not an adult. It has a very long, straight beak and fine ribs, quite close to the present young specimen.

Lacunaerhynchia palma (Szajnocha, 1879),
new combination

PLATE 8: FIGURES 2, 6

Rhynchonella palma Szajnocha, 1879:233, pl. 7: figs. 15, 16.—Rollier, 1918:170. [Not Buckman, 1882:47.—Davidson, 1884:271, pl. 19: fig. 21.]
Rhynchonella subtilis Szajnocha, 1879:234, pl. 7: fig. 17.—Rollier, 1918:170.
?Formosarhynchia palma (Szajnocha).—Wisniewska-Zelichowska, 1978:86, text-fig. 12, pl. 5: figs. 9, 10.

TYPE.—*Holotype*: Szajnocha, 1879, pl. 7: fig. 15; from the Upper Bathonian to Lower Callovian, Balin, Poland.

MATERIAL STUDIED.—13 specimens from the Bradfordian (Upper Bathonian) of England and France.

DESCRIPTION.—Shell medium, depressed, almost equally biconvex or dorsal valve slightly more convex than ventral one; young specimens generally roundly subtrigonal and adults rounded subpentagonal or subcircular in outline. Lateral commissures slightly oblique toward ventral side; anterior commissure rectimarginate in young specimens and becoming slightly arched in adults.

Beak fairly long, pointed, nearly straight to suberect; foramen relatively large, subcircular to elliptical in shape, hypothyriddid to submesothyriddid; deltidial plates conjunct, high, with or without rims; beak ridges subangular in young specimens, obtuse in adults; interareas well developed, but not as pronounced as in *L. buckmani* (Rollier).

Ventral valve gently convex posteriorly, becoming flattened anteriorly; sulcus not developed, but near anterior margin, a broad, feeble depression present in adults, hardly separable from slopes.

Dorsal valve moderately convex, with greatest convexity at midvalve; generally umbonal region more or less flattened; fold not developed, some specimens with middle portion raised slightly above slopes at anterior margin.

Costae numerous, subangular, separated by deep intervals, on each valve numbering 23–29; growth lines fine, but not as conspicuous as in *L. buckmani* (Rollier).

Measurements and counts.

Number	L	W	T	A	N
USNM 39215	16.0	16.1	8.4	95	28
USNM 39533a	23.7	24.7	12.7	97	28
USNM 39533b	18.8	18.6	10.2	98	27
USNM 39533c	19.3	19.6	11.2	98	27
USNM 64410	16.2	17.0	9.2	91	27
USNM 64500	13.0	11.9	7.3	76	24
USNM 77469	24.5	25.0	12.1	95	29

INTERIOR.—Not investigated.

REMARKS.—This is a poorly known species. Externally it is close to *Lacunaerhynchia vergissonensis* Almeras and *L. buckmani* (Rollier), but its interiors are not known. It is highly possible that some specimens previously recorded as *Kallirhynchia concinna* (Sowerby) might belong to this species, especially those that were recorded as junior specimens of *Kallirhynchia concinna* (Sowerby) from the Bradfordian of England and the Upper Bathonian of France.

As for external characters, there seems little doubt that “*Rhynchonella*” *palma* Szajnocha should be transferred into *Lacunaerhynchia* Almeras as emended here, but the matter requires further work, especially on the interiors of the topotypes. The species described here are externally similar to the specimens of *Septaliphoria* sp. described in this paper, which are from the Corallian (Oxfordian) of Fairford, England.

The only differences are that *Septaliphoria* sp. has a less convex ventral valve, less developed rims around foramen, slightly arched anterior commissure, and the shell is not thickened along the margins. Internally, *Septaliphoria* sp. is quite different from *Lacunaerhynchia* in having strongly incurved canalifer crura as well as a very narrow, deep, and short septalium.

Lacunaerhynchia palmaeformis (Lissajous in Arcelin and Roche, 1936)

PLATE 7: FIGURES 20, 21, PLATE 9: FIGURES 8–10,
PLATE 10: FIGURES 13, 14

Rhynchonella palmaeformis Lissajous in Arcelin and Roche, 1936:71, pl. 3: figs. 8, 9.
Rhynchonella sp. A, Arcelin and Roche, 1936:71, pl. 3: fig. 10.

TYPE.—*Holotype*: Lissajous in Arcelin and Roche, 1936, pl. 3: fig. 8; from the Upper Bajocian, La Roche-Vineuse, Monsard, France.

MATERIAL STUDIED.—Seven silicified specimens with good interiors (topotypes); from the Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

DESCRIPTION.—Shell medium, roundly subtrigonal to subpentagonal in outline, lenticular in anterior and lateral views; shell depressed, almost equally biconvex. Lateral commissures straight; anterior commissure rectimarginate to slightly arched; fold and sulcus absent.

Beak short, obtuse, substraight to suberect; foramen medium, subcircular, hypothyriddid to submesothyriddid; deltidial plates short, disjunct to just conjunct, with slight rims around foramen; beak ridges subangular; interareas small, slightly concave.

Ventral valve moderately convex posteriorly, tending to be flattened anteriorly.

Dorsal valve gently and uniformly convex, with greatest convexity at midvalve.

Costae wide and flattened, fine at umbonal region, increasing in width rapidly toward anterior margin; only near front margin ribs becoming subangular, on each valve numbering 27–30; growth lines fine and irregular, visible at anterior parts.

Measurements and counts.

Number	L	W	T	A	N
USNM 429275	27	28	14	98	28
USNM 429276	26	27	12	99	27
USNM 429277	26	30	14	98	29
USNM 429278	20	19	9	93	31
USNM 429279	16	17	9	94	29

INTERIOR.—No secondary thickenings in either valve. Pedicle collar short; dental plates short, splitting from ventral floor before reaching hinge zone, subparallel or slightly convergent to ventral floor; delthyrium wide, trapezoidal;

lateral cavities very short; teeth strong, mallet-like, ends expanded and crenulate, held tightly in sockets; muscle scars not very clearly impressed, located at about posterior 1/3 to 1/4 of valve, consisting of two parts, each part pyriform.

Dorsal septum well developed and blade-like, about 1.5 mm high and 5–7 mm long, occupying 1/4 to 1/5 of dorsal valve length; septalium V-shaped, generally short, wide and deep, supported by septum at posterior of apical cavity; hinge plates triangular in ventral view, not very broad, almost horizontal; inner socket ridge low, but well demarcated from hinge plates; sockets deep, with fine crenulations; crural bases poorly formed, very narrow, only existing as thickened ridges along dorsal sides of inner margins of hinge plates; crura radulifer, about 1/5 as long as dorsal valve, divergent forward and incurved ventrally, with distal ends slightly widened; sometimes very shallow furrows visible on their dorsal sides, but never deep enough to form gutters.

REMARKS.—Arcelin and Roche (1936) illustrated a specimen named *Rhynchonella* sp. A. (pl. 3: fig. 10) that was said to be different from *R. palmaeformis* in having fewer costae and a smaller, flabelliform shell. The present study shows that the young specimens of the species are usually subtrigonal to more or less flabelliform; as they grew, the shell became subcircular, subpentagonal, or transverse. The specimen illustrated by Arcelin and Roche is fairly close to present juvenile specimens and should be regarded as a young specimen of *Lacunaerhynchia palmaeformis*.

This species differs from *Lacunaerhynchia vergissonensis* Almeras in having a more depressed and rounded shell, massive beak, and rectimarginate anterior commissure. Interiorly, that species has a narrower septalium and ventrally inclined hinge plates.

Obsoletirhynchia Shi, 1992

Obsoletirhynchia Shi, 1992:143.

TYPE-SPECIES.—*Terebratula obsoleta* Sowerby, 1815:192.

DIAGNOSIS.—Shell medium to large, suboval to subpentagonal in outline and subglobose in profile; valves subequal, fold and sulcus generally weak; anterior commissure moderately uniplicate or occasionally asymmetrical; beak small, substraight to suberect; foramen large, hypothyriddid to submesothyriddid, with distinct rims; deltidial plates high, conjunct and strengthened; shell ornamented with numerous coarse costae; septum reduced; hinge plates broad; crura radulifer or close to cilifer; septalium generally absent.

AGE AND DISTRIBUTION.—Bathonian; England, France, Germany, and China.

REMARKS.—The type-species “*Terebratula*” *obsoleta* Sowerby is well known in the Upper Bathonian of England and France. It was placed previously into *Kallirhynchia*, *Burmirhynchia*, *Cymatorhynchia*, *Sphenorhynchia*, *Rhactorhynchia*, and *Kutchirhynchia* by different authors, but none of those assignments is satisfactory in consideration of both the

exteriors and interiors. This species is quite distinct in its beak character, most of the specimens studied have a very short beak, clear rims around the foramen, and high conjunct deltidial plates that are thickened inside and noticeably convex, so that the beak looks somewhat apsacline. Internally, the new genus generally has noticeable secondary thickenings, although not as strong as in *Goniorhynchia*. The septum is reduced and usually no septalium exists. The crura are of the radulifer type, but generally are depressed or flattened and are somewhat similar to cilicifer crura, formed by the taperings of the hinge plates. Some species of the genus often have an asymmetrical and slightly flexed anterior commissure.

The new genus is similar to *Kutchirhynchia*, but differs from it in the characters of beak, foramen, and deltidial plates, less developed fold and sinus, as well as internal features.

The new genus is closest to *Rhactorhynchia*, to which the species here grouped in the new genus were previously referred. *Rhactorhynchia* is one of the most unsatisfactory Jurassic genera erected by Buckman. Buckman (1918) included 32 Aalenian to Kimmeridgian species in the genus. Many of these species have later proved to belong to *Septaliphoria*, *Torquirhynchia*, *Somalirhynchia*, or *Lacunaerhynchia*, thus *Rhactorhynchia* has been preserved in a very restricted sense. Ager, Childs, and Pearson (1972) stated that *Rhactorhynchia* should be retained as a strictly Middle Jurassic genus, centering around the Bajocian type-species *Rhactorhynchia rhacta* Buckman. Unfortunately, Buckman used a unique specimen as the holotype of the type-species of *Rhactorhynchia*, and so far no other specimens have been recognized as *Rhactorhynchia rhacta* Buckman. Therefore, the interiors of the type-species are not known. Nevertheless, the similar and presumably congeneric species *Rhactorhynchia subtetrahedra* (Davidson), *R. hampenensis* (Buckman), *R. turgidula* Buckman, and *R. tumefacta* Buckman of the Upper Bajocian have been studied carefully in this paper. The present study shows that *Rhactorhynchia* internally has a well developed septum, strongly incurved radulifer crura, and generally V-shaped septalium. Externally, these species do not have a clearly rimmed foramen or conjunct thickened deltidial plates as in the new genus. Chronologically, *Rhactorhynchia* mostly concentrates in the Middle to Late Bajocian, while *Obsoletirhynchia* occurs mainly in the Late Bathonian.

The rounded and multicostate shell, poorly developed fold and sulcus, as well as the subequally biconvex valves in the new genus are reminiscent of *Burmishynchia*. However, the differences in their internal structures and in general morphology are sufficient to separate them.

The internal characters of the genus, especially the obvious secondary thickenings and thick hinge plates as well as the absence of the septalium and its related structures, show that this genus has a close relation with *Goniorhynchia*, although the two are clearly separable both in external characters and in details of their internal structures.

SPECIES INCLUDED.—The following nominal species are included in the new genus.

- Rhactorhynchia diducta* Buckman, 1918
- ?*Rhynchonella plaitea* Richardson and Walker, 1907
- ?*Rhynchonella voluta* Richardson and Walker, 1907
- Terebratula obsoleta* Sowerby, 1815
- Terebratula rostrata* Sowerby, 1815

Obsoletirhynchia diducta (Buckman, 1918),
new combination

FIGURES 52, 53; PLATE 5: FIGURES 2, 5–8, PLATE 6: FIGURES 6, 7,
PLATE 8: FIGURE 7, PLATE 16: FIGURES 19, 20

- Rhactorhynchia coriniensis* Buckman, 1918:227, pl. 14: fig. 5.
- Rhactorhynchia diducta* Buckman, 1918:227, pl. 14: figs. 9, 10.
- Rhactorhynchia faecunda* Buckman, 1918:227, pl. 14: fig. 8.
- Kutchirhynchia obsoleta obsoleta* (Sowerby).—Laurin, 1984a, pl. 11: figs. 5–9 [in part].

TYPE.—*Holotype*: Buckman, 1918, pl. 14: fig. 9; from the Bradford Clay, Bradford-on-Avon, Wiltshire, England.

MATERIAL STUDIED.—Hundreds of specimens from the Upper Bathonian of France and tens of specimens from the Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England.

DESCRIPTION.—Shell medium to large, subpentagonal in outline and subglobose in profile; valves subequal, with dorsal valve more convex than ventral one. Lateral commissures deflected ventrally; anterior commissure uniplicate; tongue high, trapezoidal to broadly rectangular in shape.

Beak long, massive, suberect; foramen medium, subcircular, hypothryidid, with clear rims; deltidial plates conjunct, but not as convex and thickened as in *O. obsoleta*; beak ridges obtuse; interareas poorly defined, but small and narrow planoareas often present, slightly concave.

Ventral valve moderately convex at posterior, tending to be flattened anteriorly; sulcus generally shallow and broad, but well separated from slopes, occurring at posterior 1/3 to 1/2 of valve.

Dorsal valve much more convex than ventral one, recurved evenly, with greatest convexity at anterior 1/3; fold low and

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 31414a	28.2	29.7	19.1	94	26	7	6
USNM 31414b	26.5	27.0	18.2	92	25	4	3
USNM 64514a	26.3	26.7	18.2	93	33	7	6
USNM 64514b	24.3	25.1	15.0	93	32	7	6
USNM 88732a	29.0	29.2	18.9	92	31	8	7
USNM 88732b	26.1	26.0	16.3	88	29	7	6
USNM 92003	28.5	27.5	17.8	100	26	6	5
USNM 92009	26.7	28.1	18.9	100	33	8	7
USNM 104682	26.5	27.0	17.8	90	33	7	6
USNM 429342	27.8	29.2	18.9	97	31	7	6
USNM 429346	25.5	25.5	18.3	100	31	6	5
USNM 429347	28.3	27.2	22.0	94	24	7	6

FIGURE 53.—Serial sections of *Obsoletirhynchia diducta* (Buckman); USNM 429348, L 26.0, W 24.3, T 19.9, A 96; (Upper Bathonian) Campagettes Quarry, Ranville, France.

FIGURE 52 (facing page).—Serial sections of *Obsoletirhynchia diducta* (Buckman); topotype, USNM 129173a, L 24.9, W 27.1, T 15.3, A 94; from the Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England.

broad, but clearly separated from and raised above slopes at anterior $\frac{1}{3}$ of valve, with stronger bordering ribs.

Costae coarser, angular, on each valve numbering 22–33, with 5–8 on fold and 4–7 in sinus; growth lines visible only at anterior margin.

INTERIOR.—Secondary thickenings in apical cavities, shell-wall thick. Pedicle collar short; dental plates thick, long, beyond hinge zone and subparallel; teeth massive, rectangular in section; accessory denticulars and dental cavities present.

Dorsal septum very short, reduced into ridge rapidly forward. Septalium absent; septalial plates clearly shown, long and pendant in topotype specimen, while absent in another one. Hinge plates broad and slightly inclined ventrally in topotype specimen; narrow and subhorizontal in another. Inner socket ridges low, but well differentiated; crural bases very narrow, in topotype specimen not well formed. Crura radulifer, about $\frac{1}{4}$ as long as dorsal valve, arising from taperings of hinge plates, flattened and wide, somewhat similar to cilifer in topotype specimen, only slightly incurved ventrally, without any specialized distal ends.

COMPARISONS.—*Obsoletirhynchia diducta* is close to *O. obsoleta* in general aspects. Laurin (1984a) thought that this species was synonymous with *O. obsoleta*. Our comparison of many specimens leads us to keep them as two separate species. The main differences between them are as follows.

1. *O. obsoleta* is generally suboval in shape, with rounded margins and subequal valves. The fold and sulcus are weak, not well separated from the slopes, and the fold is hardly raised over the flanks. The tongue is very short and the anterior commissure is arched only gently or is even nearly rectimarginate. On the other hand, *O. diducta* is generally subpentagonal in shape, with broader shell, and dorsal valve much more convex than the ventral one. The fold and sinus are clearly shown and well separated from slopes, with broader and moderately raised fold over flanks. The anterior commissure in this species is strongly uniplicate, with high, trapezoidal to rectangular tongue, although some are asymmetrical.

2. The beak of *O. obsoleta* is very short and obtuse, nearly substraight, with a larger and markedly rimmed foramen. The deltidial plates of this species is noticeably convex, making the beak slightly apsaclined in appearance. While *O. diducta* has a generally longer, massive, and suberect beak, the rims around the foramen are not as prominent as in *O. obsoleta*, and the deltidial plates are conjunct, but not as distinctly convex as in *O. obsoleta*. The planoareas are generally clearer and larger in *O. obsoleta* than in *O. diducta*.

3. *O. obsoleta* usually has more and finer, less sharp costae; while *O. diducta* possesses stronger, but fewer ribs. The concentric lines usually are more conspicuous in *O. obsoleta*.

4. The interiors of these two species are basically the

same, but *O. diducta* has generally longer dental plates and less thickened hinge plates.

Obsoletirhynchia obsoleta (Sowerby, 1815), new combination

FIGURES 54, 55; PLATE 5: FIGURES 1, 3, 4, 9, PLATE 17: FIGURES 8–10

Terebratulina obsoleta Sowerby, 1815:192, pl. 83: fig. 7.

Rhynchonella obsoleta (Sowerby).—Davidson, 1851–1852:90, pl. 17: figs. 1–5, appendix:21; 1878:207, pl. 29: fig. 4.—Oppel, 1856–1858:49.—Rollier, 1918:168. [Not Haas and Petri, 1882:215, pl. VII: figs. 8–11.—Greppin, 1900:174, pl. 19: fig. 15.]

?*Rhynchonella obsoleta* (Sowerby).—Clerc, 1904:9, pl. 3: fig. 11 [in part].

?*Cymatorhynchia obsoleta* Davidson [sic].—Buckman, 1918:54.

Kallirhynchia? obsoleta (Sowerby).—Buckman, 1918:32.

Rhactorhynchia argillacea Buckman, 1918:227, pl. 14: fig. 3.

Rhactorhynchia obsoleta (Sowerby).—Buckman, 1918:51.

Rhactorhynchia recta Douglas and Arkell, 1928:170, pl. 11: fig. 8.

Kutchirhynchia obsoleta obsoleta (Sowerby).—Laurin, 1984a:377, pl. 10: figs. 1, 2, 6, pl. 11: figs. 10–13 [in part, not pl. 10: figs. 5–9 (= *R. diducta* Buckman).]

Kutchirhynchia obsoleta divionensis Laurin, 1984a:378, pl. 10: figs. 3–5.

TYPE.—*Neotype*: Davidson, 1851–1852, pl. 17: fig. 1; designated by Laurin (1984a:378); from the Bradford Clay, Bradford-on-Avon, England.

MATERIAL STUDIED.—Hundreds of specimens from the Upper Bathonian of France and tens of specimens from the Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England.

DESCRIPTION.—Shell medium to large, with rounded antero-lateral margins; broadly suboval to roundly subpentagonal in outline, subglobose in profile; moderately biconvex, dorsal valve slightly more convex than ventral one; lateral commissures sloping toward ventral side; anterior commissure broadly arched to gently uniplicate; tongue short and low, U-shaped. Fold and sulcus feeble; some specimens almost rectimarginate, without recognizable tongue; anterior commissure of some specimens slightly asymmetrical.

Beak very small and obtuse, substraight to suberect; foramen large, oval to subcircular in shape, hypothyridid, with well developed and clear rims; deltidial plates conjunct, thickened and convex, making beak slightly apsaclined; beak ridges obtuse; interareas small, small but clear planoareas usually present.

Ventral valve moderately convex at posterior, more or less flattened anteriorly; sulcus very shallow, broad, not well separated from slopes; in some specimens sulcus only existing as depression along middle portion of valve at anterior $\frac{1}{2}$ to $\frac{1}{3}$.

Dorsal valve moderately convex, but never swollen; fold poorly developed, low and broad, only slightly differentiated from slopes at anterior $\frac{1}{3}$, in some specimens no recognizable fold present.

FIGURE 54 (facing page).—Serial sections of *Obsoletirhynchia obsoleta* (Sowerby); topotype, USNM 31006c, L 24.8, W 25.1, T 17.4, A 97; from the Bradford Clay (Upper Bathonian), Bradford-on-Avon, Dorset, England.

FIGURE 55.—Serial sections of *Obsoleterhynchia obsoleta* (Sowerby); USNM 429330, L 24.5, W 23.9, T 16.6, A 96; (Upper Bathonian) Amfreville, Calvados, France.

Costae numerous, subangular to rounded, on each valve numbering 27–38, with 5–10 on fold and 4–9 in sulcus; growth lines feeble, visible at anterior margins. Shell thickened along margins at gerontic stage, and growth lines becoming obvious.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 31006a	26.4	24.3	16.2	91	32	7	6
USNM 31006b	25.3	25.0	17.4	91	34	9	8
USNM 32107a	30.4	27.3	20.0	91	37	7	6
USNM 32107b	29.3	27.0	17.7	90	38	9	8
USNM 64405a	22.2	20.1	15.0	93	25	5	4
USNM 75577a	29.5	26.9	19.2	91	38	8	7
USNM 92009a	26.7	28.1	18.9	100	33	8	7
USNM 104680a	34.2	33.2	21.9	93	39	10	9
USNM 104682a	22.4	21.2	15.9	86	29	5	4
USNM 429331	23.1	21.3	16.0	95	30	6	5
USNM 429332	22.2	21.4	15.9	95	31	7	6
USNM 429333	20.9	20.1	14.2	94	30	7	6
USNM 429334	19.4	19.0	13.1	93	28	6	5
USNM 429335	22.0	20.8	13.0	99	31	7	6
USNM 429343	31.1	29.0	21.7	92	37	8	7
USNM 429344	23.8	21.1	17.3	95	32	6	5
USNM 429345	30.7	30.0	19.1	97	39	11	10

INTERIOR.—Secondary thickenings in umbonal cavities; shell relatively thick. Pedicle collar not seen; deltidial plates conjunct and crumpled; dental plates thick, not very long, slightly divergent or convergent to ventral floor; teeth strong, massive, rectangular in sections, with crenulations; accessory denticulars and dental cavities present; teeth tightly held in sockets.

Dorsal septum reduced into ridge; no septalium present; septalial plates short, pendant. Hinge plates broad; in one sectioned specimen, clearly thickened and slightly inclined ventrally, crural bases not well formed; in another one, hinge plates subhorizontal, crural bases well formed, but narrow. Inner socket ridges low, but well differentiated; crura radulifer, somewhat similar to cilifer in shape; arising from taperings of hinge plates; in one sectioned specimen (Figure 54) crura thick, depressed laterally and incurved ventrally, appearing as vertical plates in section (this might be the result of the specimen having been mounted diagonally in the plaster); in another specimen (Figure 55) crura rather close to cilifer, flattened in dorsal-ventral direction and only incurved slightly toward ventral valve. Crura short, about 1/4 as long as dorsal valve.

REMARKS.—Laurin (1984a:226–228, figs. 145–149) illustrated four sets of serial sections of the species. Among the sectioned specimens, the three adults show the same interiors as the present specimens and have no septalium, but the serial sections were incomplete, without showing the distal ends of the crura; one (p. 228, fig. 147), which was said to be a juvenile specimen, has a well developed septalium, high septum, and well formed crural bases. This indicates that the septalium and

septum of the species are gradually reduced with growth, becoming obsolescent at the adult stage.

This species varies considerably in exterior morphology and has been split into two subspecies by Laurin (1984a). Generally, the juvenile specimens of the subspecies *Obsoletirhynchia obsoleta obsoleta* (Sowerby) are suboval in shape and their deltidial plates are disjunct or just conjunct, not distinctly thickened (Plate 17: Figure 9, Plate 5: Figures 1, 3). Adult specimens of this subspecies usually are broadly and roundly subpentagonal, with the fold more elevated and the deltidial plates becoming conjunct and strengthened. The subspecies *O. obsoleta divionensis* Laurin is rather large and elongate, with narrowly suboval shell and more costae, somewhat suggestive of *Sphenorhynchia*. Its interior structures are the same as those of *Obsoletirhynchia obsoleta obsoleta* (Sowerby) and quite different from those of *Sphenorhynchia*.

Obsoletirhynchia rostrata (Sowerby, 1815),
new combination

PLATE 4: FIGURES 11, 18–20, PLATE 17: FIGURES 6, 7

Terebratula rostrata Sowerby, 1815:67, Tab. 537, fig. 1. [Not Zieten, 1830:55, pl. 41: fig. 6.]

?*Rhactorhynchia rostrata* (Sowerby).—Buckman, 1918:51, 227, pl. 14: fig. 4.

TYPE.—Sowerby’s original specimen, said to be from the Bathonian of Hamsey, England, is probably lost. Shi looked for it in the Natural History Museum, London, but this specimen could not be found either in the Sowerby collection or in other collections. It seems necessary to choose a neotype, but the only other specimen that has ever been illustrated is one figured by Buckman (1918, pl. 14: fig. 4) from the Bradford Clay, Bradford-on-Avon, Wiltshire, England. This specimen does not quite coincide with Sowerby’s description. Therefore, a neotype remains to be found.

MATERIAL STUDIED.—9 specimens from the Upper Bathonian of France.

DESCRIPTION.—Shell small to medium, tapering posteriorly; narrowly suboval in outline, with a narrow apical angle; valves almost equal in convexity and depth or dorsal valve slightly more convex than ventral one; subglobose in profile. Anterior commissure gently arched; tongue poorly developed and short.

Beak rather long, with massive base and pointed tip, generally substraight to suberect; foramen small, hypothyridid to submesothyridid; deltidial plates high, conjunct and strengthened, with clear rims around foramen; beak ridges obtuse; planoareas well shown.

Ventral valve moderately convex and recurved regularly; sulcus shallow, not very well separated from slopes.

Dorsal valve evenly convex; fold incipient, only recognizable at anterior 1/3, without clearly defined borders from flanks.

Ribs coarse, subangular, on each valve numbering 22–28, with 5–7 on fold and 4–6 in sinus; growth lines visible only at frontal margins.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 429350	21.9	19.2	16.6	74	27	7	6
USNM 429351	23.1	21.2	16.8	85	28	7	6
USNM 429352	21.8	19.3	16.9	88	27	6	5
USNM 429353	19.5	15.1	13.9	82	28	6	5
USNM 429354	17.8	17.5	11.3	84	25	6	5
USNM 429355	17.6	15.5	13.1	86	22	5	4
USNM 429356	22.5	19.0	16.8	77	27	6	5
USNM 429357	20.2	17.0	14.3	72	26	5	4
USNM 429358	17.4	15.2	13.0	72	25	5	4

INTERIOR.—One excavated specimen with good interiors. Secondary thickenings in umbonal cavities. Pedicle collar short; deltidial plates conjunct, thickened and crumpled internally (Plate 4: Figures 18a,b); delthyrial chamber wide, trapezoidal; lateral cavities well developed; dental plates subparallel, short, splitting from ventral floor before reaching hinge zone; teeth massive, with expanded ends and crenulations.

Dorsal septalium narrow and deep; septum reduced into ridge, running about 2/5 of valve length; hinge plates narrow, thickened secondarily and slightly declined dorsally; inner socket ridges low, but well differentiated from hinge plates; crural bases well formed along dorsal sides of inner margins of hinge plates; crura radulifer, depressed, and relatively wide, incurved ventrally forward; at distal ends crura slightly enlarged, with feeble furrows on dorsal sides of crura, but no gutters formed.

REMARKS.—This species is poorly known. Sowerby's illustration was not very clear, but he mentioned in the description that the species has a long beak and conjunct deltidial plates. The specimen illustrated by Buckman (1918) shows a short beak, large foramen, and relatively low deltidial plates. This specimen is more like a young specimen of *O. obsoleta* (Sowerby) rather than *O. rostrata* (Sowerby). The present specimens are all from France, but in character they are in close accord with Sowerby's description.

This species is similar to *O. obsoleta*, but differs from it in having a fairly long beak, highly conjunct deltidial plates, narrower shell, and a more convex ventral valve.

***Rhactorhynchia* Buckman, 1918**

Rhactorhynchia Buckman, 1918:50 [in part].—Roche, 1939:266.—Makridin, 1960:254 [in part].—Ager, 1965a:H618.—Kamyschan and Babanova, 1973:85 [in part].—Wisniewska-Zelichowska, 1978:91, 142. [Not Muir-Wood, 1936:45.—Makridin, 1964:160.—Kamyschan and Babanova, 1973:109.—Ching, Sun, and Rong, 1976:308.—Shi, 1987b:58, 59.]

?*Rhactorhynchia* Buckman.—Crickmay, 1933:880.

Formosarhynchia Buckman.—Wisniewska-Zelichowska, 1978:80, 141 [in part].

TYPE-SPECIES.—*Rhactorhynchia rhacta* Buckman, 1918:226.

EMENDED DIAGNOSIS.—Shell medium to fairly large, subglobose to globose in lateral view; fold and sulcus generally

weak; beak strong, foramen rimmed, hypothyriddid to submesothyriddid, deltidial plates conjunct; shell with many strong, sharp costae. Dorsal septum strong, crura radulifer, septalium usually present; muscle scars expanded.

AGE AND DISTRIBUTION.—Bajocian; Europe, ?India, ?Northern Africa, and ?North America.

REMARKS.—Though this genus has been founded for a long time and was supposed to be an important rhynchonellid genus in the Middle Jurassic of the Tethys, it seems seldom to be used properly in the literature. Ager, Childs, and Pearson (1972) thought that this is one of the most unsatisfactory genera erected by Buckman.

Buckman (1918), relying on the exteriors and the muscle scars, included more than 32 species in the genus. These species show great variation in morphology and a wide range in time, from the Aalenian to Kimmeridgian. Muir-Wood (1936) referred two further Bathonian species, *Rhynchonella voluta* Richardson and Walker and *Rhynchonella plateia* Richardson and Walker, to the genus with doubt. Makridin (1964) added 10 more Oxfordian to Kimmeridgian species to this genus. According to his illustrations, however, none of these Russian species appears to be morphologically coincident with the type-species or its closely related forms.

Wisniewska (1932) described *Septaliphoria* and transferred some of the *Rhactorhynchia* species into her genus. Childs (1969), in his study of the Upper Jurassic rhynchonellids of Northwestern Europe, transferred several Late Jurassic species into *Somalirhynchia* and *Torquirhynchia*. Many species in this genus remain to be verified, especially those from the Late Jurassic, which probably should be transferred to *Septaliphoria*, *Somalirhynchia*, or *Torquirhynchia*. Ager, Childs, and Pearson (1972) recommended that *Rhactorhynchia* should remain as a strictly Middle Jurassic genus, centering around the Bajocian type-species *Rhactorhynchia rhacta* Buckman.

The four species (or subspecies) depicted by Wisniewska-Zelichowska (1978) from the Bajocian of Poland are in close accord with the English forms in exterior characters, although their interiors were not investigated. From the specimens illustrated by Wisniewska-Zelichowska (1978, pl. VII-IX), nevertheless, it can be seen that all of these species have a fairly long septum or septal ridge in the dorsal valve, which runs about half of the dorsal valve length. One specimen (pl. VII: fig. 5) shows a very short septalium present in the dorsal valve and has rather large muscle scars. Unfortunately, the type-species *R. rhacta* seems to be a rare form; the only other specimens of this species, beside the holotype described by Buckman (1918), were depicted by Kamyschan and Babanova from the Lower Bajocian of the Caucasus (1973:91, pl. x: figs. 7, 8). The Russian specimens, however, do not coincide with the English specimen and are much smaller, with an arched anterior commissure and somewhat pinched, narrow beak, although they might be congeneric with the English form. Internally, the Russian specimen has a low but long septum, narrow hinge plates, radulifer crura, and no septalium (Kamyschan and Babanova, 1973:91, fig. 24).

In this paper, the genus has been preserved in a rather limited sense to include mostly Bajocian forms. The species described in this paper are all from the Upper Bajocian of England and appear close to *Rhactorhynchia rhacta* Buckman in morphology. The emended diagnosis presented herein is based mainly on those English forms, especially on *Rhactorhynchia subtetrahedra* (Davidson), which is very similar to the type-species in general characters. That species is thought to be a synonym of the latter by Colin Prosser who works on the Bajocian brachiopods of England (pers. comm. 1988, 1992).

According to the present study, the genus *Rhactorhynchia* shows a close relation with the early Middle Jurassic form *Cymatorhynchia*. Internally, both of them have well developed septum, radulifer crura, and variable septalium. Externally, they are similar in costation, folding, and general shell shape. The main differences between them seem to be that *Rhactorhynchia* usually has a stronger beak, rimmed foramen, conjunct deltidial plates, stronger costae, and less tumid dorsal valve. Gerontic specimens of this genus may have the shell thickened along the anterior margin and possess a broad and rectangular tongue. The Bathonian genus *Obsoletirhynchia* is close to this genus in the characters of beak, foramen, and deltidial plates, but differs in having a reduced dorsal septum, poorly developed septalial plates, and compressed crura. *Obsoletirhynchia* may have evolved from *Rhactorhynchia* with *Rhynchonella plaitea* and *Rhynchonella voluta* as its early forms and mainly developed in the Late Bathonian.

Rhactorhynchia hampenensis (Buckman, 1886)

FIGURE 56; PLATE 13: FIGURES 1, 3–8

Rhynchonella hampenensis Buckman, 1886:42, pl. 3: fig. 6.
Rhactorhynchia hampenensis (Buckman).—Buckman, 1918:51.
Kallirhynchia hampenensis (Buckman).—Buckman, 1918:32.

TYPE.—*Holotype*: Buckman, 1886, pl. 3: fig. 6; from the Inferior Oolite (Upper Bajocian), Notgrove station, Naunton, England.

MATERIAL STUDIED.—33 specimens from the Inferior Oolite (Upper Bajocian), England.

DESCRIPTION.—Shell medium, subtrigonal to subpentagonal in outline, subglobose in profile; dorsal valve slightly tumid, much more convex than ventral one. Anterior commissure strongly uniplicate; tongue high, rectangular in shape, with truncated termination; some specimens with slightly asymmetrical anterior commissures.

Beak long, acute, substraight to suberect; foramen medium, subcircular, hypothyridid to submesothyridid; deltidial plates high, conjunct, with rims around foramen and well separating foramen from hinge line; beak ridges rounded to subangular; interareas small, but well defined and slightly concave.

Ventral valve moderately convex; sulcus well developed, shallow and broad, occurring at anterior 1/2 of valve and turning over toward dorsal valve more or less abruptly at anterior margin.

Dorsal valve tumid, with greatest convexity at anterior 1/2 to 1/3, but not everted anteriorly; fold broad and low, only slightly elevated above slopes at anterior 1/3, with well defined borders.

Costae numerous, subangular to sharp, on each valve numbering 20–26, with 5–8 on fold and 4–7 in sulcus; growth lines not developed; shell thickened markedly along anterior margin at gerontic stage.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 30988a	17.2	16.4	13.2	86	28	7	6
USNM 64406a	17.5	18.7	13.3	101	24	6	5
USNM 75579a	18.0	17.1	14.1	80	24	7	6
USNM 88742a	18.2	18.6	14.1	87	23	6	5
USNM 89082a	18.0	18.4	14.7	96	22	6	5
USNM 89082b	18.3	18.7	13.2	89	24	7	5
USNM 89082c	17.1	18.0	14.3	92	22	6	5
USNM 89082d	18.3	21.1	16.2	96	22	7	6
USNM 92019a	17.7	19.5	13.6	94	21	7	6
USNM 104758a	17.7	18.2	15.5	96	20	6	5
USNM 104758b	17.3	21.5	16.0	100	22	6	5
USNM 180481a	17.7	18.5	14.7	97	25	7	6
USNM 429360	19.3	20.0	15.0	93	25	6	5

INTERIOR.—No secondary thickenings in either valve. No pedicle collar observed in two sectioned specimens; deltidial plates conjunct and crumpled inside; delthyrial chamber wide, rectangular in shape; lateral cavities well developed; dental plates short, splitting from ventral floor far behind hinge zone, subparallel; teeth strong, massive with expanded ends and crenulations; accessory denticulars and dental cavities present.

Dorsal septum well developed, fairly long, extending for about 1/3 to 1/2 of dorsal valve length. Septalium present, but very short; in one sectioned specimen (USNM 89082e) very shallow and narrow, only 0.5–1 mm in length; while in another (USNM 88742c, Figure 56) well developed and V-shaped, supported by stout septum. Hinge plates broad, almost horizontal; inner socket ridges poorly differentiated; crural bases not well formed; crura radulifer, about 1/4 as long as dorsal valve, arising from inner margins of hinge plates and strongly incurved toward ventral valve, appearing as vertical plates in section; in one specimen (USNM 89082e) crural terminations slightly enlarged.

REMARKS.—The species is similar to *Kallirhynchia* in general shape and size. Buckman (1886) thought that it was most nearly allied to *Kallirhynchia concinna* (Sowerby). Buckman (1918:32, 51) split this species into two parts, one of which was called *Kallirhynchia hampenensis* and the other *Rhactorhynchia hampenensis*. This is not acceptable, because Buckman in fact only illustrated one specimen in 1886 and this is the only specimen that has ever been figured for the species.

The present study shows that this species is more closely related to *Rhactorhynchia subtetrahedra* both in general character and internal structures, although it is similar to *Kallirhynchia concinna* in shape and uniplication. *Kallirhyn-*

FIGURE 56.—Serial sections of *Rhactorhynchia hampenensis* (Buckman); USNM 88742c, L 20.5, W 21.8, T 14.1, A 93; from the Inferior Oolite (Upper Bajocian), Rodborough Hill, Gloucestershire, England.

chia has a short beak, no rims around the foramen, and short deltidial plates that are disjunct to just conjunct and not thickened or strengthened. Internally, *Kallirhynchia* has a very reduced septum and long pendant septalial plates, but no septalium.

***Rhactorhynchia subtetrahedra* (Davidson, 1851)**

FIGURE 57; PLATE 5; FIGURES 10–14, PLATE 6; FIGURE 11

Rhynchonella subtetrahedra Davidson, 1851–1852:95, pl. 16: figs. 9, 10, ?11, ?12; 1878:200.—Buckman, 1886:42 [foot note].—Greppin, 1900:173, pl. 19: fig. 16.—Rollier, 1918:157.

?*Rhynchonella subtetrahedra* Davidson.—Oppel, 1856–1858:433, Tab. 53, no. 244.—Rothpletz, 1886:146, pl. X: fig. 16.

Rhactorhynchia subtetrahedra (Davidson).—Buckman, 1918:51, 226.

?*Rhactorhynchia subtetrahedra* (Davidson).—Kamyschan and Babanova, 1973:92, pl. X: fig. 9.

TYPE.—*Lectotype*: Davidson, 1851–1852, pl. 16: fig. 9; designated by Buckman, 1886:42; from the Inferior Oolite (Upper Bajocian), Dundry Hill, Somerset, England.

MATERIAL STUDIED.—6 specimens from the Inferior Oolite (Upper Bajocian) of England and Germany.

DESCRIPTION.—Shell large, transversely subpentagonal to broadly subcircular in outline, subglobose in profile; dorsal

valve slightly more convex than ventral one. Anterior commissure gently arched to moderately uniplicate; tongue variable, either very short or broadly trapezoidal; commissure variably deflected laterally.

Beak short, suberect, with broad base; foramen medium, subcircular, hypothyridid to submesothyridid; deltidial plates short, conjunct, with slight rims around foramen; beak ridges obtuse; interareas narrow, slightly concave.

Ventral valve adequately convex posteriorly, flattened anteriorly; sulcus broad and shallow, with shallow bottom, but well separated from slopes, occurring at posterior $\frac{1}{2}$ of valve.

Dorsal valve convex evenly, umbonal region less convex; fold broad and low, well defined, moderately elevated above slopes at anterior $\frac{1}{3}$ of valve.

Costae numerous, strong, subrounded, on each valve numbering 23–29, with 6–8 on fold and 4–7 in sulcus; growth lines feeble, visible only at frontal margin.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 31432	25.3	29.0	17.1	102	27	8	7
USNM 75588a	28.5	28.2	17.7	94	35	8	7
USNM 75588b	33.4	31.7	20.0	96	30	7	6
USNM 88733	32.2	35.0	19.5	106	29	8	7
USNM 88731	27.5	30.5	18.0	99	30	7	6
USNM 104779	26.2	29.2	16.9	100	23	6	5

INTERIOR.—No secondary thickenings in either valve, internal structures delicate. Pedicle collar not seen; dental plates short, splitting from ventral floor before reaching hinge zone, slightly convergent to ventral floor; delthyrial chamber wide; lateral cavities well developed; teeth small, nodular, with expanded ends, crenulations, and accessory denticulations.

Dorsal septum well developed, high and fairly long, extending about $\frac{1}{3}$ of dorsal valve length; septalium absent in sectioned specimen, septalial plates very short; hinge plates broad, subhorizontal; inner socket ridges low, but well differentiated from hinge plates; crural bases very narrow, only existing as ridges along dorsal sides of inner margins of hinge plates; crura radulifer, about $\frac{1}{4}$ as long as dorsal valve, curved slightly toward ventral valve, with slightly expanded distal ends, slightly folded and with shallow furrow on dorsal side of each crus, giving crura somewhat canalifer appearance in sections.

REMARKS.—This species is inadequately studied and its interior features are not fully known. Externally the species resembles *Rhactorhynchia rhacta* Buckman, the type-species of the genus, and was put in the same “subgroup” with the latter by Buckman (1918:226). Davidson (1851–1852) illustrated four specimens of this species, two of which (pl. 16: figs. 9, 10) are alike in uniplication, with broad and well developed tongues, as well as broad, slightly elevated fold and clear sinus. The other two (pl. 16: figs. 11, 12) bear hardly recognizable fold and sinus, and the anterior commissures are nearly

rectimarginate or slightly asymmetrical. Buckman (1918:226) thought that only fig. 9 of Davidson (1851–1852:95, pl. 16) was *Rhactorhynchia subtetrahedra*, but he did not mention whether the specimens in figs. 10–12 should be taken as a new species or referred to other species. Rollier (1918:157) doubted that the specimens illustrated by Davidson (1851–1852) in pl. 16: figs. 11, 12 were the same species as the specimens in figs. 9, 10.

The present specimens studied also fall into two morphotypes. One morphotype (Plate 5: Figures 10, 11) is broadly subpentagonal and has a widely rectangular and well defined fold and sulcus. It closely resembles specimens illustrated by Davidson (1851–1852, pl. 16: figs. 9, 10). Another morphotype (Plate 5: Figure 13, Plate 6: Figure 11) has a subcircular shell, barely recognized fold and sulcus, and slightly arched or asymmetrical anterior commissure. This morphotype is similar to the specimens illustrated by Davidson (1851–1852, pl. 16: figs. 11, 12 and also reminiscent of *Obsoletirhynchia obsoleta* (Sowerby). Nevertheless, these two morphotypes are closely related by one specimen (Plate 5: Figure 14) that shows a median character between them and is close to the lectotype of the species (Davidson, 1851–1852, pl. 16: fig. 9). We prefer, therefore, to take these two morphotypes as variations within the species and to regard the specimens illustrated by Davidson (1851–1852, pl. 16) in figs. 11, 12 as the same species illustrated in figs. 9, 10.

Regarding the interiors, a couple of specimens were sectioned in England, but none has been published until now. The present sectioned specimen is from the Inferior Oolite (*Truelli Zone*), Dundry Hill, Somerset, the type locality according to Davidson. It shows no septalium, and has short septalial plates. The crura are of the radulifer type, but with furrows on their dorsal sides and are similar to the canalifer type, except that the furrows are short and shallow. On the other hand, Colin Prosser of the Nature Conservancy for England and Ellis Owen in the Natural History Museum, London, also sectioned several specimens of the species from the Inferior Oolite at Cheltenham and Leckhampton Hill, which are not far from Dundry Hill. These specimens show that a very short, incomplete septalium or V-shaped, normal septalium may be present in the dorsal valve. The crura are typically radulifer, without obvious furrows on their dorsal sides and are strongly curved toward the ventral valve (Shi examined these sections when he visited the Natural History Museum, London), although they have the same kind of septum and hinge plates as the present specimen. These indicate that this species is internally variable, nevertheless, the septum is generally well developed and there are no secondary thickenings.

The type-species, *Rhactorhynchia rhacta* Buckman, is very rare; only the holotype, illustrated by Buckman (1918, pl. 14: fig. 16) from the Inferior Oolite, *garantiana Zone*, Upper Bajocian, Dundry Hill, Somerset, has been recorded in England. So nothing is known of the interior. Nevertheless,

FIGURE 57 (facing page).—Serial sections of *Rhactorhynchia subtetrahedra* (Davidson); topotype, USNM 104779, L 26.2, W 29.2, T 16.9, A 100; from the Inferior Oolite (Truelli Zone, Upper Bajocian), Dundry Hill, Somerset, England.

Colin Prosser thought that it might be synonymous with *Rhactorhynchia subtetrahedra* (Davidson).

Rhactorhynchia turgidula Buckman, 1918

FIGURE 58; PLATE 17: FIGURES 1–5

Rhactorhynchia turgidula Buckman, 1918:26, pl. 14: fig. 11.
? "*Rhynchonella*" sp. aff. *Globirhynchia subobsoleta* (Davidson).—Mourier and Almeras, 1986:694, pl. 2: figs. 7, 8.

TYPE.—*Holotype*: Buckman, 1918, pl. 14: fig. 11; from the Inferior Oolite (Upper Bajocian), Broad Windsor, Dorset, England.

MATERIAL STUDIED.—42 specimens from the Inferior Oolite (Upper *Trigonia* Grit, Upper Bajocian) of Leckhampton Hill, Gloucestershire; 2 specimens from the same horizon of Birdlip, England.

DESCRIPTION.—Shell small for genus; globose, with rounded antero-lateral margins; shell medium, subcircular to subpentagonal in outline; subglobose to globose in lateral view; valves subequal, dorsal valve more convex than ventral one. Anterior commissure uniplicate; tongue broad, high and rectangular in shape; shell strongly thickened along anterior margin, producing a flattened anterior region.

Beak short, obtuse, suberect; foramen small, subcircular, hypothyriddid to submesothyridid; deltidial plates conjunct, with slight rims around foramen; beak ridges obtuse; interareas small or not developed.

Ventral valve moderately convex, recurved evenly; sulcus shallow and broad, often only a slight depression at anterior 1/3 and turning toward dorsal valve more or less abruptly at anterior margin, without clearly defined borders from slopes. At gerontic stage, shell thickened markedly along anterior margin, sulcus tending to be flattened.

Dorsal valve tumid, with greatest convexity at anterior 1/3, but not everted; fold poorly developed, only slightly raised over slopes at anterior 1/3 of valve, broad and low; in some specimens hardly recognizable.

Costae numerous, subrounded to subangular, on each valve numbering 21–27, with 5–8 on fold and 4–7 in sulcus; growth lines fine and irregular, visible at anterior part.

INTERIOR.—No secondary thickenings. Dorsal muscle scars large, consisting of four attachment areas; two front scars large, subtrigonal-shaped and slightly expanded laterally, located at middle of valve; two posterior bands long and narrow, located postero-laterally to front ones. Short pedicle collar often present; dental plates short, subparallel; delthyrial chamber and lateral cavities well developed; teeth massive, mallet-like, held tightly in sockets; accessory denticulars and dental cavities present.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 130957a	18.2	19.3	16.0	94	26	5	4
USNM 130957b	18.2	19.3	18.0	96	27	6	5
USNM 268928a	19.2	20.1	15.4	99	22	6	5
USNM 268928b	18.6	21.6	16.2	106	23	7	6
USNM 268928c	17.5	18.8	13.7	96	26	6	5
USNM 268938a	21.1	21.0	17.2	96	25	6	5
USNM 268938b	19.7	22.0	14.8	106	27	6	5
USNM 268938c	21.5	23.1	17.1	104	26	7	6
USNM 429369	19.3	21.5	15.8	102	28	8	7
USNM 429370	16.5	17.8	13.9	97	26	6	5
USNM 429371	18.7	20.1	14.0	101	26	6	5

Dorsal septum well developed and high, reduced into ridge after hinge zone, which is fairly long, running about 1/3 to 1/2 of valve length. Septalium variable, in one sectioned specimen (USNM 429372, L 16.0, W 17.1, T 16.0, A 107) septalium absent and septalial plates short, pendant; while in another (USNM 258938d, L 18.2, W 20.3, T 13.4, A 106), a short, V-shaped normal septalium present. Hinge plates subhorizontal posteriorly and becoming slightly inclined anteriorly; inner socket ridges well demarcated; crural bases not very well formed, and narrow; crura radulifer, about 1/4 as long as dorsal valve, arising from inner margins of hinge plates and strongly incurved toward ventral valve at anterior parts, distal ends appearing as vertical plates in section.

REMARKS.—This species is hardly known. Buckman (1918) figured only a specimen whose outer shell was exfoliated, showing muscle scars and a long septum. The smaller specimens of the species are similar to *Globirhynchia subobsoleta* (Davidson) in shape, but differs from it in having the anterior margin thickened, a flattened anterior-view region and a high, rectangular tongue. Internally these two species are quite different. *Globirhynchia subobsoleta* has distinctly canalifer crura. Mourier and Almeras (1986, pl. 2: fig. 7) illustrated a specimen named "*Rhynchonella*" sp. aff. *Glo-*

FIGURE 58.—Serial Sections of *Rhactorhynchia turgidula* Buckman; USNM 429372, L 18.0, W 20.0, T 13.0, A 106; from the Inferior Oolite (Upper *Trigonia* Grit, Upper Bajocian), Leckhampton Hill, Gloucestershire, England.

birhynchia subobsoleta (Davidson) from the Upper Bajocian, *Parkinsoni* Zone of France, which is very similar to the present specimens and probably should be transferred to this species.

Internally, this species is close to *Rhactorhynchia hampenensis*, except that it has more strongly curved crura, which have slightly expanded distal ends. Externally, this species differs from the latter in having a more rounded and globose shell, shorter beak, as well as less developed fold and sulcus.

Rhactorhynchia tumefacta Buckman, 1918

PLATE 17: FIGURES 11–13

?*Rhactorhynchia impar* Buckman, 1918:226, pl. 14: fig. 15.

Rhactorhynchia tumefacta Buckman, 1918:226, pl. 14: fig. 12.

TYPE.—*Holotype*: Buckman, 1918, pl. 14: fig. 12; from the Inferior Oolite (*garantiana* Zone, Upper Bajocian), Stroud Hill, Gloucestershire, England.

MATERIAL STUDIED.—6 specimens from the Inferior Oolite (*Garantiana* Zone, Upper Bajocian), Leckhampton Hill, Gloucestershire; 1 specimen from the Inferior Oolite (Upper *Trigonia* Grit, Upper Bajocian), Cheltenham, Gloucestershire, England (these localities are very close to Stroud Hill, Stroud).

DESCRIPTION.—Shell medium size for genus; subpentagonal in outline and subglobose in profile; valves subequal, dorsal valve more convex than ventral one. Lateral commissures deflected ventrally at 15–5 degrees; anterior commissure uniplicate; tongue broad, rectangular or highly arched, sometimes asymmetrical.

Beak massive, short, suberect; foramen medium, subcircular, hypothyriddid, with slight rims; deltidial plates short, conjunct; beak ridges obtuse; interareas small.

Ventral valve moderately convex posteriorly, somewhat flattened anteriorly; sinus indistinct, shallow and broad, beginning about $\frac{1}{2}$ to $\frac{1}{3}$ of valve length, turning over more or less sharply toward dorsal valve at anterior margin.

Dorsal valve tumid, greatest convexity at anterior $\frac{1}{3}$ or slightly everted anteriorly; fold feeble, low and broad, but well separated from slopes at anterior $\frac{1}{3}$ of valve.

Costae numerous, coarse, subrounded, on each valve numbering 26–31, with 7–8 on fold and 6–7 in sulcus; growth lines feeble, only visible at front margin.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 429385	25.2	27.3	19.0	97	31	8	7
USNM 429386	26.0	29.1	19.9	95	28	7	6
USNM 429387	21.4	26.2	18.2	98	26	6	5
USNM 429388	20.2	21.0	14.1	95	27	8	7
USNM 429389	20.1	22.0	15.3	96	28	7	6
USNM 429390	16.2	16.0	13.1	87	30	8	7
USNM 429391	26.2	27.3	19.0	99	29	7	6

INTERIOR.—Similar to *Rhactorhynchia hampenensis* Buckman. Dorsal septum very long, about $\frac{1}{2}$ of dorsal valve length, reduced to ridge beyond hinge zone; a short V-shaped septalium present, supported by septum posteriorly; hinge plates nearly subhorizontal, with poorly demarcated inner socket ridges; crura radulifer, strongly incurved toward ventral valve, with distal ends vertical plate-like in sections. Dorsal muscle scars large; two anterior parts expanded transversely, two posterior parts narrow, elongate.

COMPARISONS.—This species is similar to *Rhactorhynchia turgidula* in some aspects, but differs in having a larger subpentagonal shell, less tumid dorsal valve, more elevated fold, and longer beak. The shell of this species is less thickened at the anterior margin in the gerontic stage.

Somalirhynchia Weir, 1925

Somalirhynchia Weir, 1925:79; 1929:38.—Muir-Wood, 1935:93.—Ager, 1965a:H614.—Childs, 1969:78.—Cooper, 1989:58.

Praecyclothyris Makridin, 1964:150 [in part].—Ager, 1965a:H617 [in part].

TYPE-SPECIES.—*Somalirhynchia africana* Weir, 1925:79.

DIAGNOSIS.—Shell large, uniplicate and multicostate; roundly subtrigonal to broadly subpentagonal in outline, subglobose in profile; fold and sulcus generally well shown; beak strong, suberect to incurved; with small and hypothyriddid foramen; interareas well developed. Septum strong and long, hinge plates subhorizontal, crura radulifer.

AGE AND DISTRIBUTION.—Oxfordian to Kimmeridgian; North and East Africa, Middle East, and Europe.

REMARKS.—This genus is similar to *Daghanirhynchia* both externally and internally; some young forms of *Somalirhynchia africana* could hardly be separated from the species of the latter. These two genera are separable mainly in chronology rather than morphology. Nevertheless, *Somalirhynchia* generally is much larger and broader than *Daghanirhynchia*, and usually has more developed and clearly defined interareas.

Somalirhynchia africana Weir, 1925

PLATE 8: FIGURE 15, PLATE 10: FIGURES 9–11, PLATE 12: FIGURE 8

Somalirhynchia africana Weir, 1925:79, pl. 12: figs. 20–23; 1929:39, pl. 4: fig. 7.—Muir-Wood, 1935:94, pl. 10: fig. 7.—Abbate et al., 1974:439, pl. 39: fig. 4.—Cooper, 1989:58, pl. 12: figs. 37–41.

Somalirhynchia smelliei Weir, 1925:83, pl. 11: figs. 32–34.

Somalirhynchia africana var. *jordanica* (Noetling).—Muir-Wood, 1935:97, pl. 10: fig. 8.

Somalirhynchia africana var. *mesoloba* Muir-Wood, 1935:100, pl. 9: fig. 2.

Somalirhynchia africana var. *smelliei* Weir; Muir-Wood, 1935:99, pl. 10: fig. 10.

TYPE.—*Lectotype*: Weir, 1929, pl. 4: fig. 7; designated by Muir-Wood, 1935:94; from the Oxfordian, Somaliland.

MATERIAL STUDIED.—12 specimens from the Oxfordian, Somaliland; 30 specimens from Ethiopia and Kenya, the Oxfordian to ?Kimmeridgian.

DESCRIPTION.—Shell large, roundly subtrigonal to transversely subpentagonal in outline; adequately biconvex, dorsal valve more convex than ventral one. Lateral commissures deflected ventrally; anterior commissure strongly uniplicate; tongue high, trapezoidal to U-shaped.

Beak strong, massive, suberect to erect; foramen large, elliptical, hypothyriddid; deltidial plates short and narrow, disjunct; beak ridges subangular to obtuse; interareas large, well defined and slightly concave, with fine transverse lines.

Ventral valve adequately convex; sinus very well developed, broad and deep, with rounded bottom, occurring at posterior $\frac{1}{3}$ of valve and well separated from slopes.

Dorsal valve evenly convex; fold distinct, broad and moderately raised over slopes, with rounded top, occurring at about $\frac{1}{2}$ of valve, making valve more or less trilobate.

Costae numerous, coarse and subangular, on each valve numbering 26–34, with 5–8 on fold and 4–7 in sulcus; growth lines fine, visible on whole shell.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 75660a	29.6	33.5	19.5	105	28	6	5
USNM 75660b	34.5	35.0	23.2	100	30	5	4
USNM 75660c	33.9	40.2	20.3	113	29	7	6
USNM 75660d	34.2	36.1	21.3	99	34	8	8
USNM 75660e	33.6	37.9	19.0	108	32	8	7
USNM 429404	30.2	33.3	22.3	95	29	6	5
USNM 429405	33.4	35.8	22.6	96	31	7	6
USNM 429406	35.1	38.8	24.9	101	27	6	5
USNM 429407	30.4	30.2	21.9	100	27	6	5
USNM 429408	30.3	32.5	20.2	90	30	6	5
USNM 429409	26.0	26.5	18.0	82	28	7	6
USNM 429410	26.1	29.4	20.5	96	29	6	5

INTERIOR.—Slight secondary thickenings in both apical cavities. Short pedicle collar present; dental plates short, splitting from ventral floor before reaching hinge zone, subparallel to each other; delthyrial chamber wide, rectangular in shape; lateral cavities short and narrow; teeth strong, massive, held tightly in sockets.

Dorsal septum very long, stout, most of length expressed as ridge. Septalium variable; generally absent in gerontic specimen and very short in young specimen, incomplete septalium occasionally visible in adults. Hinge plates broad, almost horizontal; inner socket ridges low and thin, but well demarcated from hinge plates; crural bases not well formed; crura radulifer, arising from taperings of hinge plates, with slightly enlarged and compressed distal ends.

REMARKS.—The three varieties of *S. africana* Weir described by Muir-Wood (1935), var. *aselliei*, var. *mesoloba*, and var. *jordanica*, are not much different from the species and merge from one to the other. In our opinion, none could be regarded as independent species, and are simply variations within the species.

***Sphenorhynchia* Buckman, 1918**

Sphenorhynchia Buckman, 1918:30.—Ager, 1965a:H619.—Almeras, 1980:379.

?*Sphenorhynchia* Buckman.—Cooper, 1989:60.

TYPE-SPECIES.—*Terebratula plicatella* Sowerby, 1825:167.

DIAGNOSIS.—Shell small to large, wedge-shaped, subglobose in profile; beak very short, substraight to suberect; foramen small, rimmed, hypothyriddid to submesothyriddid; deltidial plates generally conjunct; no interareas, planoareas present; anterior commissure arched variably; fold and sinus feeble; costae numerous; secondary thickenings present; septum generally reduced; septalium variable, hinge plates arched; crura radulifer.

AGE AND DISTRIBUTION.—Bajocian to Callovian and ?Oxfordian; Europe, Asia, and ?Africa.

REMARKS.—The genus was revised by Almeras (1980), with a detailed study of most of its species. Internal structures indicate that the genus should be referred to the subfamily Tetrarhynchiinae rather than Cyclothyridiinae. It is similar to *Obsoletirhynchia* and *Goniorhynchia* in characteristics of the beak, the ornamentation, and secondary thickenings. Internally, they all have obvious callus, reduced septum, and radulifer crura, although they are different in detail. This genus generally has well developed planoareas, which is unusual in the Middle Jurassic rhynchonellids and can be used to distinguish it from other genera.

The two species, *Sphenorhynchia? angulata* and *Sphenorhynchia varicostata*, depicted by Cooper (1989:60–63) from the Upper Bajocian to Lower Bathonian of Saudi Arabia are similar to the European forms in shell shape and costation, but differ in having more elongate and massive beak, as well as almost equally convex valves. Internally, *Sphenorhynchia varicostata* (Cooper, 1989, figs. 33, 34) has delicate structures, no secondary thickenings, broader and subhorizontal hinge plates, and higher septum. It seems that these two species are not quite coincident with the European forms and might be more closely related to *Conarosia* Cooper and *Strongyloria* Cooper, rather than to *Sphenorhynchia*.

***Sphenorhynchia plicatella* (Sowerby, 1825)**

PLATE 11: FIGURES 6, 8–10

Terebratula plicatella Sowerby, 1825:167, pl. 503: fig. 1.

Sphenorhynchia plicatella (Sowerby).—Almeras, 1980:329–342, text-figs. 1–4, pl. 1: figs. 1–7, pl. 2: figs. 1, 2 [synonyms cited there].

TYPE.—*Holotype*: Sowerby, 1825, pl. 503: fig. 1; from the Inferior Oolite (Upper Bajocian), Chideock, Dorset, England.

MATERIAL STUDIED.—Tens of specimens from the Inferior Oolite (Upper Bajocian), England.

DIAGNOSIS.—Shell large for genus; broadly suboval to cuneiform; dorsal valve slightly more convex than ventral one; anterior commissure slightly to adequately arched; fold feeble,

sinus broad and shallow; beak very short, pointed; foramen hypothyriddid to submesothyriddid; deltidial plates short, conjunct, with clear rims around foramen; beak ridges obtuse; no interareas, planoareas well developed; shell covered with numerous fine costae; secondary thickenings existing in both valves; septum short, reduced into ridge forward; septalium generally absent; hinge plates arched ventrally; crura radulifer.

***Sphenorhynchia matisconensis* (Lissajous in Arcelin and Roche, 1936)**

PLATE 11: FIGURES 4, 5, 7, 11, 12, PLATE 12: FIGURES 4, 5

Rhynchonella matisconensis Lissajous in Arcelin and Roche, 1936:69, 70, pl. 3: figs. 1–7, pl. 13: figs. 1, 2.

Sphenorhynchia matisconensis (Lissajous in Arcelin and Roche).—Almeras, 1980:342–352, text-figs. 5–10, pl. 2: figs. 3–10, pl. 3: figs. 1–5 [synonyms cited there].

TYPE.—*Holotype*: Arcelin and Roche, 1936, pl. 3: fig. 1; from the Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

MATERIAL STUDIED.—About 20 silicified specimens, most of them have been etched out by acid, with good interiors, from the Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

DIAGNOSIS.—Shell medium to large for genus; narrow and elongate oval or linguiform in outline; anterior commissure straight or slightly arched; fold and sinus feeble; beak very short, pointed; planoareas clear; costae many and coarse; secondary thickenings present in both apical cavities; septum long, septalium well developed; crura radulifer.

INTERIOR.—Callus existing in both valves. Short pedicle collar present; dental plates short, splitting from ventral floor before reaching hinge zone, slightly convergent to floor; teeth long, with expanded ends and crenulations, held deeply in sockets; accessory denticulars and dental cavities present.

Dorsal septum long, reaching to midvalve; in most specimens forming ridge less than 1 mm high; in some specimens septum up to 2 mm in height; in two specimens septum absorbed by secondary thickenings, only about 2–3 mm long. Septalium well developed, generally narrow and deep, V-shaped, but short; hinge plates narrow, strongly inclined ventrally; inner socket ridges very low, not very well differentiated from hinge plates; crural bases poorly formed; crura radulifer, short, about $1/5$ to $1/6$ as long as dorsal valve, arising from taperings of hinge plates, relatively wide and compressed dorso-ventrally, moderately incurved toward ventral valve, with distal ends slightly enlarged; in some specimens shallow furrows recognizable on dorsal sides of crural ends.

Subfamily INDORHYNCHIIINAE Ovtsharenko, 1975

***Moquellina* Jin, Sun, and Ye, 1979**

FIGURES 6–8, 59

Moquellina Jin, Sun, and Ye, 1979:141.—Shi, 1986:157–161.—Sun, 1990:237.

TYPE-SPECIES.—*Moquellina arcuata* Jin, Sun, and Ye, 1979:141.

EMENDED DIAGNOSIS.—Shell small to medium, fully multicostate, costellae simple; no norelliform stage; shell oval to subcircular; moderately biconvex to globose; fold and sinus usually weak, anterior commissure slightly arched to moderately uniplicate; beak short, suberect, foramen small, hypothyriddid; deltidial plates narrow, disjunct to just conjunct. Dorsal septum absent, septalial plates long, sitting parallel on dorsal floor to form septoidium; crura short, calcarifer to canalifer, about $1/5$ to $1/4$ as long as dorsal valve.

AGE AND DISTRIBUTION.—Late Bathonian to Callovian; Northern Tibet, Southern Qinghai, and Western Yunnan, China.

REMARKS.—This genus was erected by Jin, Sun, and Ye (1979:141) based on only a few poorly preserved specimens and including only the type-species *Moquellina arcuata*. The most important character of the genus was said to be the long septalial plates that extend through to the dorsal floor. The crura of the genus were defined as “vertical plate-like,” while the only set of serial sections illustrated by them were incomplete, without showing the terminal shapes of the crura (Jin, Sun, and Ye, 1979:141, fig. 78). Sun (1990:237) described another new species, *Moquellina semicostata*, from the Bathonian of western Yunnan, which shows a well developed and clear septoidium in dorsal valve, just like that in *Moquellina arcuata*. The serial sections are incomplete, without showing the terminal parts of the crura, while the last section (Sun, 1990:238, text-fig. 11) shows an obscure character suggestive of calcarifer to canalifer crura.

Recently, several hundred specimens of the genus and more than 350 serial sections of them have been systematically studied by Shi for this project, all from the Tanggula area, southern Qinghai and northern Tibet, China, where the type specimen was collected. The study shows that this genus has calcarifer crura mainly, but some specimens seem to have canalifer crura, in which the incurved secondary lamellae are longer and with a broad angle between the secondary and primary lamellae. The anterior end of some crura are strongly curved toward the ventral valve so that they appear like four vertical plates in section (Figure 7), as in *Septaliphoria* (Childs, 1969:88–92, figs. 31, 33). In one of the sectioned specimens, the crura appear clearly canalifer (Figure 8). In another (Figure 6), the crura are typically calcarifer, the secondary lamellae are longer and directed dorsally, and the primary lamellae do not extend dorsally as strongly as in *Thurmannella*. In only one of the sectioned specimens, the crura appear as vertical plates, somewhat suggesting a subfalcifer form (Figure 59, *Moquellina* cf. *arcuata* Jin, Sun, and Ye). Nevertheless, in all the sectioned specimens, the septoidium always exists. In a few specimens, the septoidium is rather short (posterior–anterior direction), less than 0.5 mm, and in one of the sectioned specimens, the septalial plates do not reach the dorsal floor, but go down through only $3/4$ of the umbonal cavity.

This genus is ordinary looking and resembles several other genera externally, such as *Burmihynchia*, *Kallirhynchia*,

Thurmannella, *Septaliphoria*, and *Indorhynchia*. Internally, however, this genus is quite distinctive and easy to distinguish from the other genera, except for *Septaliphoria*, which also has ventrally incurved canalifer crura and, occasionally, a septoidium in the dorsal valve. Generally *Septaliphoria* is a larger shell, has a stronger beak, and larger, rimmed foramen. Its deltidial plates are conjunct and strengthened, with much stronger costae and sometimes asymmetrical anterior commissure. It seems that this genus has a close affinity with *Septaliphoria*, and might be the possible ancestor of the latter. Chronologically *Moquellina* mainly occurred in the Late Bathonian to Early Callovian, while *Septaliphoria* largely appeared in the Oxfordian, with a few forms also found in the Callovian. We have put this genus in the subfamily Indorhynchiinae rather than in Cyclothyridiinae mainly because it is

more similar to *Tanggularella* and *Indorhynchia* in general characters and in distribution. *Indorhynchia* differs from this genus in having dichotomous costae and stronger dorsal septum, although it also occasionally has a septoidium in the dorsal valve.

Tanggularella Shi, 1990

Kallirhynchia Buckman.—Jin, Sun, and Ye, 1979:141 [in part].—Sun, 1981:201.—Shi, 1986:147 [in part].
Tanggularella Shi, 1990:309.

TYPE-SPECIES.—*Tanggularella feraxa* Shi, 1990:309.

DIAGNOSIS.—Shell small to medium, rounded subtrigonal to subpentagonal; unequally biconvex; shell uniplicate and fully multicostate; no norelliform stage; fold and sinus generally

FIGURE 59.—Serial sections of *Moquellina* cf. *arcuata* Jin, Sun, and Ye; Y152231, L >15.0, W 16.1, T 11.2, A 92; from upper part of the Tuotuohe Formation (Upper Bathonian) of Yanshiping, Southern Qinghai, China.

weak; beak short; foramen small, hypothyriddid; costae simple, without dichotomizing; no septalium, septum very short or reduced; crura basically calcarifer, with long secondary lamellae similar to canalifer.

AGE AND DISTRIBUTION.—Bathonian to ?Lower Callovian; North Tibet and South Qinghai, China.

SPECIES INCLUDED.—*Tanggularella feraxa* Shi, 1990, *Thurmannella rotunda* Jin, Sun, and Ye, 1979, and three more new species to be described.

REMARKS.—This is an ordinary looking rhynchonellid that shares external similarity with several contemporary forms, especially *Kallirhynchia* Buckman, to which some species included in the genus were previously referred (Jin, Sun, and Ye, 1979; Sun, 1981; Shi, 1986).

The important Bathonian genus *Kallirhynchia* was erected by Buckman (1918), who provided little information on its muscle scars, septum, and dental plates that could be observed on the shell surface. Muir-Wood (1934:526), for the first time, investigated the interiors of the genus and defined the crura type "calcarifer" based on *Kallirhynchia yaxleyensis* (Davidson). Unfortunately, Muir-Wood defined this kind of crura largely based on longitudinal sections that compared with the transverse sections, could not efficiently show the real shape of the crura. The transverse serial sections illustrated by Muir-Wood (1934:535, fig. 2) are incomplete, without showing the anterior parts of the crura. Later, Muir-Wood (1936) further studied the interiors of the genus once again, presenting two more sets of serial sections. The serial sections of *Kallirhynchia superba* Buckman (Muir-Wood, 1936:43, text-fig. 12) are incomplete without showing the anterior parts of crura, but the sections clearly show the posterior structures that are quite similar to those seen in *Kallirhynchia yaxleyensis* (Davidson). The serial sections of *K. platiloba* figured by Muir-Wood (1936:41, text-fig. 11) are complete and show typically calcarifer crura. However, the other internal characters of this species, as exhibited in the serial sections, are apparently different from those in *Kallirhynchia yaxleyensis* and *Kallirhynchia superba*, but close to those in *Rhynchonelloidella smithi* (Davidson). Ager (1965a) at first placed *Kallirhynchia* in the subfamily Lacunosellinae, but later transferred it into the subfamily Cyclothyridinae (Ager, Childs, and Pearson, 1972).

The true crural shape of *Kallirhynchia* was not known until 1984, when Laurin, based on the French specimens, proved that the crura in *Kallirhynchia* are radulifer rather than calcarifer (Laurin, 1984a:381, figs. 181–185). The Saudi Arabian specimens of the genus studied by Cooper (1989:45) also have radulifer crura. In this paper, the type-species of *Kallirhynchia* has been studied with topotype materials. The study demonstrates sufficiently that *Kallirhynchia yaxleyensis* (Davidson), *Kallirhynchia concinna* (Sowerby), and *Kallirhynchia multicostata* Douglas and Arkell all have typical radulifer crura as understood by most brachiopodologists now, in which the distal ends of the crura are curved strongly toward the ventral

valve and the crura are relatively long, about $\frac{1}{3}$ of the dorsal valve length.

It is clear that the genus *Tanggularella* mainly differs from *Kallirhynchia* internally, especially by having crura of the calcarifer to canalifer type. The septum, hinge plates, septalium, and the inner socket ridges in the dorsal valve as well as the interior features of the ventral valve are only slightly different from those in *Kallirhynchia*. Chronologically, these two genera are almost the same, from Bathonian to ?Early Callovian.

COMPARISONS.—This genus resembles *Indorhynchia* Ovtsharenko, 1975, in some aspects. The main differences are that the latter has conspicuously dichotomizing costae and many shells are asymmetrical. Internally, the latter has a short septalium in the dorsal valve and very short dental plates in the ventral valve; its crura are not shaped as peculiarly as in the present genus. Chronologically, *Indorhynchia* is later, ranging from the Middle to Late Callovian. From *Moquellina* the present genus differs in having no septoidium but a stronger septum. The specimens identified as *Kutchirhynchia kutchiensis* (Kitchin) by Ovtsharenko (1975) from the Pamirs may not be congeneric with the Indian form. *Kutchirhynchia* has radulifer crura and simple costae (Laurin, 1984a; Cooper, 1989; and this paper). In contrast, the specimens from the Pamirs have dichotomizing costae and calcarifer to arculifer crura, according to the description of Ovtsharenko (1975:130–132, text-fig. 5). The specimens identified by Ovtsharenko as *Indorhynchia indica* (Orbigny) from the Pamirs are probably not conspecific with the Indian form either.

Tanggularella feraxa Shi, 1990

FIGURES 60–64

Tanggularella feraxa Shi, 1990:309, text-fig. 2, pl. 1: figs. 4–10.

TYPE.—*Holotype*: Shi, 1990, pl. 1: fig. 6; *Paratype*: pl. 1: fig. 5; from the Upper part of the Tuotuohe Formation (Upper Bathonian), Yanshiping, Southern Qinghai, China.

DIAGNOSIS.—Shell large for genus; subtrigonal to subpentagonal in outline and subglobose to globose in profile; dorsal valve much more convex than ventral one; shell with stout beak and stronger costae; fold and sinus feeble; crura longer.

DESCRIPTION.—Shell medium; subglobose to globose in profile and subtrigonal to rounded subpentagonal in outline; unequally biconvex, dorsal valve much more convex than ventral one. Lateral commissure variably deflected toward ventral valve; anterior commissure low arched to highly uniplicate, with arcuate to trapezoidal tongue.

Beak stout, substraight to suberect; foramen small, circular, hypothyriddid; deltidial plates disjunct to just conjunct, without noticeable rim; beak ridges obtuse to subangular; planoareas usually not developed.

Ventral valve moderately convex at posterior part and becoming less convex or somewhat flattened anteriorly; sinus

FIGURE 60.—*Tanggularella feraxa* Shi; holotype, Y152164, L 17.0, W 19.0, T 15.0, A 88; from the upper part of the Tuotuohe Formation (Upper Bathonian) of Yanshiping, Southern Qinghai, China. A-C, dorsal, side, and anterior views of the shell showing general morphology and muscle scars ($\times 1.5$); D, showing beak and foramen character ($\times 4$).

FIGURE 61.—Serial sections of *Tanggularella feraxa* Shi; Y152167, L 16.1, W 17.3, T 13.2, A 96; from the upper part of the Tuotuohe Formation (Upper Bathonian) of Yanshiping, Southern Qinghai, China.

FIGURE 62.—Serial sections of *Tanggularella feraxa* Shi; Y152170, L 18.8, W 20.8, T 12.9, A 99; from the upper part of the Tuotuohe Formation (Upper Bathonian) of Yanshiping, Southern Qinghai, China.

shallow and broad, starting at anterior $\frac{1}{2}$ to $\frac{1}{3}$ of valve, well defined in young form and tending to be flattened by shell thickening in the gerontic stage. Shell obviously thickened at anterior margins at gerontic stage.

Dorsal valve high convex to moderately inflated; umbonal region less tumid, with highest convexity at middle or anterior part, but reverted instead of everted; fold indistinct, only visible at anterior margin.

Costae rather coarse and subangular, on each valve numbering 16–22, with 4–7 on scarcely raised fold and 3–6 in sinus; no posterior smooth area present on either valve and no

sulcation in dorsal umbo; costae becoming finer near umbones; shell also with fine growth lines. Dorsal muscle scars clear, consisting of four parts: two front ones larger, subtrigonal in shape; two posterior ones narrowly strip-like, located postolaterally to front ones.

MEASUREMENTS.—The average dimensions of 78 measured specimens are: L 17.5 (15.5–21), W 17.6 (14.7–21), T 13.4 (12–15.8), A 94 (83–102); W/L 1.01, T/L 0.77, T/W 0.76; *holotype*: L 17, W 19, T 15, A 88; *paratype*: L 18, W 17, T 16, A 84.

INTERIOR.—Slight secondary thickenings often present in

FIGURE 63.—Serial sections of *Tanggularella feraxa* Shi; Y152171, L 18.1, W 18.4, T 11.5, A 97; from the upper part of the Tuotuohe Formation (Upper Bathonian) of Yanshiping, Southern Qinghai, China.

umbonal chambers, shell relatively thick. Pedicle collar variable, often present and very short; dental plates long, reaching or even exceeding hinge zone; subparallel or slightly divergent or convergent to floor; teeth fairly strong, massive, mallet-like, with expanded ends and denticulars.

No septalium in dorsal valve; septalial plates well developed and pendant; septum short, generally less than 1.5 mm in length

and reduced into ridge rapidly forward; hinge plates narrow, subhorizontal or slightly arched; inner socket ridges low, but clearly demarcated from hinge plates; crural bases variable, in most cases well formed but short. Crura essentially calcarifer, with wide angle between primary and secondary lamellae; in some specimens typically canalifer in appearance; 13 completely sectioned specimens showing CL/DL (crural length/

FIGURE 64.—Serial sections of *Tanggularella feraxa* Shi; Y152160, L 17.2, W 18.1, T 14.6, A 96; from the upper part of the Tuotuohe Formation (Upper Bathonian) of Yanshiping, Southern Qinghai, China.

dorsal valve length) 0.20, 0.22, 0.22, 0.22, 0.24, 0.24, 0.25, 0.254, 0.26, 0.27, 0.30, 0.34, 0.32, respectively.

REMARKS.—There are a large number of complete specimens of the species, but in most the shell surfaces have been exfoliated, obscuring the umbonal costae. Nevertheless, we are sure that they have no recognizable norelliform stages.

The abundant specimens show a considerable variation in morphology. After an extensive comparison, however, it has been found that they can be grouped into the following three major morphotypes. Morphotype A has broad suboval to rounded trigonal shape, the dorsal valve is less tumid, with a clear sinus in the ventral valve and weakly raised fold on the

dorsal valve. Morphotype B shows the typical character of the species: shell subtrigonal in outline, dorsal valve inflated, feeble sinus, and fold only recognizable at anterior margin, with noticeable thickening at anterior margin and high trapezoidal tongue, costae strong, and subangular. Morphotype C generally has the shell rounded subpentagonal to broad subcircular in shape, dorsal valve highly convex, but not inflated, and ventral valve more or less flattened anteriorly, with hardly recognizable sinus and fold, anterior commissure becoming broadly arched. Internally, these three morphotypes are basically the same, but the relative length of crura (CL/LD) shows three obvious groups. Morphotype A shows CL/LD

respectively 0.20, 0.21, 0.22, 0.22; morphotype B shows 0.30, 0.314, 0.32; morphotype C ranges typically between them, showing 0.24, 0.24, 0.24, 0.25, 0.254, 0.27. Externally, there are many transitional forms among these three morphotypes, so it is difficult to put rigid boundaries between them. These forms are, perhaps, only showing different stages in the development of the species, but the crural length increasing gradually may have significance in the evolution of the genus.

COMPARISONS.—Externally, the species resembles *Kallirhynchia yaxleyensis* (Davidson) and *Kallirhynchia concinna* (Sowerby). It seems the only differences are that the European species have finer costae and more clearly defined fold and sinus, although internally they are quite different from the present species.

Subfamily CYCLOTHYRIDINAE Makridin, 1955

Bicepsirhynchia Shi, 1990

"*Rhynchonella*" Childs, 1969:107.

Lotharingella Laurin.—Shi, 1986:123 [in part].

Bicepsirhynchia Shi, 1990:310.

TYPE-SPECIES.—*Bicepsirhynchia asperata* Shi, 1990:311.

DIAGNOSIS.—Small to medium, suboval to pyriform; somewhat pinched posteriorly; shell fully costate; fold and sinus feeble; beak relatively strong; foramen hypothyriddid to submesothyriddid with conjunct and thickened deltidial plates. No septalium; septum and septalial plates extremely reduced; crura short, canalifer, incurved strongly toward ventral valve.

AGE AND DISTRIBUTION.—Oxfordian; China and England.

SPECIES INCLUDED.—The following species are included in the genus.

"*Rhynchonella*" *ordinaria* Childs, 1969

? "*Rhynchonella*" *pyrenaei* Childs, 1969

Bicepsirhynchia asperata Shi, 1990

REMARKS.—The generic diagnosis is mainly based on the type-species, but the two English species must be included. Unlike any other species of Oxfordian age, these two species, as noted by Childs (1969), having ordinary appearance and

narrower shell, are somewhat similar to *Burmishynchia*, but may have a stronger beak with conjunct deltidial plates and rimmed large foramen. Similar to *Bicepsirhynchia asperata* Shi, the two English species also have rather coarse and sharp ribs and numerous fine growth lines or even lamellae, with pinched or tapering posterior of the shell and perhaps asymmetrical low uniplication. All these characters are reminiscent of *Septaliphoria*, to which the type-species was initially referred. Internally, the two English species are basically the same as the type-species and are also characterized by having the septum greatly reduced, and poorly developed septalial plates, as well as strongly incurved crura.

COMPARISONS.—This genus resembles *Moquellina* externally, but the latter has finer costae and unthickened deltidial plates. Internally, this genus differs from the latter in having no septoidium and related structures, and the crura are curved much more strongly, although the latter sometimes also has canalifer crura. *Burmishynchia* has numerous fine costellae and a short beak, its interior is quite different from the present genus and has typically radulifer crura. *Lotharingella* is internally characterized by having no septum or its related structures, but it has calcarifer crura instead of canalifer. Externally, *Lotharingella* has clear posterior smooth areas on both valves and well developed sulcation in dorsal umbone. From *Septaliphoria* the present genus differs largely externally. *Septaliphoria* has a broad shell and large foramen that is rimmed clearly. Internally the present genus has the septum and septalial plates so greatly reduced as to be absent in some specimens.

Bicepsirhynchia asperata Shi, 1990

FIGURES 65–67

Bicepsirhynchia asperata Shi, 1990:311, text-fig. 3, pl. 1: figs. 11–13.

TYPE.—*Holotype*: Shi, 1990, pl. 1: fig. 13; from the Lower Oxfordian of Geladandong, southern Qinghai, China; *Paratype*: pl. 1: fig. 12; from the Oxfordian of Wenquan, southern Qinghai, China.

DIAGNOSIS.—Shell medium for genus; shell pyriform and globose; coarsely ribbed, with stout beak and high arched anterior commissure; no dorsal septum and its related structures

FIGURE 65.—*Bicepsirhynchia asperata* Shi; holotype, Y154191 L 18.7, W 18.3, T 13.5, A 93; from the Lower part of the Suwa Formation (Oxfordian), south of Wenquan, Southern Qinghai, China. A–C, dorsal, side, and anterior views of the shell, showing general morphology ($\times 1.5$); D, showing beak and foramen character ($\times 3$).

in dorsal valve; crura canalifer, strongly incurved toward ventral valve and fork-like in section.

DESCRIPTION.—Shell small to medium in size, suboval to pyriform in outline and globose in profile; valves unequally biconvex, dorsal valve much more convex than ventral one. Anterior commissure uniplicate; tongue arched to rectangular in shape.

Beak stout, substraight; foramen small, circular, submesothyriddid, with slight rim; deltidial plates conjunct and thickened.

Ventral valve moderately convex, with shallow sinus at anterior $\frac{1}{3}$.

Dorsal valve tumid, umbonal region slightly swollen, with lower fold.

Costae coarse, on each valve numbering 10–16, with 3–5 on fold and 2–4 in sinus. At gerontic stage shell also with fine imbricated growth lamellae. Dorsal muscle scars clearly impressed, consisting of 4 parts: two front ones pear-shaped and located at middle of valve; two posterior ones narrow stripes.

MEASUREMENTS.—The average dimensions of 11 specimens are: L 17.5 (16–19), W 17.1 (13.6–18), T 12.9 (11.7–13.6), A 83 (75–90); W/L 0.97, T/L 0.74, T/W 0.75;

holotype: L 18.7, W 18.3, T 13.5, A 93; *paratype*: L 17.2, W 15.7, T 13, A 75.

INTERIOR.—Shell thick, with slight secondary thickenings in apical cavities. Short pedicle collar present in young specimens, becoming resorbed in adults; deltidial plates conjunct, strongly thickened and buttressed by short septum in adult; dental plates short, behind hinge zone.

No septalium or septum in dorsal valve; septalial plates not developed; hinge plates narrow, subhorizontal posteriorly and slightly arched anteriorly; inner socket ridges poorly demarcated; crural bases poorly formed. Crura short, canalifer, abruptly curved ventrally at anterior ends of hinge plates, appearing fork-like to four vertical plate-like in section; furrows on dorsal sides of crura narrow and shallow; three sectioned specimens have the ratios CL/LD 0.22, 0.24, and 0.26.

COMPARISONS.—Interior features of the species are so distinctive that no other species known can be compared with it, but its exteriors are similar to *Burmihynchia* and *Moquellina*, especially *B. parva* Buckman, *B. subcostata* Buckman, and *M. arcuata* Jin, Sun, and Ye. Generally, *Burmihynchia* has a hypothyriddid foramen without rim, unthickened deltidial plates, and has finer costae. *Moquellina arcuata* is narrower and has finer costellae than the present species. The present

FIGURE 66.—Serial sections of *Bicepsirhynchia asperata* Shi; paratype, Y154192, L 17.2, W 15.7, T 13.0, A 75; from the Suwa Formation (Oxfordian), Wenquan, Southern Qinghai, China.

species differs from "*Rhynchonella*" *ordinaria* Childs in having a stout beak and fewer, but stronger costae; from "*Rhynchonella*" *pyrenaei* Childs in having a much more gibbous shell and stronger ribs.

Flabellirhynchia Buckman, 1918

Flabellirhynchia Buckman, 1918:65.—Ager, 1965a:H617. [Not Crickmay, 1933:881.—Quilty, 1972:142.—Mourier and Almeras, 1986:694, pl. 2: fig. 10.—Shi, 1987b:45.]

?*Flabellirhynchia* Buckman.—Roche, 1939:269.

TYPE-SPECIES.—*Rhynchonella* *lycetti* Davidson, 1851–1852:81.

EMENDED DIAGNOSIS.—Shell medium, subtrigonal or flabelliform; fold and sinus weak, anterior commissure low uniplicate or arched; anterior margin thickened; beak strong, with large and rimmed foramen; deltidial plates conjunct and

thickened; shell ornamented with strong, angular ribs; concentric lines or layers well developed. Dorsal septum reduced, very short; septalium absent; crura canalifer; teeth very strong.

AGE AND DISTRIBUTION.—Aalenian to Bajocian; England, France, and ?China.

REMARKS.—The genus is externally quite distinctive and easy to distinguish from other genera. Buckman (1918) included two species, *Flabellirhynchia delicata* Buckman and *F. lycetti* (Davidson), in the genus, but none was known internally. Crickmay (1933) recorded several specimens from the North America and identified them as *Flabellirhynchia*. However, these specimens are far from the European forms in morphology and could hardly be put in the same genus. Quilty (1972) also described a species of the genus from the Antarctic. Those specimens are very small and internally quite different from the type-species, and can not be regarded as congeneric with *Flabellirhynchia lycetti*.

FIGURE 67.—Serial sections of *Bicepsirhynchia asperata* Shi; Y154198, L 17.9, W 17.3, T 14.1, A 88; from the Suwa Formation (Lower Oxfordian), south of Wenquan, Southern Qinghai, China.

So far, the type-species has been recorded only from the Aalenian of England, with a restricted distribution. On the other hand, however, *Flabellirhynchia delicata* Buckman seems to have a wider distribution. It has been found in France and also recently in Tibet, China, although its interior has not been studied yet.

***Flabellirhynchia lycetti* (Davidson, 1852)**

FIGURE 68; PLATE 14: FIGURES 11–13

Rhynchonella lycetti Davidson, 1851–1852:81, pl. 15: fig. 6; 1878:203.

Flabellirhynchia lycetti (Davidson).—Buckman, 1918:65, pl. 19: figs. 14, 15.

Not *Flabellithyris lycetti* (Davidson).—Shi, 1987b:45, pl. 11: fig. 16.

TYPE.—*Holotype*: Davidson, 1851–1852, pl. 15: fig. 6; from the Inferior Oolite (Aalenian), Minchinhampton, Gloucestershire, England.

MATERIAL STUDIED.—15 well preserved specimens from the Inferior Oolite (Oolite Marl, Aalenian), Notgrove Station, Minchinhampton, and Leckhampton Hill, Gloucestershire, England.

DESCRIPTION.—Shell medium, rounded subtrigonal to transversely flabelliform in outline; subglobose in profile, valves from almost equally biconvex to nearly convexo-planate. Anterior commissure slightly arched to moderately uniplicate; tongue very short or not developed; shell generally depressed.

Beak long, acute, substraight and slightly pinched; foramen large, hypothyriddid to submesothyriddid; deltidial plates short, conjunct and thickened, with marked rims around foramen; beak ridges subangular; interareas small but well defined, with transverse growth lines.

Ventral valve planate to moderately convex at posterior, tending to be flattened anteriorly; sulcus weak, only existing as a shallow depression in adults at anterior $\frac{1}{3}$.

Dorsal valve gently to highly convex, some specimens slightly everted anteriorly; fold not very well developed, only recognizable at anterior $\frac{1}{3}$ in adults, usually very low.

Costae few but strong and angular, on each valve numbering 12–17, with 2–3 in sulcus and 3–4 on fold; shell also with quite distinct concentric lamellae at anterior parts; numerous fine, and regularly placed growth lines clearly shown on whole shell, generally 11–18 per millimeter. Shell thickened markedly along anterior margin at gerontic stage.

INTERIOR.—Shell thick, slight secondary thickenings in both valves. No pedicle collar observed in sections; dental plates subparallel, long, beyond hinge zone; delthyrial chamber wide, trapezoidal; lateral cavities small; teeth very strong, flabelliform, with extraordinarily expanded ends and crenulations; accessory denticulars and dental cavities present.

Dorsal septum very short, reduced into ridge rapidly forward, only about $\frac{1}{6}$ as long as dorsal valve; no septalium or septalial plates; hinge plates thick, narrow, slightly inclined ventrally; inner socket ridges strong, massive, and relatively high, consisting of shallow troughs with inclined hinge plates; fulcral plates very thick; crural bases not well formed; crura

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 75591a	18.3	20.0	11.1	94	14	4	3
USNM 75591b	15.0	17.6	9.8	97	15	3	2
USNM 88711a	16.8	19.0	10.5	98	14	3	2
USNM 88711b	16.4	18.9	12.3	97	13	4	3
USNM 88711c	16.3	19.5	13.1	95	13	3	2
USNM 123684a	18.9	21.8	14.2	106	14	3	2
USNM 123684b	16.5	18.2	12.5	93	16	4	3
USNM 429411	19.0	21.7	16.1	102	12	3	2
USNM 429412	19.2	22.3	16.2	104	14	3	2
USNM 429413	20.1	21.6	13.0	97	15	4	3
USNM 429414	18.3	19.5	14.7	101	12	3	2
USNM 429415	17.2	18.5	13.1	98	14	3	2

canalifer, about $\frac{1}{4}$ as long as dorsal valve, arising from tapered hinge plates and only incurved slightly toward ventral valve; furrows on dorsal sides of crura deep and relatively wide.

REMARKS.—This species was not known internally and so far has only been recorded from England. Externally, it is quite distinctive, especially by having few very strong angular ribs, distinct concentric lamellae, and dense, elegant growth lines, which make it easy to distinguish from the other contemporary species. The thick shell, strong ribs, large rimmed foramen, and the strong teeth indicate that this species lived in shallow water, near shore, in a rough environment, probably just below the tidal zone.

The specimen illustrated by Davidson (1851–1852) is slightly different from the present specimens. It has a broader and somewhat depressed shell, with less developed fold and sinus, less prominent concentric lamellae, and larger interareas. Buckman (1918) illustrated two specimens collected from Notgrove Station and Charlton Common, one of which (Buckman, 1918, pl. 14: fig. 14) is similar to the present specimens (Plate 14: Figures 11, 12) and is relatively depressed; while another (Buckman, 1918, pl. 14: fig. 15) is apparently a young form. The present specimen figured in Plate 14: Figure 13 is much more globose and has strongly lamellose shell. It is strongly thickened and imbricated along the anterior margin, and probably represents a gerontic specimen.

***Globirhynchia* Buckman, 1918**

Globirhynchia Buckman, 1918:48.—Ager, 1965a:H617.—Cooper, 1989:39.

[Not Crickmay, 1933:878.—Kamyschan and Babanova, 1973:83.—Almeras and Peybernes, 1979:65.—Mourier and Almeras, 1986, pl. 2.]

?*Globirhynchia* Buckman.—Walter and Almeras, 1977:926; 1981:368.

TYPE-SPECIES.—*Rhynchonella subobsoleta* Davidson, 1851–1852:91.

EMENDED DIAGNOSIS.—Shell small to medium; globose and uniplicate; fold low; beak short, massive; foramen large, rimmed, hypothyriddid to submesothyriddid; deltidial plates conjunct; costae coarse, subangular; growth lines fine. Dorsal septum short or reduced into ridge; hinge plates broad; crura canalifer; septalium variable.

FIGURE 68.—Serial sections of *Flabellirhynchia lycetti* (Davidson); USNM 88711b, L 16.4, W 18.9, T 12.3, A 97; from the Inferior Oolite (Oolite Marl, Aalenian), Notgrove Station, Gloucestershire, England.

AGE AND DISTRIBUTION.—Aalenian to Bajocian and ?Bathonian; Europe, Saudi Arabia, and ?North America.

REMARKS.—*Globirhynchia* is an important rhynchonellid genus of early Middle Jurassic age. Although it was founded by Buckman in 1918, its internal structure has not yet been properly studied. Ager (1965a) illustrated a set of serial sections of the type-species, in which no septalium is recognizable and the crura are not very well shown, but the septum is clearly developed. In the definition of the genus, Ager stated that the genus has “no septalium; dorsal muscle scars linear; crura radulifer, hooked dorsally.” On the other hand, Almeras and Peybernes (1979:67) illustrated a set of complete serial sections made from a French specimen that was identified as *Globirhynchia subobsoleta*. In this specimen, the

septalium is very well developed and deeply V-shaped, supported by a high and long septum, and the crura are clearly of the radulifer type. Walter and Almeras (1977, 1981) studied some silicified specimens from the Aalenian of France, most of which are juvenile specimens with good interiors that have been etched out. These specimens, as mentioned by them, all have radulifer crura and characteristically are not quite coincident with those described by Ager (1965a). Our examination of the topotype material of the type-species shows that the genus has definitely canalifer crura, but its septalium is variable, which, just like in some other genera, may not be used as a good criterion for this genus. The dorsal septum may be reduced to a ridge.

Five more new species were described by Cooper (1989:

39–41) from the Upper Bajocian to Upper Bathonian of Saudi Arabia. Among these species, however, *Globirhynchia? dubia* (Cooper, 1989, pl. 10: figs. 31–36) and *Globirhynchia triangulata* (pl. 11: figs. 1–5) are similar to *Globirhynchia subobsoleta* (Davidson) in general shell shape and folding, but differ in beak characters as well as in having fewer and stronger ribs. *Globirhynchia concinna* (Cooper, 1989, pl. 10: figs. 37–44), *Globirhynchia? crassa* (pl. 10: figs. 7–12) and *Globirhynchia subtriangulata* (pl. 10: figs. 45–55, pl. 17: figs. 28–37) have somewhat depressed shells, fewer and stronger ribs, and externally resemble *Eurysites* Cooper. The interiors of these Saudi Arabian species, as shown by *Globirhynchia subtriangulata* (Cooper, 1989:41, fig. 21) and *Globirhynchia triangulata* (Cooper, 1989:42, fig. 22), are close to those of *Globirhynchia subobsoleta*, except that they have less incurved crura and a slightly stronger dorsal septum.

The two species, *Globirhynchia? parva* (Rothpletz) and *Globirhynchia davidsoni* Kamyschan and Babanova, depicted by Kamyschan and Babanova (1973:83–85) from the Aalenian of the Caucasus may not belong to this genus. The specimens illustrated by them (1973, pl. IX: fig. 11, pl. X: figs. 1, 2) have fairly strong ribs, obtuse beak, and high tongue. Internally they have a well developed dorsal septum and radulifer to calcarifer rather than canalifer crura (Kamyschan and Babanova, 1973:85, fig. 21).

Globirhynchia subobsoleta (Davidson, 1852)

FIGURE 69; PLATE 14: FIGURES 1–6, PLATE 18: FIGURES 5, 6

Rhynchonella subobsoleta Davidson, 1851–1852:91, pl. 17: fig. 14; 1878:207, pl. 28: figs. 42–44.—Richardson, 1904:244, pl. 17: fig. 3.—Rollier, 1918:167. [Not Charles, 1948:89, pl. 5: fig. 10; 1950:2.—Pevny, 1964:168, pl. 5: fig. 5.—Almeras and Peybernes, 1979:65, text-fig. 18, pl. 2: figs. 1–6.] *Globirhynchia subobsoleta* (Davidson).—Buckman, 1918:48, pl. 18: fig. 12. Not *Globirhynchia davidsoni* Kamyschan and Babanova, 1973:84, text-fig. 21, pl. X: figs. 1, 2. *?Globirhynchia subobsoleta* (Davidson).—Walter and Almeras, 1977:926, pl. 5: figs. 9, 15, 16, pl. 6: figs. 2, 3; 1981:368, pl. 5: figs. 18–23.

TYPE.—*Lectotype*: Davidson, 1878, pl. 28: fig. 42; designated by Almeras, 1977:926; from the Inferior Oolite (Oolite Marl, Aalenian), Cleeve Hill, Cheltenham, Gloucestershire, England.

MATERIAL STUDIED.—83 specimens from the Inferior Oolite (Oolite Marl, Aalenian) of Minchinhampton, Cleeve Hill, Cheltenham, Notgrove Station, Painswick, Stroud, and Birdlip, Gloucestershire, England.

DESCRIPTION.—Shell small to medium in size, subcircular to transversely rounded subpentagonal in outline and subglobose to globose in profile; valves almost equally biconvex or dorsal valve slightly more convex than ventral. Lateral commissures oblique ventrally at 10–20 degrees; anterior commissure slightly arched to moderately uniplicate; tongue short and low, not very well shown, some specimens with asymmetrical anterior commissures.

Beak short, obtuse, with broad base, suberect; foramen subcircular, hypothyriddid to submesothyriddid; deltidial plates short, conjunct, with clear rims; beak ridges obtuse to subangular; interareas small, but well defined and slightly concave.

Ventral valve convex adequately; sulcus broad and shallow, occurring at posterior $\frac{1}{3}$ to anterior $\frac{1}{3}$, without distinct borders from slopes; in some specimens sulcus only slight anterior depression.

Dorsal valve tumid, umbonal region generally swollen, valve recurved regularly forward; fold not very well developed, usually low and broad, only slightly raised above slopes at anterior $\frac{1}{3}$. In young specimens fold hardly recognizable even at anterior margin.

Costae coarse, subangular to sharp, on each valve numbering 17–27, with 4–7 on fold and 3–6 in sulcus; growth lines clear, fine and innumerable, regularly displayed, becoming more conspicuous near anterior margin.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 64486a	17.5	17.5	14.5	93	22	5	4
USNM 64486b	16.5	16.2	13.4	87	28	6	5
USNM 75580a	19.0	20.3	15.2	109	26	6	5
USNM 75580b	17.2	19.3	12.8	113	22	5	4
USNM 76022a	14.5	16.0	10.2	106	25	6	5
USNM 88717a	18.1	20.3	14.9	94	25	6	5
USNM 88717b	17.5	19.0	13.3	98	22	5	4
USNM 104778a	16.8	17.4	12.3	101	21	5	4
USNM 104778b	14.2	15.7	10.4	98	18	4	3
USNM 106317a	19.1	21.2	13.7	109	21	5	4
USNM 429416	20.0	20.2	15.5	100	23	4	3
USNM 429417	18.2	20.1	13.3	112	24	5	4
USNM 429418	15.7	16.2	11.5	97	18	4	3
USNM 429419	19.2	20.5	14.3	112	21	4	3
USNM 429420	19.5	21.4	14.0	97	21	4	3
USNM 429421	18.8	19.8	14.7	104	23	5	4
USNM 429422	17.3	17.6	13.1	103	23	5	4
USNM 429423	16.8	17.0	12.5	97	18	5	4

INTERIOR.—No secondary thickenings in either valve. In three sectioned specimens, one with short pedicle collar, other two without definite collars; delthyrial chamber generally wide, subrectangular in shape; lateral cavities well developed; dental plates short, delicate, and subparallel; teeth strong, massive, flabelliformed, with crenulations; accessory denticulars and dental cavities present.

Dorsal septum short, only supporting hinge plates or septalium at posterior of apical cavity, reduced into ridge after hinge zone, fairly long, reaching $\frac{1}{3}$ to $\frac{1}{2}$ of valve length. Septalium variable, in one sectioned specimen, no septalium at all; in second, very short, narrowly V-shaped septalium present;

FIGURE 69 (facing page).—Serial sections of *Globirhynchia subobsoleta* (Davidson); USNM 429428, L 19.9, W 21.2, T 13.7, A 101; from the Inferior Oolite (Oolite Marl, Aalenian), Notgrove Station, Gloucestershire, England.

and in third (Figure 69) very short and incomplete septalium present. Septalial plates generally short, pendant; hinge plates broad, nearly horizontal or slightly arched ventrally; inner socket ridges low, but clearly differentiated from hinge plates; crural bases very narrow, clearly formed; crura canalifer, about $\frac{1}{4}$ as long as dorsal valve, arising from taperings of hinge plates and strongly incurved toward ventral valve anteriorly, appearing as four vertical plates in section at distal ends; furrows on dorsal sides of crura deep and wide.

REMARKS.—The species is not very well known internally. Ager (1965a:H616, fig. 499-2) illustrated a set of incomplete serial sections of the species. In those sections, no septalium exists, the septum is long and low, and the crura are not completely shown. Ager mentioned that the crura are radulifer and hooked dorsally. From his sections, we judge that the crura might be partly broken off and that the hooked ends probably indicate the original canalifer crura.

Walter and Almeras (1977) illustrated several specimens of *G. subobsoleta*. These specimens were poorly preserved and did not show clear characteristics of the species, but they mentioned that these specimens all have radulifer crura (Walter and Almeras, 1977:927). Almeras and Peybernes (1979) again studied this species and illustrated a good set of serial sections. In these sections, a very deep, V-shaped septalium is very well shown, the septum is fairly high and long, and the crura are obviously radulifer, with strongly incurved terminations. Comparing their sections with the present ones, we are quite sure that the sectioned specimen illustrated by them does not belong to *Globirhynchia*, but to a genus of the subfamily Rhynchonellinae. The present sectioned specimens all have canalifer crura, although the crura in the other two specimens are not shaped as distinctively as those in the figured specimen, which was from the Inferior Oolite (Pea Grit, Aalenian), Crickley Hill, Cheltenham, a locality not far from Cleeve Hill.

Globirhynchia tatei (Davidson, 1878)

PLATE 18: FIGURES 1-4, 7-10

Rhynchonella tatei Davidson, 1878:218, pl. 28: fig. 45.—Rollier, 1918:167.

Globirhynchia tatei (Davidson).—Buckman, 1918:49.

TYPE.—*Holotype*: Davidson, 1878, pl. 28: fig. 45; from the Inferior Oolite (Oolite Marl, Aalenian), Seven Springs, Cubberfield, Cheltenham, England.

MATERIAL STUDIED.—28 specimens from the Inferior Oolite (Oolite Marl, Aalenian), Painswick, Stroud, Gloucestershire; 19 specimens from the Inferior Oolite (Gryphite Grit, Bajocian), Scottsquar Hill, Painswick, Gloucestershire, England.

DESCRIPTION.—Shell very small, globose; subcircular to transversely subpentagonal in outline; dorsal valve more convex than ventral one and slightly everted anteriorly. Anterior commissure strongly uniplicate; tongue well developed, highly arched to trapezoidal in shape.

Beak massive, longer than in *Globirhynchia subobsoleta*,

suberect to incurved; foramen small, hypothyridid; deltidial plates very short, conjunct, with rims around foramen; beak ridges obtuse; interareas not developed.

Ventral valve moderately convex at posterior, slightly flattened anteriorly; sulcus well developed, broad and shallow, occurring at anterior $\frac{1}{2}$ to $\frac{1}{3}$; in some specimens sulcus abruptly turning over toward dorsal valve at anterior margin, forming high tongue.

Dorsal valve swollen, slightly everted anteriorly in some specimens; fold broad and low, but well elevated above slopes at anterior $\frac{1}{3}$ of valve, with well defined borders.

Costae coarse and subangular, on each valve numbering 16–19, with 5–6 on fold and 4–5 in sulcus; growth lines fine, regular.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 89801a	9.6	10.8	7.5	107	18	6	5
USNM 89801b	10.8	11.2	8.5	108	16	6	5
USNM 89801c	9.3	9.8	6.9	97	17	5	4
USNM 89801d	8.8	9.7	7.2	96	19	6	5
USNM 89801e	7.2	9.2	6.6	100	18	6	5
USNM 429440	9.1	10.3	8.6	107	16	5	4
USNM 429441	9.4	10.0	7.4	97	16	5	4
USNM 429442	9.3	10.5	7.8	102	18	6	5
USNM 429443	9.2	9.2	6.7	97	17	5	4
USNM 429444	9.7	8.8	6.4	87	18	6	5

INTERIOR.—No secondary thickenings in either valve. No pedicle collar observed in sectioned specimen; delthyrial chamber wide; lateral cavities well developed; deltidial plates conjunct; dental plates delicate, subparallel and short, splitting from ventral floor before reaching hinge zone; teeth short, massive, quadrate in section, with crenulations; accessory denticulars and dental cavities present.

No septalium present in sectioned specimen; septum short, supporting hinge plates only at posterior of umbonal cavity, reduced abruptly forward to ridge; hinge plates narrow, slightly inclined ventrally; inner socket ridges very low, poorly differentiated from hinge plates; crural bases narrow, well formed and extending as ridges along dorsal sides of inner margins of hinge plates; crura canalifer, about $\frac{1}{3}$ as long as dorsal valve, not shaped as distinctively as in *G. subobsoleta*, only incurved slightly toward ventral valve at anterior.

REMARKS.—*Globirhynchia tatei* is a barely known species, the only illustration was by Davidson (1878), with which the present specimens are in close accord. The specimens studied herein include two populations, one from the Aalenian of Painswick and the other from the Middle Bajocian (*Sowerbyi* Zone) of Scottsquar Hill. These two populations have no significant differences in character, but differ in age.

This species is close to *G. subobsoleta* in general aspects, the main differences between them are that this species is much smaller, with a more swollen dorsal valve, more incurved and longer beak, and has a more elevated fold as well as a clearly

defined sulcus. Interiorly these two species are basically the same, except that *G. tatei* has a more delicate and shorter septum, and less incurved canalifer crura.

Granulirhynchia Buckman, 1918

Granulirhynchia Buckman, 1918:64.—Roche, 1939:270.—Ager, 1965a:H611.

TYPE-SPECIES.—*Rhynchonella granula* Upton, 1905:83.

EMENDED DIAGNOSIS.—Shell small, subtrigonal to transverse; dorsal valve much more convex than ventral one, with anterior commissure strongly uniplicate; shell more or less trilobate; beak strong, suberect to substraight; foramen large, rimmed; deltidial plates conjunct and strengthened; ribs strong and angular, numerous; growth lines dense, fine and regular. Dorsal septum well developed; hinge plates broad; crura canalifer.

AGE AND DISTRIBUTION.—Aalenian to ?Bajocian; England and France.

REMARKS.—The genus was erected by Buckman based on Upton's species *Rhynchonella granula*. One of its most important characteristics was said to be its granulate shell. The present topotype materials have been carefully examined under the microscope and it is clear that these granules actually result from weathering and erosion of the numerous fine growth lines. The granules are visible only at the anterior parts of the shell in some specimens and are not very constant. Therefore, the granulation is not regarded as a genuine generic character.

Ager (1965a) put this genus in the subfamily Acanthothyridinae Schuchert, which implied a close relation of this genus with *Acanthothiris*. Later, Ager, Childs, and Pearson (1972) mentioned that the genus had not been investigated internally, so its position was not certain. The present study shows that this genus actually has nothing to do with Acanthothyridinae and that the granules are not original structures and have no relation with the spinose shells of the Acanthothyridinae. The internal structures of this genus place it definitely in the subfamily Cyclothyridinae Makridin.

The genus is similar to *Flabellirhynchia* in many respects, except the type-species of the latter, *Flabellirhynchia lycetti*, has conspicuous lamellae and a strongly thickened shell. *Flabellirhynchia delicata* Buckman is close to *Granulirhynchia granula* (Upton) in all external characters and probably should be transferred into this genus rather than placed in *Flabellirhynchia*. This is especially significant when their micro-ornaments and beak characters are compared, although the interiors of *Flabellirhynchia delicata* are not known yet.

Granulirhynchia granula (Upton, 1905)

FIGURE 70; PLATE 14: FIGURES 7–10

Rhynchonella granula Upton, 1905:83, pl. 3: figs. 1–6.

Granulirhynchia granula (Upton).—Buckman, 1918:64, pl. 19: figs. 17, 18.

Rhynchonella (*Granulirhynchia*) *granula* Upton.—Roche, 1939:207, pl. 7: figs. 7, 9, 17.

TYPE.—*Holotype*: Upton, 1905, pl. 3: figs. 1–3; from the Lower Limestone (Pea Grit, Inferior Oolite, Aalenian), Crickley Hill, Cheltenham, Gloucestershire, England.

MATERIAL STUDIED.—23 well preserved specimens from the Inferior Oolite (Pea Grit, Aalenian), Crickley Hill, Leckhampton Hill, near Cheltenham, Gloucestershire, England.

DESCRIPTION.—Shell small to medium, inequivalve; subtrigonal, roundly subpentagonal to transverse in outline and subglobose in profile; dorsal valve much more convex than ventral one and slightly everted anteriorly in adults. Lateral commissures deflected ventrally at 10–15 degrees; anterior commissure uniplicate; tongue short and arched in young specimens, while high and trapezoidal in adults.

Beak generally short and massive, substraight to suberect; in some specimens beak long and pointed; foramen large, hypothyrilid to submesothyrilid, clearly rimmed; deltidial plates conjunct and high; beak ridges subangular; interareas small, but well defined and slightly concave.

Ventral valve gently convex at posterior and tending to be flattened anteriorly; sulcus well developed, broad and deep in adults, with rounded bottom and well defined borders.

Dorsal valve adequately convex, greatest convexity at anterior part; fold prominent and well elevated above slopes in adults, occurring at anterior $\frac{1}{2}$, making valve more or less trilobate; while feeble in young forms, only slightly raised over slopes.

Costae strong, angular, on each valve numbering 17–20, with 3–6 on fold and 2–5 in sulcus; whole shell covered with innumerable fine growth lines. Gerontic shells thickened at anterior margins, with heavier growth lines imbricated at anterior parts of shell, fine granules visible in some specimens.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 64420	16.0	17.5	11.2	95	18	4	3
USNM 75603a	17.0	21.5	12.8	107	17	5	4
USNM 75603b	14.8	16.6	10.7	100	18	4	3
USNM 75603c	13.1	13.2	8.9	87	19	4	3
USNM 104770a	19.2	20.5	12.4	94	20	4	3
USNM 104770b	17.8	18.3	16.4	93	20	6	5
USNM 104770c	14.2	15.0	9.7	92	27	4	3
USNM 429448	16.5	16.5	11.0	92	17	4	3
USNM 429449	18.5	21.1	13.1	104	22	5	4
USNM 429450	16.1	16.8	10.2	94	19	4	3
USNM 429451	17.5	20.3	10.5	104	20	5	4
USNM 429452	10.6	13.5	7.8	113	18	5	4

INTERIOR.—No secondary thickenings in either valve. No clear pedicle collar present in sectioned specimen; foramen margins thickened; delthyrial chamber wide; lateral cavities well developed; dental plates subparallel, reaching hinge zone; teeth very strong, long and massive, with expanded and

flabelliform ends and crenulations; accessory denticulars and dental cavities present.

Very short, incomplete septalium in dorsal valve; septalial plates long, pendant; septum well developed, reduced into ridge after hinge zone and fairly long, beyond crura; hinge plates broad, slightly inclined ventrally; inner socket ridges low, well differentiated from hinge plates; crural bases narrow, well formed; crura canalifer, about $\frac{1}{3}$ as long as dorsal valve, arising from taperings of hinge plates and slightly incurved toward ventral valve anteriorly; furrows on dorsal sides of crura very deep and distinct; angle between two folded lamellae of each crus about 45 degrees.

REMARKS.—At present, only the type-species can be put into the genus confidently, therefore no comparisons can be made

within the genus. Buckman (1918) mentioned that there were various new species in the genus, but none but the type has been formally described. The juvenile specimens of the species are somewhat depressed and flabelliform, the fold on the dorsal valve is lower, and the anterior commissure is only slightly arched. In gerontic specimens, the fold becomes highly elevated above the flanks and the anterior commissure becomes strongly uniplicate. Some young specimens of *Flabellirhynchia lycetti* (Davidson) are similar to this species in shell shape and folding, but generally the former has more conspicuous concentric lamellae.

Flabellirhynchia delicata Buckman is externally similar to this species in having dense, fine, and regularly placed growth lines, as well as a similar general shape, size, costation, and

FIGURE 70.—Serial sections of *Granulirhynchia granula* (Upton); topotype, USNM 104770d, L 15.9, W 16.7, T 10.6, A 86; from the Inferior Oolite (Pea Grit, *Murchisonae* Zone, Aalenian), Cleeve Hill, Cheltenham, Gloucestershire, England.

uniplication. The main differences are that *Flabellirhynchia delicata* Buckman has a slightly more transverse shell and shorter beak, and its rims around foramen are not as clear as in this species. It was put in the genus *Flabellirhynchia* mainly because no clear granules were observed on the shell at that time. As mentioned above, the granules on the shell of *Granulirhynchia* are not original structures but result from weathering or erosion, therefore the generic position of *Flabellirhynchia delicata* Buckman remains to be verified, which might be partly synonymous with *Granulirhynchia granula*.

Pararhactorhynchia Shi, 1990

Rhactorhynchia Buckman.—Shi, 1987b:58, 59.

Pararhactorhynchia Shi, 1990:311.

TYPE-SPECIES.—*Pararhactorhynchia trigona* Shi, 1990:312.

DIAGNOSIS.—Shell medium, inequivalve and uniplicate; subtrigonal to subpentagonal in outline; dorsal valve slightly everted anteriorly and feebly subcynocephalous in profile; beak short, suberect; foramen small, hypothyridid; deltidial plates narrow, disjunct to just conjunct; fold and sinus variably developed; ribs few but strong; septum and septalium well developed; crura canalifer, incurved ventrally.

AGE AND DISTRIBUTION.—Bajocian; Southern Tibet, China.

REMARKS.—The genus, as its name implies, resembles *Rhactorhynchia* Buckman, 1918, externally. The two species included here in this genus were originally recorded as ?*Rhactorhynchia* cf. *turgidula* Buckman and ?*Rhactorhynchia* sp. indet. (Shi, 1987b:58, 59). At that time, for lack of information available on the internal structures of *Rhactorhynchia*, these two species were placed in *Rhactorhynchia* solely on the basis of their exterior similarities with *Rhactorhynchia turgidula* Buckman and *Rhactorhynchia brevis* Buckman. Although the type-species of *Rhactorhynchia* has not yet been internally investigated, several closely related species have been studied through topotype materials in this paper. These species prove to have radulifer crura, so the genus has been partly emended. The present genus differs from *Rhactorhynchia* in having canalifer crura and well developed septalium and high septum in the dorsal valve. Externally this genus is close to *Rhactorhynchia* in having a few strong ribs, widely uniplicate anterior commissure, and no smooth areas, but its beak, deltidial plates, and foramen differ from the latter.

Generally, the new genus is easy to distinguish from any other genera of Bajocian age by its distinctive interiors and exteriors. *Deltarhynchia* Cooper, 1989, is externally similar to this genus, but differs in having radulifer crura, stronger septum, and no septalium. *Flabellirhynchia* differs from the new genus in having a reduced septum and no septalium, although it also has strong ribs and canalifer crura. *Globirhynchia* is distinguished from this genus by having finer and more

costae, rounded and globose shell, as well as less developed septum and strongly incurved crura inside.

Pararhactorhynchia tibetica Shi, 1990

FIGURE 71

Rhactorhynchia cf. *turgidula* Buckman.—Shi, 1987b:58, text-fig. 13, pl. II: fig. 12a-d.

Pararhactorhynchia tibetica Shi, 1990:312, pl. I: fig. 15a-d.

TYPE.—*Holotype*: Shi, 1990, pl. I: fig. 15a-d (= Shi, 1987b:58, pl. II: fig. 12a-d); from the Bajocian of Nyalam, near Mt. Everest, Southern Tibet, China.

DIAGNOSIS.—Small-sized *Pararhactorhynchia*, with subpentagonal and highly uniplicate shell; fold and sulcus well developed; without anterior and lateral flattened regions; ribs fewer.

DESCRIPTION.—Shell small to medium, inequivalve; subpentagonal in outline and subcynocephalous in profile. Lateral commissures deflected ventrally; anterior commissure strongly uniplicate.

Beak short and obtuse, suberect; foramen small, hypothyridid; deltidial plates short, disjunct to just conjunct; beak ridges and interareas not developed.

Ventral valve moderately convex; sulcus wide and deep, occurring at posterior $\frac{1}{3}$ of valve and turning over toward dorsal valve abruptly at anterior margin; tongue wide and high, subtrapezoidal in shape.

Dorsal valve much more convex than ventral one and moderately everted anteriorly; fold broad, well elevated above slopes at anterior $\frac{1}{3}$, with borders well defined from flanks.

Costae strong, subangular, on each valve numbering 11–12, with 4 on fold and 3 in sulcus; concentric growth lines feeble.

MEASUREMENT.—*Holotype*: N1245050-1, L 16.8, W 19.5, T 14.2, A 103.

INTERIOR.—No secondary thickenings in either valve. No pedicle collar observed in sectioned specimens; delthyrial chamber broad, trapezoidal in shape; lateral cavities well developed; dental plates short, splitting from ventral floor before reaching hinge zone and slightly divergent to floor; teeth long, with expanded ends and crenulations, inserting deeply into sockets; accessory denticulars and dental cavities present.

Dorsal septum high and fairly long, extending beyond crura; septalium narrow and shallow, V-shaped, about 1 mm long, supported by septum; hinge plates broad, subhorizontal or slightly inclined ventrally; inner socket ridges low, but well demarcated from hinge plates; crural bases not well formed; crura canalifer, short, about $\frac{1}{5}$ as long as dorsal valve (two sectioned specimens, crural length/dorsal valve length = 0.18, 0.20 respectively); arising from inner margins of hinge plates and incurved strongly toward ventral valve at anterior parts; furrows on dorsal sides of crura very shallow and narrow, not showing U- or V-shape in sections.

REMARKS.—The species is externally similar to *Rhactorhyn-*

FIGURE 71.—Serial sections of *Pararhactorhynchia tibetica* Shi; N124050-1, L 16.8, W 19.5, T 14.2, A 103; (Bajocian) Nyalam, near Mt. Everest, South Tibet, China.

chia turgidula Buckman, but differs in having fewer and stronger costae, a less tumid dorsal valve, and wider, deeper sulcus. Internally, this species has canalifer crura, well developed septum, and V-shaped septalium in dorsal valve, while *Rhactorhynchia turgidula*, as revealed in this paper, has

radulifer crura and the reduced septum that mostly exists as a ridge. *Cirpa himalaica* Ching, Sun, and Rong (1976:286, text-fig. 3, pl. 1: figs. 24–30,) is close to this species in exterior, which was from the same horizon and same locality as the present species. According to the original description and

illustration, however, that species has joined hinge plates, doubled deltidial plates, and prefalcifer crura (Ching, Sun, and Rong, 1976:286–288). *Rhactorhynchia brevis* Buckman resembles this species in shell shape and folding, but differs in having a somewhat depressed dorsal valve that is scarcely everted.

Pararhactorhynchia tibetica differs from *Pararhactorhynchia trigona* in having smaller and subpentagonal shell, with fewer ribs, deeper sulcus, and well defined fold. The former has no anterior and lateral flattened regions, its internal structures, especially the crura, are also slightly different from those in the latter.

COMPARISONS.—Although *P. tibetica* is close to *Pararhactorhynchia trigona* in general aspects, its crura are not as typical for the genus as those in *Pararhactorhynchia trigona*. The crura of *P. trigona* are somewhat aberrant, but should no doubt be regarded as of the canalifer type, while the crura of *P. tibetica* are somewhat similar to the radulifer type. The furrows on the dorsal sides of the crura are so shallow and narrow that the crura appear almost as vertical plates rather than curved gutters. Compared with those in *Rhactorhynchia turgidula* Buckman, it seems clear that this species has different crura from that species, while in *Rhactorhynchia subtetrahedra* (Sowerby), the crura do possess very shallow furrows on their dorsal sides, although they do not incurve toward the ventral valve as strongly as in this species. More information on the interiors, especially the crura, is needed for comparison.

Pararhactorhynchia trigona Shi, 1990

FIGURES 72, 73

Rhactorhynchia sp. indet. Shi, 1987b:59, text-fig. 14, pl. III: fig. 9a–d.
Pararhactorhynchia trigona Shi, 1990:312, text-fig. 4, pl. I: fig. 14a–d.

TYPE.—*Holotype*: Shi 1990, pl. I: fig. 14a–d (= Shi, 1987b:59, pl. III: fig. 9a–d); from the Upper Bajocian, Nyalam, near Mt. Everest, Southern Tibet, China.

DIAGNOSIS.—Shell large for genus, subtrigonal in shape, with well developed anterior and lateral flattened regions; fold and sinus feeble; anterior commissure strongly zigzagging.

DESCRIPTION.—Shell medium, subtrigonal in outline and feebly subcyncephalous in profile. Lateral commissure deflected ventrally; anterior commissure uniplicate and strongly zigzagging; shell strongly thickened along margins, lateral sides parallel, giving shell rectangular appearance in anterior view.

Beak small, suberect; foramen small, hypothyriddid; deltidial plates narrow, just conjunct; interareas not developed.

Ventral valve gently convex; sulcus feeble, only existing as a depression at anterior margin, hardly separated from slopes; at anterior margin, ventral valve turning over toward dorsal valve abruptly and resulting in a flattened anterior region.

Dorsal valve much more convex than ventral one and slightly everted anteriorly; fold feeble and flat, elevated only slightly above slopes at anterior $\frac{1}{3}$ of valve, with well defined borders.

Shell covered with strong and angular ribs, on each valve numbering 12–14, with 5 on fold and 4 in sulcus; no smooth areas present on either valve; concentric lines visible.

MEASUREMENT.—*Holotype*: N124051-1, L 25.6, W 24.0, T 18.2, A 85.

INTERIOR.—Shell thick, slightly thickened at umbonal cavities. Pedicle collar short, and feeble, very short septal ridge present in ventral valve; delthyrial chamber wide; lateral cavities narrow and short; dental plates short, splitting from ventral floor before reaching hinge zone, slightly divergent to floor; teeth long, inserting deeply into sockets, with expanded ends and crenulations; accessory denticulars and dental cavities present.

Dorsal septum massive, supporting long and V-shaped septalium, reduced into ridge after hinge zone; hinge plates thick and broad, concave posteriorly, becoming ventrally inclined at anterior and tapering forward; inner socket ridges high, well demarcated from hinge plates; crural bases not well formed; crura canalifer, about $\frac{1}{5}$ to $\frac{1}{4}$ as long as dorsal valve (crural length/dorsal valve length = 0.22), arising from prolongations of hinge plates and somewhat similar to cilifer at their posterior parts; crura strongly incurved toward ventral valve and folded longitudinally at their anterior parts; crural ends deeply V-shaped, each primary lamella with a short tip directed ventrally; furrows on dorsal sides of crura deep and narrow.

REMARKS.—The new species is somewhat similar in shape to *Cirpa langi* Ager, especially by having well developed lateral and anterior flattened regions, as well as few but strong costae. Internally, however, they are quite different, *Cirpa langi* has double deltidial plates, prefalcifer crura, extremely reduced septum, and no septalium. *Rhactorhynchia regalis* Buckman shares some resemblances with this species externally, but differs in having a much larger and broader shell, as well as many more costae, and a stronger beak. *Rhactorhynchia brevis* Buckman differs from this species in having a depressed dorsal valve, well developed rectangular tongue, and broader shell.

Pycnoria Cooper, 1989

Pycnoria Cooper, 1989:51.

Burmishynchia Buckman.—Cooper, 1989:15 [in part].

Gibbirhynchia Buckman.—Cooper, 1989:33 [in part].

TYPE-SPECIES.—*Pycnoria magna* Cooper, 1989:53.

DIAGNOSIS.—Shell small to medium, thick-shelled, subangular to subpentagonal; unequally biconvex to globose; uniplicate; fold and sinus weak. Beak very small, low, erect to incurved; foramen small, pin-hole like, hypothyriddid and rimmed. Shell covered with strong subangular ribs. Hinge plates thick and narrow; septum reduced; septalium very short or absent; crura short, ?radulifer to canalifer.

AGE AND DISTRIBUTION.—Bathonian to Early Callovian; Saudi Arabia, Israel, and Egypt.

FIGURE 73.—*Pararhactorhynchia trigona* Shi; holotype, N124051-1, L 25.6, W 24.0 T 18.2, A 85. A–C, dorsal, side, and anterior views of shell ($\times 1.5$); D, showing beak and foramen character ($\times 3$).

REMARKS.—The genus was erected by Cooper, 1989, including only two Saudi Arabian species. Here one more new species from Israel and Egypt has been added, and several species from Saudi Arabia, formerly put in *Burmishynchia* and *Gibbirhynchia*, have been transferred into this genus.

In the original diagnosis, the crura of the genus were defined as “radulifer” and the genus was placed in the subfamily Tetrarhynchiinae Ager, 1965a. In Cooper’s paper, the two sets of serial sections of the genus (Cooper, 1989:52, 53, figs. 29, 30, *Pycnoria magna* Cooper) were incomplete, nevertheless, one of them (fig. 29) shows canalifer crura as defined in this paper, although they are not as distinctive as those in *Globirhynchia subobsoleta* (Davidson) and in *Granulirhynchia granula* (Upton). Another set of serial sections illustrated by Cooper as *Burmishynchia angustata* (p. 16, text-fig. 7), which show the same interiors as *Pycnoria magna* and also possesses a very thick shell, should be transferred into the genus without much doubt. This species actually also shows signs of canalifer crura rather than radulifer, although the canalifer has been regarded as one of the variants of radulifer type. In this paper, five more sets of serial sections of the genus have been made. As shown by the serial sections presented herein, *Pycnoria magna* Cooper clearly has canalifer crura, but the gutters on the dorsal sides of the crura are narrow and shallow. One of the sectioned specimens of *Pycnoria depressa*, new species (Figure 74), does not show well the gutters on the dorsal sides of the crura, while another (Figure 75) shows clearly canalifer crura. Based on the characteristics, such as strong costation, rimmed foramen, reduced septum, as well as canalifer crura, this genus seems better placed in the subfamily Cyclothyridiinae than in the Tetrarhynchiinae as Cooper suggested.

COMPARISONS.—The genus is similar to *Globirhynchia* in having a globose shell, but differs in having much stronger and fewer ribs, much shorter beak, poorly defined interareas, and much smaller foramen. Internally, *Globirhynchia* has no secondary thickenings, a stronger septum, and distinct canalifer crura; the furrows on the dorsal sides of the crura are much

wider and deeper. Externally the genus is somewhat similar to *Daghanirhynchia*, but their interiors, as revealed in this paper, are quite different. *Burmishynchia* has more and finer costellae, longer incurved beak, and no rimmed foramen, internally it has radulifer crura and wider hinge plates. Compared with the Burmese and Chinese specimens, some of the species described by Cooper as *Burmishynchia* seem to be related to *Pycnoria* more closely than to typical *Burmishynchia*. *Gibbirhynchia* also shares some resemblance with the genus, but it has radulifer crura, a high septum, finer and more costae, and is restricted chronologically to the Early Jurassic. The two sets of serial sections of the *Gibbirhynchia* from Saudi Arabia illustrated by Cooper are also incomplete, not showing the terminal parts of the crura. Nevertheless, the interior of *Gibbirhynchia pulcher* Cooper is comparable to that of *Pycnoria magna* (Cooper, 1989:36, fig. 19, compare with p. 52, 53, figs. 29, 30). Cooper’s other species *Gibbirhynchia rotundata* (Cooper, 1989:38, fig. 20) has a longer septum, but also has noticeable secondary thickenings and thick, narrow hinge plates. Externally, these species look more similar to *Pycnoria magna* than to *Gibbirhynchia gibbosa* Buckman.

Pycnoria depressa, new species

FIGURES 74, 75; PLATE 10: FIGURES 1–3, PLATE 18: FIGURES 11–14

TYPE.—*Holotype*: USNM 429539; *Paratype*: USNM 429540; from the Zohar Shales (near base, Upper Bathonian), NW side of Hamatesh Hagadol, southern Israel.

MATERIAL STUDIED.—22 specimens from the Zohar Shales (Upper Bathonian to Lower Callovian), Hamaktesh Hagadol, southern Israel; hundreds of specimens from the Upper Bathonian of Gebel Maghara, northern Sinai, Egypt.

DIAGNOSIS.—Small-sized *Pycnoria* with depressed shell; fold and sulcus well developed; beak very small, pointed; shell with few, but strong and sharp ribs; crura canalifer, septum reduced, generally no septalium.

DESCRIPTION.—Shell small to medium, depressed, wider than long; rounded subtrigonal to transversely subpentagonal in outline; valves subequal, dorsal valve slightly more convex than ventral one. Lateral commissures sloping ventrally;

FIGURE 72 (facing page).—Serial sections of *Pararhactorhynchia trigona* Shi; holotype, N124051-1, L 25.6, W 24.8, T 18.2, A 85; (Upper Bajocian) Nyalam, near Mt. Everest, South Tibet, China.

anterior commissure well uniplicate; tongue short, broad, rectangular to subtrapezoidal in shape.

Beak short, suberect to incurved, or even touching dorsal umbo; foramen minute, hypothyridd, circular to elliptical in shape; deltidial plates rather low, disjunct to just conjunct, with slight to well developed rims around foramen; beak ridges blunt; interareas very small or not developed.

Ventral valve gently convex at posterior and tending to be flattened anteriorly; sulcus well developed, broad and moderately deep, fairly deep and prominent in some specimens.

Dorsal valve gently and evenly convex; fold broad and low, moderately raised above slopes at anterior $\frac{1}{2}$ to $\frac{1}{3}$, with well defined borders from slopes.

Costae few, strong and sharp, on each valve numbering 11–18, with 3–5 on fold and 2–4 in sulcus; ribs on fold and in sulcus usually stronger than those on slopes; growth lines fine, regularly displaced on whole shell, generally well preserved and clearly shown in intervals, becoming more obvious at anterior parts.

INTERIOR.—Shell thick, without noticeable secondary thickenings in either valve. Short pedicle collar often present; dental plates divergent or subparallel, very short; delthyrial chamber wide; lateral cavities clear, but short; teeth long, nodular, with expanded ends and crenulations; accessory denticulars and dental cavities present.

Dorsal septum very short, reduced into ridge rapidly

FIGURE 74.—Serial sections of *Pycnorhynchus depressa*, new species; USNM 429549, L 17.1, W 18.9, T 12.8, A 94; from the Zohar Shales (near base, Upper Bathonian to Lower Callovian), NW side of Hamaktesh Hagadol, Southern Israel.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 429539	17.2	18.8	10.6	102	11	3	2
USNM 429540	17.5	18.5	10.7	103	15	4	3
USNM 429541	19.7	18.0	12.8	90	14	4	3
USNM 429542	18.5	18.0	12.8	97	12	4	3
USNM 429543	14.6	17.5	11.2	100	13	4	3
USNM 429544	15.7	16.8	11.0	101	15	4	3
USNM 429545	14.9	12.3	10.6	106	10	3	2
USNM 429546	17.1	18.9	12.8	94	14	4	3
USNM 429550	17.4	19.6	12.0	108	14	5	4
USNM 429551	15.8	17.6	11.2	101	11	4	3
USNM 429552	18.0	19.4	10.3	103	16	4	3
USNM 429553	17.3	17.6	11.2	90	18	4	3
USNM 429554	17.2	18.3	10.6	97	15	3	2
USNM 429555	16.4	16.6	11.3	91	11	3	2
USNM 429556	20.1	22.2	13.4	91	11	3	2
USNM 429557	16.2	17.3	11.2	96	14	3	2
USNM 429558	18.8	19.5	13.2	98	12	3	2

forward; no septalium observed in sectioned specimens; hinge plates wide, nearly horizontal; inner socket ridges well developed, high and erect; socket fulcral plates long. Crural bases poorly formed in one sectioned specimen, well formed in another, generally narrow. Crura canalifer, in one specimen (from Israel) furrows on dorsal sides of crura shallow and incipient, while in another (from Egypt) deeper and narrow; crura short, only about 1/5 as long as dorsal valve, incurved feebly toward ventral valve.

REMARKS.—The new species is characterized by having a rather depressed shell, well developed fold and sulcus, and shell not strongly thickened along the margins. The ribs of the species are generally stronger and sharper, but fewer than in

Pycnoria magna. It is similar to the specimen described by Cooper as *Pycnoria compacta*, but the latter has strongly swollen and tumid valves. The new species is also somewhat suggestive of *Eurysites* (Cooper, 1989, pl. 8: figs. 50–59, pl. 9: figs. 1–16), but that genus has a long and strong beak, widely divergent and long dental plates, well developed septalium, as well as radulifer crura.

Pycnoria magna Cooper, 1989

FIGURE 76–78; PLATE 10: FIGURES 4, 5, PLATE 15: FIGURE 19, PLATE 18: FIGURES 15–18

Pycnoria magna Cooper, 1989:53, text-fig. 29, 30, pl. 12: figs. 11–36, pl. 18: figs. 26–36.

Pycnoria compacta Cooper, 1989:51, pl. 12: figs. 6–10. [New synonymy.]

TYPE.—*Holotype*: Cooper, 1989, pl. 12: figs. 31–35; from the Upper Bathonian, Saudi Arabia.

MATERIAL STUDIED.—35 specimens from the Zohar Shales (Upper Bathonian to Lower Callovian), Hamaktesh Hagadol, southern Israel; hundreds of specimens from the Upper Bathonian of Gebel Naghara, northern Sinai, Egypt.

DESCRIPTION.—Shell medium, globose, width and length almost equal; dorsal valve tumid and much more convex than ventral; shell thickened markedly along margins, with two sides nearly parallel, quadrate in anterior view. Lateral commissures deflected ventrally at 5–15 degrees; anterior commissure uniplicate; tongue high, rectangular in shape.

Beak very small, erect to incurved or even touching dorsal umbo; foramen minute, subcircular, hypothyriddid; deltidial plates narrow, disjunct to just conjunct, with slight rims around foramen; beak ridges blunt, interareas not developed.

FIGURE 75.—Serial sections of *Pycnoria depressa*, new species; USNM 429562, L 15.3, W 16.8, T 10, A 100; (Upper Bathonian) Gebel Maghara, northern Sinai, Egypt.

FIGURE 76.—Serial sections of *Pycnorina magna* Cooper; USNM 429462, L 18.9, W 17.8, T 15.4, A 93; from the Zohar Shales (near base, Upper Bathonian to Lower Callovian), NW side of Hamaktesh Hagadol, southern Israel.

Ventral valve moderately convex; sulcus very shallow, occurring at posterior $\frac{1}{3}$ of valve, usually existing only as a depression not abruptly separated from slopes and turning over toward dorsal valve sharply at anterior margin.

Dorsal valve tumid and domed in anterior view, umbonal region swollen, with greatest convexity at anterior part, but not everted anteriorly; fold low and broad, slightly raised above slopes at anterior $\frac{1}{3}$, with borders poorly defined from flanks.

Shell with a few subangular to angular ribs, on each valve numbering 14–17, with 3–5 on fold and 2–4 in sulcus; growth lines fine, visible at anterior parts. Becoming conspicuous or even feebly imbricate at gerontic stage.

INTERIOR.—Shell rather thick, markedly secondary thickenings present in both valves. No pedicle collar observed in sectioned specimens; dental plates short, subparallel or convergent to ventral floor; delthyrial chamber wide; lateral

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 429455	19.0	17.5	16.7	90	14	3	2
USNM 429456	15.7	14.8	13.2	92	16	4	3
USNM 429457	18.8	17.8	15.4	97	15	3	2
USNM 429458	17.5	15.1	15.3	92	14	3	2
USNM 429459	17.8	16.0	16.5	91	16	4	3
USNM 429460	16.2	14.3	14.3	90	15	4	3
USNM 429461	16.3	16.1	12.5	98	15	4	3
USNM 429489	19.6	18.3	18.1	93	16	5	4
USNM 429490	18.7	17.8	16.2	99	15	4	3
USNM 429491	18.7	18.6	16.0	98	14	4	3
USNM 429492	19.7	18.7	16.1	98	14	4	3
USNM 429493	17.8	17.5	18.6	98	15	4	3
USNM 429494	19.4	19.1	16.6	94	16	4	3
USNM 429495	18.2	19.0	14.2	106	16	5	4
USNM 429496	18.0	19.1	14.0	104	17	5	4

FIGURE 77.—Serial sections of *Pycnorhina magna* Cooper; USNM 429497, L 15.0, W 14.0, T 14.0, A 88; (Upper Bathonian) Gebel Maghara, northern Sinai, Egypt.

FIGURE 78.—Serial sections of *Pycnorhina magna* Cooper; USNM 429498, L 21.0, W 20.0, T 19.0, A 97; (Upper Bathonian) NW of Gebel Maghara, northern Sinai, Egypt.

cavities short; teeth very strong, massive and mallet-like, with expanded ends and crenulations, held tightly in sockets.

Very short and narrow septalium present in dorsal valve, incomplete to V-shaped; dorsal septum very short, only supporting septalium at posterior of umbonal cavity and reduced into ridge rapidly forward; hinge plates narrow, thick at posterior and tapering toward each other at anterior, subhorizontal or slightly declined dorsally at anterior; inner socket ridges very low, feebly differentiated; socket fulcral plates very long; crural bases not well formed; crura canalifer,

but very short, less than $\frac{1}{4}$ of dorsal valve length; dorsal furrows on crura narrow and shallow.

REMARKS.—The present specimens are quite close to those described by Cooper in general characters, except that the Saudi Arabia specimens are generally larger and slightly transverse. The adult specimens from Israel and Egypt, however, are strongly thickened at the margins so the fold and sulcus tend to be flattened, with flattened frontal region and parallel sides.

Pycnorhina compacta Cooper is in close external accord with

this species, which was created on the basis of only one specimen. According to the original definition (Cooper, 1989:51, 52), *Pycnoria compacta* differs from *Pycnoria magna* in having a smaller and narrower shell, and stronger, more angular and fewer costae.

When comparing hundreds of specimens from Egypt and Israel, however, we found it difficult to put a strict boundary between these two species, and that all the characteristics mentioned by Cooper are transitional, without abrupt distinction. We prefer, therefore, to combine them in a single species and to take *Pycnoria compacta* as a synonym of *Pycnoria magna* Cooper.

The specimens depicted by Parnes (1981:21, pl. 2: figs. 16–18) as *Burmihynchia* sp. “group *hopkinsi*” from South Israel are somewhat similar to the present species in general character, except they have a smaller and narrower shell, but stronger beak. Possibly these specimens represent a new species of this genus rather than a species of *Burmihynchia*.

The specimen illustrated by Muir-Wood as *Cymatorhynchia* (?) *quadriplicata* (Hartman) (Muir-Wood, 1925:182, pl. 1: fig. 8) from the Upper Bajocian of the Jordan Valley is very similar to the present species in ornament and beak character, but has less tumid valves and a deeper sulcus. Probably that specimen also belongs to a species of this genus, although its interior is not known.

Septaliphoria Leidhold, 1921

Septaliphoria Leidhold, 1921:354, 355.—Wisniewska, 1932:18–20.—Makridin, 1960:251, 252; 1964:96, 97 [in part].—Ager, 1965a:H619.—Dagis, 1968:84.—Childs, 1969:85.—Kamyschan and Babanova, 1973:111 [in part].—Laurin, 1984a:400 [in part].—Shi, 1986:162.—Smirnova, 1990:29. [Not Ching, Sun, and Rong, 1976:304.—Jin, Sun, and Ye, 1979:158.]

TYPE-SPECIES.—*Rhynchonella arduennensis* Oppel, 1856–1858:615.

EMENDED DIAGNOSIS.—Shell medium to large, subpentagonal to subcircular, with coarse and simple subangular ribs; foramen large, rimmed; deltidial plates conjunct; anterior commissure uniplicate or slightly asymmetrical. Dorsal septum short or reduced, septalium generally short or absent; crura canalifer.

AGE AND DISTRIBUTION.—Callovian to Oxfordian, ?Kimmeridgian; Europe, Asia, and ?Africa.

REMARKS.—*Septaliphoria* is a very important genus in the Late Jurassic and is also widespread in the Tethys. The genus was described by Leidhold (1921); one of its most important characteristics was said to be having a septalium in the dorsal valve. As can be seen in this paper, however, the septalium is a variable structure in Jurassic rhynchonellids, often varying so considerably within a genus or even at species level that it can hardly be used as a key character. In this genus the septalium varies greatly.

Leidhold (1921, pl. 5: fig. 2a–d) presented four illustrations to show the interiors of the genus, among which figs. 2c,d show a short, widely V-shaped septalium with a long septal ridge, but crura were broken off. The others have no clear septalium.

Wisniewska (1932:6, fig. 1c and p. 19, fig. 4) also illustrated the interior of *Septaliphoria asteriana*, showing a well developed V-shaped septalium and a long septum and canalifer crura. Another species, *Septaliphoria pinguis*, according to illustrations by Wisniewska (1932:6, fig. 1b and p. 26, fig. 6), either has a V-shaped septalium or the septalial plates sit directly on the dorsal floor rather than being supported by a septum.

Childs illustrated two sets of serial sections of *Septaliphoria arduennensis* (Oppel), one of which (Childs, 1969:88, fig. 31) shows an incomplete, very short septalium and ventrally incurved canalifer crura; while the other (1969:89, fig. 32) shows no septalium at all, but has a long septum, pendant septalial plates, and ventrally incurved canalifer crura. *Septaliphoria paucicosta* Childs (1969:92, fig. 33), has no septalium either, but has a reduced septum and clearly canalifer crura. However, Childs (1969:85) still defined this genus as “septalium present, crura radulifer” in his emended diagnosis.

Makridin sectioned two Russian species of the genus, *S. sobolevi* Makridin and *S. pectunculoides* (Etallon) (Makridin, 1964:98, fig. 25 and p. 104, fig. 28), both of them with short septalium, canalifer crura, and variable dorsal septum.

In addition, Laurin (1984a) illustrated several sets of serial sections of *Septaliphoria mourdoni* Laurin and *S. orbignyana* (Oppel) from the Callovian of France (1984a:317, figs. 202, 203, p. 322, fig. 204, p. 324, fig. 205, p. 325, fig. 206). These sections show that the septalium exists only in the young specimens of *S. mourdoni*, and becomes obsolete or disappears in the adults. In this species, the septum is apparently reduced, but the crura are variable, showing calcarifer to canalifer types. In *S. orbignyana* the septalium exists only in the juvenile stage and disappears in adults, the septum is reduced, but the crura are calcarifer to subfalcifer with quite distinct and long crural bases. These make us believe that *S. orbignyana* and *S. mourdoni* are probably more closely related to the Bathonian genus *Bradfordirhynchia* than to the Oxfordian genus *Septaliphoria*.

Recently, one of us (Shi) has sectioned two specimens of *Septaliphoria arduennensis* from the Lower Oxfordian of Southern Qinghai, China. One of them shows a short septoidium in the dorsal valve, in which the septalial plates are extended parallel to rest directly on the dorsal floor; while the other has no septalium at all. Nevertheless, both of them have very short, reduced dorsal septum and canalifer crura.

Considering all the information available on the interiors of *Septaliphoria*, it seems clear that in the genus the dorsal septum is generally short or reduced, the crura are canalifer rather than radulifer, and the septalium is variable, usually short or absent. An emended diagnosis for the genus is therefore presented.

Septaliphoria arduennensis (Oppel, 1858)

PLATE 15: FIGURES 1, 4

Rhynchonella arduennensis, Oppel, 1856-1858:615, 639, 654.—Rollier, 1918:171.

Septaliphoria arduennensis (Oppel).—Leidhold, 1921:354, pl. 5: fig. 2.—Wisniewska, 1932:18.—Childs, 1969:86, text-figs. 31, 32, pl. 8: figs. 4, 5.—Shi, 1986:162, text-fig. 90, pl. 4: figs. 5, 6.—Smirnova, 1990:30, text-fig. 16, pl. IV, fig. 5a-c.

TYPE.—*Neotype*: Childs, 1969, pl. 8: fig. 4; from the Oxfordian (Terrain a Chilles), Pagny-Sur-Meuse (Meurthe et Moselle), France.

MATERIAL STUDIED.—8 well preserved specimens from the Oxfordian of France and England.

DESCRIPTION.—Shell medium, subcircular in outline, subglobose in profile; with dorsal valve slightly more convex than ventral one. Lateral commissures slightly deflected ventrally; anterior commissure uniplicate; tongue short, arched or asymmetrical.

Beak strong and long, suberect; foramen large, circular and rimmed, hypothyriddid to submesothyriddid; deltidial plates conjunct; beak ridges obtuse; interareas small but well defined.

Ventral valve adequately convex; sulcus shallow and short, not very well separated from slopes, often only slight depression; in some specimens, sulcus hardly recognizable.

Dorsal valve convex evenly or slightly inflated; fold low and ill-defined, recognizable only at anterior margin; in some specimens, fold absent.

Costae numerous, coarse, subangular, on each valve numbering 23-27, with 5-6 on fold and 4-5 in sulcus; growth lines fine, well developed, more conspicuous at anterior parts.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 31012a	19.5	22.4	14.0	106	24		-
USNM 31012b	21.1	22.5	16.8	103	23		-
USNM 92938a	19.5	21.2	13.3	98	25		-
USNM 92938b	17.3	17.5	14.1	103	26	6	5
USNM 429572	23.5	22.0	17.4	85	22	6	5
USNM 429573	23.5	24.8	14.3	97	22	5	4
USNM 429574	19.2	20.4	14.2	103	25		-
USNM 429575	19.0	19.8	14.2	104	26		-

INTERIOR.—The European specimens were not investigated. On the shell surface, very short, divergent dental plates are visible running about 1/5 as long as ventral valve. The dorsal septum or ridge is weak, about 1/4 as long as dorsal valve.

REMARKS.—A Chinese specimen from the Lower Oxfordian of Southern Qinghai was serially sectioned and illustrated in Figure 12 to show the interior. The Chinese specimen shows basically the same internal structures as those illustrated by Childs (1969), but its crura are not shaped as distinctively as in

the European specimen. Besides, the Chinese specimen has a very short, but clearly formed septoidium in the dorsal valve and a extremely short septal ridge in the ventral valve. In one of the sectioned specimens illustrated by Childs (1969:88, text-fig. 31), it seems the short septoidium also exists, but it is not as clear as in the Chinese specimen. Childs mentioned (1969:16) "...the septalium in *Septaliphoria arduennensis* is only developed at the extreme posterior end of the valve and is either supported by a very low septum or sometimes appears to rest directly on the floor of the valve." Wisniewska (1932:26, fig. 6) also figured similar structures in *Septaliphoria pinguis* (Roemer), although this has been largely exaggerated by the orientation of the sectioned specimen. All these facts indicate that the septalium is variable in the genus, and sometimes the septalial plates can sit directly on the dorsal floor to form a very short septoidium, although it is not as persistent as in *Moquellina*.

Septaliphoria cf. corallina (Leymerie, 1846)

FIGURE 79; PLATE 8: FIGURE 1

?*Rhynchonella inconstans* var. *pectunculoides* Etallon.—Davidson, 1878:191, pl. 26: figs. 8-12.

Rhynchonella inconstans Sowerby.—Haas, 1888:107, pl. IX: figs. 1, 2, 4, 7.

Rhynchonella corallina Leymerie, 1846:256, pl. 10: figs. 16, 17.—Haas, 1889:23, pl. 1: figs. 13-20.—Rollier, 1918:81, 172.

Rhactorhynchia corallina (Leymerie).—Buckman, 1918:51.

?*Septaliphoria corallina* (Leymerie).—Makridin, 1952:58, pl. 4: fig. 3.

?*Rhactorhynchia corallina* (Leymerie).—Makridin, 1964:170, pl. 8: fig. 5.—Kamyschan and Babanova, 1973:109, pl. 8: fig. 7.

Septaliphoria corallina (Leymerie).—Fischer, 1980:178, 179, pl. 79: figs. 7, 8.

TYPE.—*Holotype*: Leymerie 1846, pl. 10: figs. 16, 17; from the Coral Rag (Rauracian, Upper Oxfordian), Aube, France.

MATERIAL STUDIED.—4 specimens from the Jurassic Coral-lian (Upper Oxfordian to Lower Kimmeridgian), Fairfield, England.

DESCRIPTION.—Shell medium, subcircular; depressed, valve gently and almost equally biconvex or dorsal valve slightly more convex than ventral one. Lateral commissures feebly deflected toward ventral valve; anterior commissure slightly arched; tongue poorly developed, very short; fold and sinus ill-defined.

Beak long, pointed, substraight; foramen large, elliptical in shape, hypothyriddid to submesothyriddid; deltidial plates narrow, conjunct, with clear rims around foramen; beak ridges subangular; interareas small but well defined.

Ventral valve moderately convex at umbonal region and more or less flattened anteriorly; sulcus absent in young forms and only existing as a broad depression at anterior 1/4 of valve in adults, without clear borders from slopes.

Dorsal valve gently and evenly convex, with greatest convexity at middle part; fold not developed, recognizable only at anterior margin, without clearly defined borders.

FIGURE 79.—Serial sections of *Septaliphoria* cf. *corallina* (Leymerie); USNM 64485a, L 22.3, W 22.8, T 10.3, A 97; from the Jurassic Corallian (Upper Oxfordian to Lower Kimmeridgian), Fairford, England.

Cosate numerous, subangular, on each valve numbering 24–28, with 5–7 on fold and 4–6 in sinus; growth lines feeble, visible at anterior part.

INTERIOR.—Slight secondary thickenings only in umbonal cavities. Pedicle collar short; deltidial plates conjunct and crumpled inside; delthyrial chamber wide, rectangular in shape; lateral cavities well developed; dental plates short, subparallel;

Measurements and counts.							
Number	L	W	T	A	N	F	S
USNM 64485a	22.3	22.8	10.3	97	26	5	4
USNM 64485b	23.8	22.8	12.6	86	25	7	6
USNM 64485c	20.9	22.3	20.6	93	23		
USNM 64485d	19.5	18.2	10.5	87	23	–	–

teeth short, massive, with expanded ends and crenulations; accessory denticulars and dental cavities present.

Dorsal septum low, reduced; only supporting septalium at very posterior part of umbonal cavity, mostly existing as a ridge, running about $\frac{1}{3}$ of valve length; septalium very short, narrow and fairly deep; septalial plates long, pendant; hinge plates broad, almost horizontal at posterior, and tapering anteriorly; inner socket ridges low, but clearly differentiated; crural bases poorly formed, only existing as thickened ridges along dorsal sides of inner margins of hinge plates; crura canalifer, short, about $\frac{1}{5}$ as long as dorsal valve, incurved toward ventral valve at anterior; furrows on dorsal sides of crura narrow and shallow, crura appearing as four vertical plates.

REMARKS.—The specimens described here are from the Oxfordian of England. Externally they are reminiscent of *Lacunaerhynchia*, especially similar to *Lacunaerhynchia palma* (Szajnocha), in having a depressed and almost equally biconvex shell, with slightly arched anterior commissure, poorly defined fold and sinus, as well as long, pointed beak. Internally, however, the present specimen shows the typical characteristics of *Septaliphoria*, with canalifer crura, reduced septum, and a short, deep septalium that is somewhat similar to a septoidium. These characteristics suggest that this species is closely related to *Septaliphoria arduennensis* (Oppel) and *Septaliphoria pinguis* (Roemer) rather than to *Lacunaerhynchia palma* (Szajnocha).

In general character the present specimens are close to *Septaliphoria corallina* (Leymerie), especially close to the specimens illustrated by Haas (1887, pl. IX: figs. 1, 2, 4, 7; 1889, pl. I: figs. 3–14). However, this species, as mentioned by Rollier (1918:81, 172), is not properly known and there are a lot of species confused with it. We were unable to find the original description and the illustrations of Leymerie, but noticed that the specimens illustrated subsequently by various authors are quite different from one another. According to the illustrations of Fischer (1980), the French specimen is slightly more convex than the present specimens, has a shorter beak, a smaller submesothyriddid foramen, and fewer, but stronger costae.

Septaliphoria? mourdoni Laurin, 1984

PLATE 15: FIGURES 2, 3, PLATE 16: FIGURE 7, PLATE 18: FIGURE 19

Septaliphoria mourdoni Laurin, 1984a:400, pl. 14: figs. 1–10.

TYPE.—*Holotype*: Laurin, 1984a, pl. 14: fig. 1; from the Lower Callovian, Gisement d'Escoville, Calvados, France.

MATERIAL STUDIED.—8 well preserved specimens from the Lower Callovian, Argences and Ranville, Calvados, France.

DESCRIPTION.—Shell small to medium, outline subtrigonal or slightly subpentagonal; dorsal valve much more convex than ventral and slightly everted anteriorly, giving a subcynocephalous profile in adults. Lateral commissure deflected ventrally

at 10–25 degrees; anterior commissure uniplicate; tongue high, subtrapezoidal.

Beak acute, suberect; foramen large, subcircular, hypothyridid; deltidial plates disjunct to conjunct, with well developed rims around foramen; beak ridges obtuse; interareas small but well defined, slightly concave and with fine transverse lines.

Ventral valve moderately convex posteriorly, tending to be flattened anteriorly; sulcus deep and broad, occurring at anterior $\frac{1}{2}$ of valve and increasing in width and depth forward rapidly.

Dorsal valve slightly everted anteriorly; fold well developed, occurring at anterior $\frac{1}{2}$ of valve and well elevated above slopes.

Costae many and angular, on each valve numbering 18–22, with 3–6 on fold and 2–5 in sulcus; growth lines very well developed, dense, and regularly displaced, which become more conspicuous at anterior parts or even feebly imbricated at anterior margin.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 75065a	19.7	22.7	13.4	95	22	6	5
USNM 75065b	17.8	18.8	13.2	104	18	5	4
USNM 429582	16.3	19.0	13.8	97	20	5	4
USNM 429583	17.0	18.8	12.8	98	22	6	5
USNM 429584	16.8	20.1	12.2	103	21	5	4
USNM 429585	15.3	16.4	10.5	92	19	5	4
USNM 429586	14.8	14.0	10.6	95	16	3	2

INTERIOR.—Not investigated.

REMARKS.—This species has very well developed growth lines, which are dense, fine and regularly spaced or even micro-imbricated, large and rimmed foramen, as well as well developed fold and sulcus. All these characteristics are quite coincident with *Bradfordirhynchia*, especially close to *B. ecardensis* (Laurin). Externally this species is also similar to *Rhynchonelloidella alemanica* (Rollier) and *R. smithi* (Davidson), but the well developed, rimmed foramen and micro-ornament exclude the possibility of belonging to that genus. In general, this species and *S. orbignyana* (Oppel) are more similar to *Bradfordirhynchia* in exterior character.

The interior of the species was described by Laurin (1984a:410): "Internal structures very fine, with very short septum, septalium well developed; crural bases long, directed dorsally, crura radulifer." In his illustrations (Laurin, 1984a:317, fig. 202), the juvenile specimen shows a deep septalium and has falcifer or subfalcifer crura, with very long crural bases that are very similar to those in *Bradfordirhynchia*. The adult specimen shows no septalium and seems to have calcarifer to canalifer crura. This species seems more closely related to *Bradfordirhynchia* than to *Septaliphoria*, especially by having the crura similar to subfalcifer and well developed micro-ornament.

Septaliphoria pinguis (Roemer, 1836)

FIGURE 80; PLATE 15: FIGURE 7, 8

Terebratula pinguis Roemer, 1836:41, pl. 2: fig. 15.
Terebratula inconstans Sowerby.—Quenstedt, 1868–1871:141, pl. 40: figs. 55–59.
Rhynchonella pinguis (Roemer).—Davidson, 1878:193, pl. 26: fig. 7.—Haas, 1894, pl. 23: figs. 9, 10.—Rollier, 1918:173.
Septaliphoria pinguis (Roemer).—Wisniewska, 1932:24, pl. 1: figs. 1–18 [in part].—Childs, 1969:86.

TYPE.—*Holotype*: Roemer, 1836, pl. 2: fig. 15; from the Upper Jurassic (Oxfordian), northern Germany.

MATERIAL STUDIED.—10 specimens from the Oxfordian of Poland; 2 from Switzerland.

DESCRIPTION.—Shell medium to large, rounded subtrigonal to transversely subpentagonal in outline; subglobose in profile; dorsal valve more convex than ventral one. Lateral commissures oblique ventrally at 10 to 20 degrees; anterior commissure lower uniplicate to broadly arched; tongue short, low or asymmetrical.

Beak strong, massive, suberect; foramen circular, rimmed, hypothyriddid to submesothyriddid, just below beak tip; deltidial plates high, conjunct; beak ridges obtuse; interareas narrow, slightly concave.

Ventral valve adequately convex at posterior 1/3 and slightly flattened anteriorly; sulcus shallow and broad, without abrupt borders from slopes; in most specimens sulcus existing only as a slight depression at anterior 1/3; some specimens asymmetrical or with slight twisted anterior commissure.

Dorsal valve much more convex than ventral one, with umbonal region less tumid or slightly flattened; greatest convexity located at anterior part; fold poorly developed, only recognizable at anterior margin in some specimens.

Costae many and coarse, on each valve numbering 16–25, with 4–5 on fold and 3–4 in sulcus when recognizable; growth lines fine, visible at anterior margins.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 87228a	23.0	28.0	16.2	93	20	6	5
USNM 87228b	20.3	24.1	14.0	108	19	5	4
USNM 87228c	18.5	19.9	12.2	93	18	5	4
USNM 87228d	20.8	20.3	12.2	94	23		
USNM 87228e	20.2	21.4	13.6	106	17		
USNM 87228f	18.1	18.3	11.4	87	16		–
USNM 87228g	17.4	20.2	12.0	105	21		–
USNM 429576	22.1	24.0	18.2	88	25		–
USNM 429577	20.8	21.9	13.1	89	22	5	4

INTERIOR.—No secondary thickenings in either valve. No pedicle collar observed in sectioned specimen; foramen marginate, with thickened rims visible inside; deltidial plates conjunct and slightly thickened; delthyrial chamber broad; lateral cavities short; dental plates very short, less than 1/5 of

valve length and splitting from ventral floor before reaching hinge zone; teeth fairly long, massive and mallet-like, with expanded ends and crenulations; accessory denticulars and dental cavities present.

No septalium in dorsal valve; septalial plates absent in sectioned specimen; septum reduced into ridge, which is fairly long, about half of valve length; hinge plates broad, inclined ventrally; inner socket ridges low, clearly differentiated from hinge plates; crural bases very narrow, weakly formed as ridges along dorsal sides of inner margins of hinge plates; crura canalifer, short, about 1/4 to 1/5 as long as dorsal valve, strongly incurved toward ventral valve, furrows on dorsal sides of crura narrow and shallow; crural ends appearing as four vertical plates in section.

Dorsal muscle scars large, located at midvalve; two front ones rounded trigonal in shape, located closely to each other; two posterior scars narrow strips.

REMARKS.—This species is variable in shape, Roemer's original specimen is more or less depressed and small, with a long beak. The present specimens are more close to the specimens illustrated by Wisniewska. Internally the species also varies, especially the septalium. The orientation of the serial sections presented by Wisniewska (1932:26, fig. 6) make the septalium look wider and to sit on the dorsal floor directly, the hinge plates and the crura are inclined strongly toward the ventral valve.

Family ACANTHOTHYRIDIDAE Schuchert, 1913

Subfamily ACANTHOTHYRIDINAE Schuchert, 1913

Acanthothiris d'Orbigny, 1850

TYPE-SPECIES.—*Anomia spinosa* Linnaeus, 1788:3346.

Acanthothiris spinosa (Linnaeus), 1788

PLATE 11: FIGURES 1–3

Anomia spinosa Linnaeus, 1788:3346.
Terebratulites spinosa.—Schlotheim, 1813:73.
Terebratula spinosa.—Von Buch, 1834:58.—Brown, 1849:142, pl. 56: fig. 1.—Zieten, 1834:44, fig. 1; 1852:36, fig. 37.—Davidson, 1851–1852:71, pl. 15: figs. 15–20.—Quenstedt, 1858:426, pl. 58: figs. 21–27.
Acanthothiris spinosa.—d'Orbigny, 1850:343.—Buckman and Walker, 1889:50–51.—Lissajous, 1911: pl. 16: figs. 5, 6.—Buckman, 1918:70, pl. 19: fig. 26.—Rollier, 1918:76.—Muir-Wood, 1936:28.—Arcelin and Roche, 1936:54, pl. 1: figs. 1–18, pl. 12: fig. 2.—Roche, 1939:272.—Charles, 1950:2.—Ager, 1965a:H611, fig. 493-1.—Almeras, 1966b:277–279, pl. 17: figs. 1–3.—Childs, 1969:55, text-figs. 21, 22, pl. 5: figs. 12–17.
Rhynchonella spinosa.—Haas and Petri, 1882:226, pl. 4: figs. 7–9.—Greppin, 1900:178–180 pl. 19: figs. 3, 8.
Hemithyris spinosa.—Bouillierie, 1920:76, pl. 2: figs. 43–46.

TYPE.—*Neotype*: Childs, 1969, pl. 5: fig. 12a–d; from the Upper Trigonia Grit or Clypeus Grit (Bajocian), Rodborough Hill, Gloucestershire, England.

FIGURE 80.—Serial sections of *Septaliphoria pinguis* (Roemer); USNM 429577, L 20.8, W 21.9, T 13.1, A 89; (Oxfordian) Sobkow, Kłielc, Poland.

MATERIAL STUDIED.—89 specimens from the Bajocian and Bathonian of England, France, Switzerland, and Germany.

DESCRIPTION.—Shell small to medium, roundly subtrigonal to subpentagonal in outline; subglobose to globose in profile, valves almost equally biconvex. Lateral commissures straight or slightly oblique toward ventral side; anterior commissure generally rectimarginate to gently arched; tongue very short or

absent. Generally no fold clearly recognizable on dorsal valve; sulcus very shallow, usually existing as depression at anterior part, not abruptly separated from slopes.

Beak short, acute, erect to incurved, touching or almost touching dorsal umbo; foramen and deltidial plates concealed.

Costae many and irregularly branching, on each valve numbering 25–45 at anterior margin; innumerable coarse

spines displaced on costae; shell also covered with fine and clear growth lines.

Measurements and counts.

Number	L	W	T	A
USNM 429587	22.0	24.1	15.4	105
USNM 429588	17.5	19.6	13.2	97
USNM 429589	20.0	23.2	15.0	99
USNM 429590	21.1	23.6	16.6	101
USNM 429591	24.0	24.2	28.5	96
USNM 429592	23.5	24.1	18.5	96
USNM 429593	16.0	16.7	12.3	94
USNM 429594	14.2	15.0	11.7	96

INTERIOR.—No secondary thickenings in either valve. Pedicle collar short; delthyrial chamber wide; lateral cavities well developed, but relatively short; dental plates variable, subparallel, divergent or convergent to floor; generally splitting from ventral floor at hinge zone or nearby; teeth long, with expanded ends and crenulations, inserting deeply into sockets.

Dorsal septalium short, shallow and narrow; septum short, supporting septalium only at very posterior part of cavity and reduced into ridge forward, running about $\frac{1}{4}$ to $\frac{1}{3}$ of dorsal valve length; hinge plates narrow, slightly arched or inclined ventrally; inner socket ridges low, well differentiated from hinge plates at posterior parts and becoming less eminent anteriorly; crural bases well formed and relatively long, arising dorsally from inner margins of hinge plates; crura radulifer, about $\frac{1}{5}$ to $\frac{1}{4}$ as long as dorsal valve, strongly incurved toward ventral valve at anterior parts; on their dorsal sides, incipient and very shallow furrows present.

OBSERVATIONS.—In the young specimens of the species, the beak is suberect, a fold and sulcus are not developed, and the anterior commissure is nearly rectimarginate. With growth, the beak becomes incurved and anterior commissure arched, in some specimens the sulcus can be relatively deep, giving the anterior margin a shallow notch. Internally, the young specimens usually have a deeper and wider septalium, while in adults it becomes narrow and short or obsolescent, and the crural ends tend to be somewhat variable.

In adult specimens the beak is strongly incurved and conceals the foramen. This probably indicates that the species lost its functional pedicle at the adult stage, but stabilized on the substrata by spines instead.

REMARKS.—The species name "*spinosa*" was originally proposed by Linnaeus in 1788, but most literature cites it as *Terebratulula* (*Rhynchonella*) *spinosa* Schlotheim, because this species was first formally described by Schlotheim. The genotype was designated by Buckman and Walker (1889:43) as *Anomia spinosa* Linnaeus that was generally thought to be slightly different from *Terebratulites spinosa* Schlotheim, 1813 (Rollier, 1918; Buckman and Walker, 1889; Muir-Wood, 1936), which was designated as the type-species by Rollier (1918). Unfortunately, the original specimen of *Anomia spinosa* Linnaeus was not preserved, so that the character of

Anomia spinosa could not be fixed. Nevertheless the species *Anomia spinosa* Linnaeus was generally thought to be congeneric with *Terebratulites spinosa* Schlotheim. Childs (1969) chose a neotype from the Upper Bajocian of England and took *Terebratulites spinosa* Schlotheim as a synonym of *Anomia spinosa* Linnaeus. Here the sense of *Acanthothiris spinosa* is basically that of *Terebratulites spinosa* Schlotheim.

Family ERYMNARIIDAE Cooper, 1959

Subfamily CRYPTORHYNCHIIDAE, new subfamily

***Aethirhynchia* Shi, 1990**

Aethirhynchia Shi, 1990:314.

TYPE-SPECIES.—*Aethirhynchia lenticulata* Shi, 1990:314.

DIAGNOSIS.—Shell medium, fully costate, nearly rectimarginate; oval to sphenoidal, with numerous fine costellae. No septalium, septum stout; crura septifer, lateral septa short, partially fused with fulcral plates.

AGE AND DISTRIBUTION.—Callovian; South Qinghai, China.

COMPARISONS.—This genus differs from the Triassic genus *Crurirhynchia* in having a larger oval shell with rectimarginate anterior commissure, as well as finer and more costellae. Internally, *Crurirhynchia* has longer lateral septa that split from the dorsal floor much later in ontogeny. *Cryptorhynchia* differs from the present genus externally in having a uniplicate and smaller shell with conspicuous reticulate ornament; internally, the lateral septa are totally fused with the fulcral plates. Externally, the present genus resembles *Sphenorhynchia* in some respects, but their interiors are quite different. *Strongylo-*
ria Cooper (1989) and *Schizoria* Cooper (1989) also have oval-shaped and multicostate shells with rectimarginate anterior commissures, but both of them have radulifer crura and belong to the family Rhynchonellidae.

***Aethirhynchia lenticulata* Shi, 1990**

FIGURES 81, 82

Aethirhynchia lenticulata Shi, 1990:314, text-fig. 5, pl. 1: figs. 19, 20.

TYPE.—*Holotype*: Shi, 1990: pl. 1: fig. 20; from the Xiali Formation (Middle to Upper Callovian) of Geladandong, Southern Qinghai, China.

MATERIAL STUDIED.—3 specimens, one of which was sectioned serially; from the Xiali Formation (Middle to Upper Callovian) of Geladandong, Southern Qinghai, China.

DIAGNOSIS.—Medium sized *Aethirhynchia* with sphenoidal shell and straight lateral commissures; lentiform both in lateral and anterior views; with short beak and numerous finer costellae.

DESCRIPTION.—Shell medium, moderately biconvex and nearly equivalve; sphenoidal in shape and lentiform in lateral and anterior views. Lateral commissure straight; anterior commissure rectimarginate to feebly arched; fold and sulcus absent.

FIGURE 81.—*Aethirhynchia lenticulata* Shi; holotype, Y14750, L 27, W 24, T 14, A 84; from the Xiali Formation (Middle to Upper Callovian), Geladandong, Southern Qinghai, China. A–C, dorsal, side, and anterior views of shell, showing the general morphology and costation ($\times 1.5$); D, showing beak and foramen character ($\times 3$).

FIGURE 82.—Serial sections of *Aethirhynchia lenticulata* Shi; holotype, Y14750, L 27, W 24, T 14, A 84; from the Xiali Formation (Middle to Upper Callovian), Geladandong, Southern Qinghai, China.

Beak short, suberect; foramen small, circular, hypothyridd; deltidial plates disjunct to just conjunct, very low; beak ridges and planoareas not developed.

Ventral valve gently convex, with greatest convexity at midvalve; sulcus not shown.

Dorsal valve evenly convex, without recognizable fold.

Numerous fine costellae, on each valve numbering 30–35, occasionally bifurcating and intercalating; growth lines feeble, visible at anterior.

MEASUREMENTS.—The average dimensions of the 3 specimens are: L 24 (21–27), W 22 (18–24), T 13 (12–14), A 83 (78–86); W/L 0.92, T/L 0.54, T/W 0.59; *holotype*: Y14750, L 27, W 24, T 14, A 84.

INTERIOR.—Shell thick, slight secondary thickenings in apical cavities. Pedicle collar short; lateral cavities small; dental plates long, reaching hinge zone; teeth small, mallet-like.

Septalium absent in dorsal valve, septum stout, reduced into

ridge forward; septalial plates well developed and pendant; crura septifer; lateral septa short, partially fused with fulcral plates posteriorly, becoming separate and pendant anteriorly.

REMARKS.—This species is externally similar to *Spheonorhynchia dominulla* (Rollier) and *Spheonorhynchia bugeysica* (Riche) in general outline and costation, as well as in having a somewhat depressed shell. However, the interiors of the latter two are quite different from the present species. That genus has radulifer crura and a well developed dorsal septum, and belongs to the subfamily Tetrarhynchiinae of the Rhynchonellidae. Internally this species is so peculiar that, at this moment, no known species can be compared with it.

Cryptorhynchia Buckman, 1918

Cryptorhynchia Buckman, 1918:66 [in part].—Trechmann, 1923:283.—Allan, 1945:10.—Roger, 1952:93.—Ager, 1965a:H612.—Mitra and Ghosh, 1973:178.—Ovtsharenko, 1983:30 [in part]. [Not Li and Gu, 1982:51.]
?*Cryptorhynchia* Buckman.—Reed, 1927:260.—Perry, 1979:1002.

TYPE-SPECIES.—*Rhynchonella pulcherrina* Kitchin, 1900:52.

EMENDED DIAGNOSIS.—Shell small, uniplicate; with many costae reticulated with conspicuous concentric lines, no smooth areas on valves; beak short, suberect; foramen large, rimmed. Dorsal septum reduced; crura septifer, lateral septa totally fused with socket fulcral plates.

AGE AND DISTRIBUTION.—Bathonian; India, Pamirs, ?China, New Zealand, and ?North America.

REMARKS.—Buckman (1918) erected this genus with *Rhynchonella pulcherrina* Kitchin, 1900, as type-species, and included two Indian species and three European species. At that time none of these species were properly studied with interiors.

Ager (1965a:H612) mentioned that "the genus has appearance of lateral septa; no septalium; crura radulifer, blade-like, converging ventrally." However, he was not able to present any sections and put the genus into the subfamily Tetrarhynchiinae. Ager, Childs, and Pearson (1972) later transferred this genus into the subfamily Septocrurellinae, without further comments on its interior.

Mitra and Ghosh (1973) were first to illustrate a set of serial sections of the type-species *Rhynchonella pulcherrina*, made from a topotype specimen, and emended the genus based on the interior. Unfortunately, these serial sections were too rough, with long intervals between sections, and are not complete, so that the details of the crura, septalium, as well as the crural bases can not be figured out with certainty. Mitra and Ghosh (1973:179) stated that the type-species has "short and shallow septalium; median septum short; crural bases given off dorsally from the distal ends of hinge plates, recurved at a high angle from the hinge plates; crura radulifer, extending about $\frac{1}{3}$ of the brachial valve length, anteriorly diverging at a low angle." According to the only set of incomplete serial sections presented by them (Mitra and Ghosh, 1973:178, fig. 2), we are quite sure that the crura of the species are not radulifer, but septifer and are similar to those seen in *Crurirhynchia* Dagus, 1961.

On the other hand, Laurin (1984a) combined Buckman's three species, *Cryptorhynchia bradfordensis*, *C. vauhani*, and *C. avonensis* into a single species, "*Rhynchonella*" *bradfordensis*, and compared it with *Septaliphoria mourdoni* Laurin. The present study on the topotypes shows that the interiors of *Cryptorhynchia bradfordensis* are so different from those of *Cryptorhynchia pulcherrina* that a new genus *Bradfordirhynchia* has been suggested and that they have been placed in different families.

The present study on topotype specimens shows that *Cryptorhynchia* actually has septifer crura, but the dorsal lateral septa are totally fused with the socket fulcral plates so that in sections the crura look like they arise directly from the extensions of the socket fulcral plates. The crura of *Crurirhynchia* are similar to those of *Cryptorhynchia*, but in *Crurirhynchia* the lateral septa fuse incompletely with the socket fulcral plates, there remain small chambers between the lateral septa

and the socket fulcral plates. The lateral septa in *Crurirhynchia* do not join the dorsal floor as directly as in *Septocrurella*.

Cryptorhynchia pulcherrina (Kitchin, 1900)

FIGURE 83; PLATE 13: FIGURES 13–18, PLATE 16: FIGURES 3–6

Rhynchonella pulcherrina Kitchin, 1900:52, pl. 11: figs. 1–9, 16.

Cryptorhynchia pulcherrina (Kitchin).—Buckman, 1918:66, pl. 19: fig. 8.—Mitra and Ghosh, 1973:178–181, fig. 2, fig. 4A–D.

?*Cryptorhynchia pulcherrina* (Kitchin).—Ovtsharenko, 1983:31, text-fig. 8a–d, pl. 2: figs. 5–12.

TYPE.—*Lectotype* (here designated): Kitchin, 1900, pl. 11: fig. 1; from the Upper Beds of Putchum Group (Callovian) of Jumara, Kutch, India.

MATERIAL STUDIED.—6 well preserved specimens from the Putchum Group (Upper Beds, Callovian), Jumara, Kutch, India.

DESCRIPTION.—Shell small, subcircular to transverse in outline; gently biconvex to subglobose in side view; dorsal valve slightly more convex than ventral one. Lateral commissures deflected ventrally at 5–20 degrees; anterior commissure uniplicate; tongue short, subtrapezoidal. In junior specimens, anterior commissure only arched gently.

Beak short, substraight to suberect; foramen large, circular, hypothryidid; deltidial plates narrow, disjunct to just conjunct, with well developed rims around foramen; beak ridges subangular; interareas small, but well defined, with clearly transverse lines.

Ventral valve moderately convex; sulcus well developed, deep, with rounded bottom, occurring at posterior $\frac{1}{3}$ and well separated from slopes.

Dorsal valve convex evenly; fold variably developed, in young specimens low and short, while in adults generally well elevated above slopes at anterior $\frac{1}{3}$ to $\frac{1}{2}$ of valve.

Subangular costae numbering 13–16, crossed by quite distinct concentric lines or lamellae that are imbricated and so produce a reticulate pattern. In adult specimens, at intersections with costae, lamellae slightly protruding as granules or even short spines; between coarser lamellae, fine growth lines also clearly shown and regularly spaced.

Measurements and counts.

Number	L	W	T	A	N	F	S
USNM 76009a	10.0	11.1	8.0	101	15	3	2
USNM 76009b	9.2	12.1	7.7	99	16	4	3
USNM 76009c	10.6	10.8	6.2	100	14	4	3
USNM 76009d	10.5	12.5	6.1	120	16	4	3
USNM 429604	10.3	11.5	7.4	110	15	4	3
USNM 429605	9.2	11.0	6.3	118	13	3	2

INTERIOR.—No secondary thickenings in either valve, but shell relatively thick. Beak of sectioned specimen cut off so pedicle collar not seen; dental plates short; delthyrial chamber

FIGURE 83.—Serial sections of *Cryptorhynchia pulcherrima* (Kitchin); topotype, USNM 76009b, L 9.2, W 12.1, T 7.7, A 99; from the Putchum Group (Upper Beds) of Jumara, Kutch, India.

and lateral cavities well developed; teeth very strong and massive, rectangular, inserting tightly into sockets.

Dorsal septum short, reduced to ridge forward; septalium absent in sectioned specimen; hinge plates broad, subhorizontal posteriorly, and becoming strongly inclined toward ventral valve at anterior part, which are tapering forward and constitute parts of the crura; crural bases not well formed; crura septifer; lateral septa, instead of sitting straight on dorsal floor as in *Septocrurella*, fused totally with very long and forwardly divergent socket fulcral plates; crura arising from distal ends of fused lateral septa, appearing as vertical plates in section.

REMARKS.—The crura of the species are septifer, but the lateral septa are fused with the socket fulcral plates so they look like they arise directly from the socket fulcral plates. When compared with *Crurirhynchia* it becomes clear that the crura of *Cryptorhynchia* are actually similar to those of that genus and that these two genera are closely related.

Perry (1979) described a species of the genus from North America. This species was illustrated with interiors of silicified

specimens that show similar interiors with the present specimen, although its crura were described as radulifer (Perry, 1979:1002). Ovtsharenko (1983) also described two species of the genus from the Middle Jurassic of the Pamirs, one of which, *Cryptorhynchia karadzhilgensis* Ovtsharenko, shows crura similar to those of the present specimen, but the fused lateral septa are short. The other, which was described as *Cryptorhynchia pulcherrina*, seems to be different from the present specimens both in crura and exteriors (Ovtsharenko, 1983:28–30, text-fig. 7; 31–33, text-fig. 8, pl. 2: figs. 5–12). Externally, these specimens have weakly concentric lines and no clear reticulate ornament. Internally, their crura are not as distinctive as those in the present specimen and are somewhat similar to calcarifer. Makridin (1964:193, fig. 64A, B) illustrated two sets of serial sections of *Cardinirhynchia roissica* Makridin. One set (fig. 64A), made from a juvenile specimen, shows crura quite close to the present species, but another (fig. 64B) has clearly calcarifer crura. We suspect that the juvenile specimen might belong to this genus rather than to *Cardinirhynchia*.

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Plates

PLATE 1

FIGURES 1–3.—*Ptyctorhynchia pentaptycha* (Buckman): 1a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429121; 2a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429122; 3a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429123. Inferior Oolite (lower part, Aalenian), Chideock Quarry Hill, Dorset, England.

FIGURES 4–6.—*Costirhynchia costigera* Buckman: 4a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 88709a (sectioned); 5a–c, dorsal, side, and anterior views, $\times 1$, USNM 123711; 6a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 88709b. Inferior Oolite (Pea Grit, Aalenian); 4, 6, from Crickley Hill, Cheltenham, Gloucestershire; 5, from Leckhampton Hill, Gloucestershire, England.

FIGURES 7–12.—*Rhynchonelloidea subangulata* (Davidson): 7a,b, dorsal and anterior views, $\times 1$, USNM 312350a; 8a–c, dorsal, side, and anterior views, $\times 1$, USNM 312350b; 9a–c, dorsal, side, and anterior views, $\times 1$, USNM 429147; 10a–c, dorsal, side, and anterior views, $\times 1$, USNM 429148; 11a–c, dorsal, side, and anterior views, $\times 1$, USNM 429152; 12a–c, dorsal, side, and anterior views, $\times 1$, USNM 429146. Inferior Oolite (Pea Grit, Aalenian); 7, 8, from Selsley Common, Stroud, Gloucestershire; 9, 10, 12, from Crickley Hill, Cheltenham; 11, from Leckhampton Hill, Gloucestershire, England.

FIGURES 13–17.—*Rhynchonelloidea angulata* (Sowerby): 13a–c, dorsal, side, and anterior views, $\times 1$, USNM 429156; 14a–c, dorsal, side, and anterior views, $\times 1$, USNM 429157; 15a–c, dorsal, side, and anterior views, $\times 1$, USNM 429158; 16a–c, dorsal, side, and anterior views, $\times 1$, USNM 429159; 17a–c, dorsal, side, and anterior views, $\times 1$, USNM 104764. Inferior Oolite (Pea Grit, Aalenian); 13–16, from Crickley Hill, Cheltenham; 17, from Stroud Common, Gloucestershire, England.

FIGURES 18, 19.—*Aalenirhynchia subdecorata* (Davidson): 18a–c, dorsal, side, and anterior views, $\times 1$, USNM 123721a; 19a–c, dorsal, side, and anterior views, $\times 1$, USNM 123721b (sectioned). Inferior Oolite (Pea Grit, Aalenian), Leckhampton Hill, Gloucestershire, England.

FIGURES 20, 21.—*Isjuminella decorata* (Schlotheim): 20a–c, dorsal, side, and anterior views, $\times 1$, USNM 31331; 21a–c, dorsal, side, and anterior views, $\times 1$, USNM 75850. Bathonian; 20, from Poix Ardenne, France; 21, from Langer Berg, Bad Harzburg, Germany.

PLATE 2

FIGURES 1–4.—*Bradfordirhynchia bradfordensis* (Buckman): 1a–c, dorsal, side, and anterior views, ×1, topotype, USNM 104765a; 2a–c, dorsal, side, and anterior views, ×1, USNM 429128; 3a–c, dorsal, side, and anterior views, ×1, USNM 429129; 4a–c, dorsal, side, anterior views, ×1, topotype, USNM 104765b. 1, 4, from the Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England; 2, 3, Upper Bathonian, Campagnettes Quarry, Ranville, France.

FIGURES 5–10.—*Bradfordirhynchia ecardensis* (Laurin): 5a–c, dorsal, side, and anterior views, ×1, USNM 429138; 6a–c, dorsal, side, and anterior views, ×1, USNM 92005a; 7a–c, dorsal, side, and anterior views, ×1, USNM 429139; 8a–c, dorsal, side, and anterior views, ×1, USNM 429140; 9a–c, dorsal, side, and anterior views, ×1, USNM 429135; 10a–c, dorsal, side, and anterior views, ×1, USNM 104587a. Upper Bathonian, Ranville and Langueville, Calvados, France.

FIGURES 11–13.—*Bradfordirhynchia ecardensis* (Laurin): 11a–c, dorsal, side, and anterior views, ×1, USNM 104687c; 12a–c, dorsal, side, and anterior views, ×1, USNM 429137; 13a–c, dorsal, side, and anterior views, ×1, USNM 104687d. Upper Bathonian, Ranville and Langueville, Calvados, France.

FIGURE 14.—*Bradfordirhynchia ecardensis* (Laurin): 14a–c, dorsal, side, and anterior views, ×1, USNM 104687b. Upper Bathonian, Langueville, Calvados, France.

FIGURES 15–17.—*Sharpirhynchia sharpi* (Muir-Wood): 15a–c, dorsal, side, and anterior views, ×1, USNM 429193; 16a–c, dorsal, side, and anterior views, ×1, USNM 429199; 17, dorsal view, ×1, USNM 429194. Base of the Great Oolite (Lower Bathonian); 15, 17, from Cranford South Quarry, Kettering; 16, from Corby, Lincolnshire, England.

FIGURE 18.—*Sharpirhynchia acutiplicata* (Brown): 18a–c, dorsal, side, and anterior views, ×1, USNM 89082a. Inferior Oolite (Upper *Trigonia* Grit, Upper Bajocian), Buckholt Wood, Cranham near Painswick, England.

FIGURE 19.—*Sharpirhynchia sharpi* (Muir-Wood): 19a–c, dorsal, side, and anterior views, ×1, USNM 429195. Base of the Great Oolite (Lower Bathonian), Cranford South Quarry, Kettering, England.

FIGURES 20–23.—*Sharpirhynchia acutiplicata* (Brown): 20a–c, dorsal, side, and anterior views, ×1, USNM 75590a; 21a–c, dorsal, side, and anterior views, ×1, USNM 89082b; 22a–c, dorsal, side, and anterior views, ×1, USNM 75590b; 23a–c, dorsal, side, and anterior views, ×1, USNM 123758. Inferior Oolite (Upper *Trigonia* Grit, Upper Bajocian); 20, 22, from Birdlip Hill, Gloucestershire, England; 21, Buckholt Wood, Cranham by Painswick, England; 23, Lorraine, France.

FIGURES 24–27.—*Thurmannella obtrita* (Defrance): 24a–c, dorsal, side, and anterior views, ×1, USNM 306011a; 25a,b, dorsal and anterior views, ×1, USNM 306011e; 26a–c, dorsal, side, and anterior views, ×1, USNM 429212; 27a–c, dorsal, side, and anterior views, ×1, USNM 306011b. Lower Oxfordian; 24, 25, 27, from Park near Benoit, Besancon, France; 26, from Woodham Pit, Buckingham, England.

PLATE 3

FIGURES 1–6.—*Rhynchonelloidella alemanica* (Rollier): 1a–c, dorsal, side, and anterior views, $\times 1$, USNM 429173; 2a–c, dorsal, side, and anterior views, $\times 1$, USNM 429174; 3a–c, dorsal, side, and anterior views, $\times 1$, USNM 429175; 4a–c, dorsal, side, and anterior views, $\times 1$, USNM 429178; 5a–c, dorsal, side, and anterior views, $\times 1$, USNM 429179; 6a–c, dorsal, side, and anterior views, $\times 1$, USNM 429180. Varais Bed (Upper Bathonian to Lower Callovian); 1, 2, 3, from Leisberg alte, Fabrik; 4, from Kahlen-Teniken; 5, from Roggenweid-Oensing; 6, from Lostorf-Dottenberg, Switzerland.

FIGURES 7–11.—*Rhynchonelloidella smithi* (Davidson): 7a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 75628a; 8a–c, dorsal, side, and anterior views, $\times 1$, USNM 75630; 9a–c, dorsal, side, and anterior views, $\times 1$, USNM 104786; 10a–c, dorsal, side, and anterior views, $\times 1$, USNM 18969; 11a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 75628b. Fuller's Earth Rock (Bathonian); 7, 11, from Bath, Somerset; 8, from Box Tunnel, Wiltshire; 9, from Bradford-on-Avon, Wiltshire; 10, from Bruton, Somerset, England.

FIGURE 12.—*Rhynchonelloidella mesoloba* Muir-Wood: 12a–c, dorsal, side, and anterior views, $\times 1$, USNM 429172. Fuller's Earth Rock (Bathonian), near Frome, Somerset, England.

FIGURE 13.—*Rhynchonelloidella wattonensis* Muir-Wood: 13a–c, dorsal, side, and anterior views, $\times 1$, USNM 129175a. Fuller's Earth Rock (Bathonian), Bath, Somerset, England.

FIGURES 14, 15.—*Rhynchonelloidella alemanica* (Rollier): 14a–c, dorsal, side, and anterior views, $\times 1$, USNM 123762a; 15a–c, dorsal, side, and anterior views, $\times 1$, USNM 123762b. Upper Bathonian, Villey (Lorraine), France.

FIGURES 16, 17.—*Rhynchonelloidella curviviarians* (Buckman): 16a–c, dorsal, side, and anterior views, $\times 1$, USNM 88741a; 17a–c, dorsal, side, and anterior views, $\times 1$, USNM 88741b. Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England.

FIGURE 18.—*Rhynchonelloidella wattonensis* Muir-Wood: 18a–c, dorsal, side, and anterior views, $\times 1$, USNM 129175b. Fuller's Earth Rock (Bathonian), Bath, Somerset, England.

FIGURES 19, 20.—*Lotharingella leedsi* (Davidson): 19a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429167; 20a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429166. Combrash (upper part, Lower Callovian), Peterborough, Cambridgeshire, England.

FIGURE 21.—*Lotharingella leedsi* (Davidson) (= *Rhynchonelloidea inflata* Douglas and Arkell): 21a–c, dorsal, side, and anterior views, $\times 1$, USNM 429169. Combrash (upper part, Lower Callovian), Milton near Peterborough, Cambridgeshire, England.

FIGURES 22–28.—*Thurmannella acuticosta* Childs: 22a–c, dorsal, side, and anterior views, $\times 1$, USNM 88738b; 23a–c, dorsal, side, and anterior views, $\times 1$, USNM 88738c; 24a–c, dorsal, side, and anterior views, $\times 1$, USNM 88738d; 25a–c, dorsal, side, and anterior views, $\times 1$, USNM 64412a; 26a–c, dorsal, side, and anterior views, $\times 1$, USNM 429218; 27a–c, dorsal, side, and anterior views, $\times 1$, USNM 429219; 28a–c, dorsal, side, and anterior views, $\times 1$, USNM 64412b. Lower Oxfordian; 22, 23, 24, from the Lower Calcareous Grit, Waydale Snainton, England; 25, 28, from Wagrion (Ardeunne), France; 26, 27, from Villers-Sur-Mer, Calvados, France.

FIGURE 29.—? *Lotharingella woevrica* Laurin: 29a–c, dorsal, side, and anterior views, $\times 1$, USNM 31018. Bathonian, Langueville, Calvados, France.

PLATE 4

FIGURES 1, 2.—*Burmihynchia* (*Burmihynchia*) *gutta* Buckman: 1a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429222; 2a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 123602 (sectioned). Namyau Beds (Bathonian), Northern Shan States, Burma.

FIGURES 3–5.—*Burmihynchia* (*Hopkinsirynchia*) *hopkinsi* (Davidson): 3a–c, dorsal, side, and anterior views, $\times 1$, USNM 104676a; 4a–c, dorsal, side, and anterior views, $\times 1$, USNM 104676b; 5a–c, dorsal, side, and anterior views, $\times 1$, USNM 32112. Bathonian, Les Callande, Pas de Calais, France.

FIGURES 6–10.—*Burmihynchia* (*Hopkinsirynchia*) *latiscensis* Laurin: 6a–c, dorsal, side, and anterior views, 6c showing interiors, $\times 1$, topotype, USNM 429240; 7a,b, dorsal and anterior views, $\times 1$, topotype, USNM 429226; 8a–c, dorsal, side, and anterior views, $\times 1$, 8d showing interiors $\times 2$, topotype, USNM 429227; 9a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429228; 10a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429229. Lower Callovian, Chatillon-Sur-Seine, Cote d'Or, France.

FIGURE 11.—*Obsoletirynchia* *rostrata* (Sowerby): 11a–c, dorsal, side, and anterior views, $\times 1$, USNM 429359. Bathonian, France.

FIGURES 12, 13.—*Burmihynchia* (*Hopkinsirynchia*) *elegantula* (Deslongchamps): 12a–c, dorsal, side, and anterior views, $\times 1$, USNM 19886; 13a–c, dorsal, side, and anterior views, $\times 1$, USNM 75584. Bathonian, Marquise, Pas de Calais, France.

FIGURES 14, 15.—*Burmihynchia* (*Hopkinsirynchia*) *latiscensis* Laurin: 14a–c, interiors of dorsal valve, $\times 1.5$, topotype, USNM 429239; 15a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429230. Lower Callovian, Chatillon-Sur-Seine, Cote d'Or, France.

FIGURE 16.—*Burmihynchia* (*Hopkinsirynchia*) *hopkinsi* (Davidson): 16a–c, dorsal, side, and anterior views, $\times 1$, USNM 429223. Bathonian, Ancy of France.

FIGURE 17.—*Burmihynchia* (*Hopkinsirynchia*) *latiscensis* Laurin: anterior view, same specimen as FIGURE 6, showing interiors, $\times 1.7$, topotype, USNM 429240. Lower Callovian, Chatillon-Sur-Seine, Cote d'Or, France.

FIGURE 18.—*Obsoletirynchia* *rostrata* (Sowerby): two valves of one specimen; 18a–b, interior of a ventral valve, $\times 1.7$; 18c–g, interiors of a dorsal valve, $\times 1.7$, USNM 429359. The same specimen as FIGURE 11. Bathonian, France.

FIGURES 19, 20.—*Obsoletirynchia* *rostrata* (Sowerby): 19a–c, dorsal, side, and anterior views, $\times 1$, USNM 429351; 20a–c, dorsal, side, and anterior views, $\times 1$, USNM 429350. Upper Bathonian, Langueville, Calvados, France.

PLATE 5

FIGURE 1.—*Obsoletirhynchia obsoleta* (Sowerby): 1a–c, dorsal, side, and anterior views, $\times 1$, USNM 429331. Upper Bathonian, Amfreville, Caen, Calvados, France.

FIGURE 2.—*Obsoletirhynchia diducta* (Buckman): 2a–c, dorsal, side, and anterior views, $\times 1$, USNM 429342. Upper Bathonian, Amfreville, Calvados, France.

FIGURES 3, 4.—*Obsoletirhynchia obsoleta* (Sowerby): 3a–c, dorsal, side, and anterior views, $\times 1$, USNM 75577a; 4a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 31006a. 3, Upper Bathonian, Ranville, Calvados, France; 4, Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England.

FIGURES 5, 6.—*Obsoletirhynchia diducta* (Buckman): 5a–c, dorsal, side, and anterior views, $\times 1$, USNM 64514; 6a–c, dorsal, side, and anterior views, $\times 1$, USNM 88732. Bradford Clay (Upper Bathonian), from Bradford-on-Avon, Wiltshire, England.

FIGURES 7, 8.—*Obsoletirhynchia diducta* (Buckman): 7a–c, dorsal, side, and anterior views, $\times 1$, USNM 104682; 8a–c, dorsal, side, and anterior views, $\times 1$, USNM 92003. Upper Bathonian; 7, from Ranville; 8, from Beaune, Cote d'Or, France.

FIGURE 9.—*Obsoletirhynchia obsoleta* (Sowerby): 9a–c, dorsal, side, and anterior views, $\times 1$, USNM 104680. Upper Bathonian, Le Pichottes, Pas de Calais, France.

FIGURES 10, 11.—*Rhactorhynchia subtetrahedra* (Davidson): 10a–c, dorsal, side, and anterior views, $\times 1$, USNM 88731; 11a–c, dorsal, side, and anterior views, $\times 1$, USNM 31432. 10, Inferior Oolite (upper part, Upper Bajocian), Leckhampton Hill, Gloucestershire, England; 11, Upper Bajocian, Wuttingburg, Germany.

FIGURES 12, 13.—*Rhactorhynchia subtetrahedra* (Davidson): 12a–c, dorsal, side, and anterior views, $\times 1$, USNM 75588a; 13a,b, dorsal and anterior views, $\times 1$, USNM 88733. Inferior Oolite (upper part, Upper Bajocian), Sherborne, Dorset, England.

FIGURE 14.—*Rhactorhynchia subtetrahedra* (Davidson): anterior view, $\times 1$, topotype, USNM 104779 (sectioned). Inferior Oolite (Truelli Zone, Upper Bajocian), Dundry Hill, Somerset, England.

PLATE 6

FIGURES 1–3.—*Goniorhynchia boueti goniaeae* Buckman: 1a–c, dorsal, side, and anterior views, $\times 1$, USNM 355632; 2a–c, dorsal, side, and anterior views, $\times 1$, USNM 429283; 3a–c, dorsal, side, and anterior views, $\times 1$, USNM 429284. Upper Bathonian; 1, 3, from Langton Herring, Dorset; 2, from Herbury Peninsula, East Fleet Chesil, Dorset, England.

FIGURES 4, 5.—*Goniorhynchia boueti boueti* (Davidson): 4a–c, dorsal, side, and anterior views, $\times 1$, USNM 19893; 5a–c, dorsal, side, and anterior views, $\times 1$, USNM 92005. Upper Bathonian, Ranville, Caen, Calvados, France.

FIGURES 6, 7.—*Obsoletirhynchia diducta* (Buckman): 6a–c, dorsal, side, and anterior views, $\times 1$, USNM 429346; 7a–c, dorsal, side, and anterior views, $\times 1$, USNM 429347. Upper Bathonian, Campagnettes Quarry, near Ranville, France.

FIGURE 8.—*Kutchirhynchia morrieri* (Davidson): 8a–c, dorsal, side, and anterior views, $\times 1$, USNM 104680. Upper Bathonian, Pitchottes, Pas de Calais, France.

FIGURE 9.—*Kutchirhynchia kutchiensis* (Kitchin): 9a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 75997. Charee Group (bottom bed, Upper Bathonian), Jooria, Kutch, India.

FIGURE 10.—? *Goniorhynchia maxima legirica* Laurin: 10a–c, dorsal, side, and anterior views, $\times 1$, USNM 64407. Upper Bathonian, Benouville, Calvados, France.

FIGURE 11.—*Rhactorhynchia subtetrahedra* (Davidson): 11a–c, dorsal, side, and anterior views, $\times 1$, USNM 75588b. Inferior Oolite (Upper Bajocian), Sherborne, Dorset, England.

FIGURE 12.—*Kutchirhynchia morrieri* (Davidson): 12a–c, dorsal, side, and anterior views, $\times 1$, USNM 429328. Upper Bathonian, Selongey, Cote d'Or, France.

FIGURE 13.—*Isjuminella decorata* (Schlotheim): 13a–c, dorsal, side, and anterior views, $\times 1$, USNM 31331b. Bathonian, Poix Ardenne, France.

PLATE 7

FIGURES 1–6.—*Kallirhynchia yaxleyensis* (Davidson): 1a–c, dorsal, side, and anterior views, $\times 1$, USNM 123765b; 2a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429305; 3a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429308; 4a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429311; 5a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429303; 6a–c, dorsal, side, and anterior views, $\times 1$, USNM 429309. 1, Upper Bathonian, Lorraine, France; 2, 3, 4, 5, from the Lower Cornbrash (Upper Bathonian), Yaxley near Peterborough, Cambridgeshire, England; 6, from the Lower Cornbrash (Upper Bathonian), Dorset, England.

FIGURES 7–9.—*Kallirhynchia multicostata* Douglas and Arkell: 7a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429317; 8a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429318; 9a–c, dorsal, side, and anterior views, $\times 1$, USNM 223474a. 7, 8, from the Lower Cornbrash (Upper Bathonian), Dorset, England; 9, from the Upper Bathonian, Amfreville, Caen, Calvados, France.

FIGURES 10, 11.—*Kallirhynchia indentata* Buckman: 10a–c, dorsal, side, and anterior views, $\times 1$, USNM 104670; 11a–c, dorsal, side, and anterior views, $\times 1$, USNM 429320. Upper Bathonian; 10, from Le Baque, Pas de Calais; 11, from Amfreville, Caen, Calvados, France.

FIGURES 12, 13.—*Kallirhynchia concinna* (Sowerby): 12a–c, dorsal, side, and anterior views, $\times 1$, USNM 104762a; 13a–c, dorsal, side, and anterior views, $\times 1$, USNM 104762b. Upper Bathonian, Hidreguent, Pas de Calais, France.

FIGURES 14, 15.—*Kallirhynchia concinna* (Sowerby): 14a–c, dorsal, side, and anterior views, $\times 1$, USNM 77399; 15a–c, dorsal, side, and anterior views, $\times 1$, USNM 429314. 14, Great Oolite (Upper Bathonian), Weymouth, England; 15, Jurassic Homomyenmergel (Upper Bathonian), Liesberg Qrub W. ob Strasses nach Delsberg, Switzerland.

FIGURE 16.—*Kallirhynchia concinna* (Sowerby): 16a–c, dorsal, side, and anterior views, $\times 1$, juvenile, USNM 429329. Lower Cornbrash (Upper Bathonian), Sapperton, England.

FIGURES 17, 18.—*Cymatorhynchia quadriplicata* (Zieten): 17a,b, ventral and side views of dorsal valve, $\times 1$, USNM 380741; 18a–c, ventral, side, and anterior views inside of a dorsal valve, $\times 1$, USNM 429268. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURE 19.—*Cymatorhynchia quadriplicata* (Zieten): interior, showing dental plates and low dorsal septum, $\times 1.3$, USNM 429269. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURES 20, 21.—*Lacunaerhynchia palmaeformis* (Lissajous in Arcelin and Roche): 20, interior, showing the radulifer crura and low dorsal septum, $\times 1.8$, topotype, USNM 429275; 21, interior, showing the septalium and dental plates, $\times 1.8$, topotype, USNM 429276. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

PLATE 8

FIGURE 1.—*Septaliphoria* cf. *corallina* (Leymerie): 1a–c, dorsal, side, and anterior views, $\times 1$, USNM 64485a (sectioned). Jurassic Corallian (Oxfordian), Fairford, England.

FIGURE 2.—*Lacunaerhynchia palma* (Szajnocha): 2a–c, dorsal, side, and anterior views, $\times 1$, USNM 39533. Bathonian, Benouville, France.

FIGURES 3–5.—*Lacunaerhynchia buckmani* (Rollier): 3a–c, dorsal, side, and anterior views, $\times 1$, USNM 429280; 4a–c, dorsal, side, and anterior views, $\times 1$, USNM 104773a; 5a,b, dorsal and anterior views, $\times 1$, USNM 104773b. Inferior Oolite (*Truelli* Zone, Aalenian), Dundry Hill, Somerset, England.

FIGURE 6.—*Lacunaerhynchia palma* (Szajnocha): 6a–c, dorsal, side, and anterior views, $\times 1$, USNM 77469. Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England.

FIGURE 7.—*Obsoletirhynchia diducta* (Buckman): 7a–c, dorsal, side, and anterior views, $\times 1$, USNM 31414c. Upper Bathonian, Ranville, France.

FIGURES 8–10.—*Cymatorhynchia quadriplicata* (Zieten): 8a–c, dorsal, side, and anterior views, $\times 1$, USNM 429256; 9a–c, dorsal, side, and anterior views, $\times 1$, USNM 429257; 10a–c, dorsal, side, and anterior views, $\times 1$, USNM 429258. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURE 11.—*Cymatorhynchia quadriplicata* (Zieten): 11a,b, interior of a ventral valve, the same specimen as FIGURES 10a–c, showing the dental plates and foramen, $\times 1.2$, USNM 429258. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURE 12.—*Cymatorhynchia quadriplicata* (Zieten): 12a,b, interior of a ventral valve, $\times 1.2$, USNM 380741. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURE 13.—*Cymatorhynchia quadriplicata* (Zieten): side view of a dorsal valve, the same specimen as FIGURES 10a–c, showing the radulifer crura, $\times 1$, USNM 429258. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURE 14.—*Hopkinsirhynchia latiscensis* (Laurin): side view of a dorsal valve, showing the radulifer crura, $\times 2$, topotype, USNM 429240. Lower Callovian, Chatillon-Sur-Seine, Cote d'Or, France.

FIGURE 15.—*Somalirhynchia* cf. *africana* Weir: interior, showing radulifer crura and long dorsal septum, $\times 2$, USNM 107068. Kimmeridgian, Dire Daoua, Abyssinia (Ethiopia).

PLATE 9

FIGURES 1–7.—*Cymatorhynchia quadriplicata* (Zieten): 1, interior, showing radulifer crura and dorsal septum, $\times 1.2$, USNM 429270; 2, interior, $\times 1$, USNM 429271; 3a,b, interiors, $\times 1$, USNM 429272; 4a,b, interior of a dorsal valve, showing radulifer crura, $\times 1$, USNM 380741; 5, interior of ventral valve, the same specimen as FIGURE 4a,b, $\times 1$, USNM 380741; 6, interior, $\times 1$, USNM 429273; 7a,b, interior of a dorsal valve, showing radulifer crura and short septalium, $\times 1$, USNM 429274. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURES 8–10.—*Lacunaerhynchia palmaeformis* (Lissajous in Arcelin and Roche); 8a, dorsal view of a silicified specimen, 8b–d, interior of preceding, showing radulifer crura and short septalium, $\times 1$, topotype, USNM 429275; 9, interior, $\times 1$, topotype, USNM 429277; 10, interior, $\times 1$, topotype, USNM 429276. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURES 11–15.—*Cymatorhynchia quadriplicata* (Zieten): 11a–c, interior of a dorsal valve, $\times 0.85$, USNM 429258; 12, ventral valve of preceding, $\times 0.85$, USNM 429258; 13, interior of a dorsal valve, $\times 1.6$, USNM 429268; 14, interior of a dorsal valve, $\times 1.2$, USNM 429258; 15a,b, interior of a dorsal valve, $\times 1.8$, USNM 429268. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURE 16.—*Cymatorhynchia quadriplicata* (Zieten): 16a–c, interior of a dorsal valve, showing radulifer crura and septum, $\times 1.8$, USNM 380741. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURE 17.—*Cymatorhynchia quadriplicata* (Zieten): interior of a dorsal valve, showing radulifer crura, $\times 1.2$, USNM 429258. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

PLATE 10

FIGURES 1–3.—*Pycnoria depressa*, new species: 1a–c, dorsal, side, and anterior views, $\times 1$, paratype, USNM 429540; 2a–c, dorsal, side, and anterior views, $\times 1$, holotype, USNM 429539; 3a–c, dorsal, side, and anterior views, $\times 1$, paratype, USNM 429541. Zohar Shales (Upper Bathonian to Lower Callovian, near base), Hamaktesh Hagadol, southern Israel.

FIGURES 4, 5.—*Pycnoria magna* Cooper: 4a–c, dorsal, side, and anterior views, $\times 1$, juvenile, USNM 429456; 5a–c, dorsal, side, and anterior views, $\times 1$, USNM 429455. Zohar Shales (Upper Bathonian to Lower Callovian, near base), Hamaktesh Hagadol, southern Israel.

FIGURES 6–8.—*Daghanirhynchia daghaniensis* Muir-Wood: 6a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 75666a; 7a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 75666b (sectioned); 8a–c, dorsal, side, and anterior views, $\times 1$, juvenile, topotype, USNM 75666c. Lower Callovian, Daghani section 227, Somaliland (Somalia).

FIGURES 9, 10.—*Somalirhynchia africana* Weir: 9a–c, dorsal, side, and anterior views, $\times 1$, USNM 429404; 10a–c, dorsal, side, and anterior views, $\times 1$, USNM 75660. Oxfordian; 9, from Gahodleh Shale, Bihendula; 10, from Bosti, NW of Bihendula, Somaliland (Somalia).

FIGURE 11.—*Somalirhynchia* cf. *africana* Weir: 11a, interior, $\times 1$, 11b, interior, $\times 2$, USNM 197068. Kimmeridgian, Dire Daoua, Abyssinia (Ethiopia).

FIGURE 12.—*Rhynchonelloidella proxima* (Roche): 12a, interior of ventral valve, showing dental plates and foramen, $\times 1.8$, 12b–d, dorsal valve of preceding, showing calcarifer crura, $\times 1.8$, USNM 429402. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURES 13, 14.—*Lacunaerhynchia palmaeformis* (Lissajous in Arcelin and Roche): 13a, dorsal view, $\times 1$, 13b, interior of preceding, showing radulifer crura and septalium, $\times 1.8$, topotype, USNM 429277; 14a,b, interiors of a specimen, $\times 2$, topotype, USNM 429276. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

PLATE 11

FIGURES 1, 2.—*Acanthothiris spinosa* (Linnaeus): 1a–c, dorsal, side, and anterior views, $\times 1$, USNM 429588; 2a–c, dorsal, side, and anterior views, $\times 1$, USNM 429587. Jurassic Varians Bed (Bathonian to Lower Callovian), Liesberg ob alte Fabrik, Switzerland.

FIGURE 3.—*Acanthothiris spinosa* (Linnaeus): interiors of a silicified specimen; 3a–c, showing radulifer crura and septum, $\times 1.7$, 3d, e, two views of preceding, $\times 1$, USNM 429603. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURES 4, 5, 7.—*Sphenorhynchia matisconensis* (Arcelin and Roche): 4a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429392; 5a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429393; 7a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429398. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURES 6, 8–10.—*Sphenorhynchia plicatella* (Sowerby): 6a–c, dorsal, side, and anterior views, $\times 1$, USNM 88733a; 8a–c, dorsal, side, and anterior views, $\times 1$, USNM 88733b; 9a–c, dorsal, side, and anterior views, $\times 1$, USNM 75523; 10a–c, dorsal, side, and anterior views, $\times 1$, USNM 31014. Inferior Oolite (upper beds, Upper Bajocian); 6, 8, 9, from Broad Windsor, Dorset; 10, from Dundry, Somersetshire, England.

FIGURES 11, 12.—*Sphenorhynchia matisconensis* (Arcelin and Roche): two valves of one specimen, 11, dorsal view of ventral valve, showing dental plates, $\times 1$; 12a,b, ventral and side views of dorsal valve, showing radulifer crura and septum, $\times 1$, topotype, USNM 429399. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

PLATE 12

FIGURES 1, 2.—*Cymatorhynchia quadriplicata* (Zieten): 1a–c, ventral, side, and anterior views of a dorsal valve, $\times 1.8$, USNM 429274a; 2a–d, ventral, side, anterior, and side views of a dorsal valve, $\times 1.8$, USNM 429274b. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURE 3.—*Rhynchonelloidella proxima* (Roche): 3a–d, ventral, anterior, and two side views of a dorsal valve, showing calcarifer crura and septum, $\times 1.8$, USNM 429403. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURES 4, 5.—*Sphenorhynchia matisconensis* (Arcelin and Roche): two valves of one specimen; 4a–d, ventral, side, and two anterior views of dorsal valve; 5a,b, two views of ventral valve, $\times 1.8$, topotype, USNM 429399. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURES 6, 7.—*Cymatorhynchia quadriplicata* (Zieten): 6, interior of a specimen, $\times 1.8$, USNM 429270; 7, interior of another specimen, $\times 1.8$, 429273. Upper Bajocian, La Roche-Vineuse Quarry, Monsard, Saone-et-Loire, France.

FIGURE 8.—*Somalirhynchia* cf. *africana* Weir: 8a,b, interior of one specimen, 8a $\times 1$, 8b $\times 1.8$, USNM 107068. Kimmeridgian, Dire Daoua, Abyssinia (Ethiopia).

PLATE 13

FIGURE 1.—*Rhactorhynchia hampenensis* (Buckman): 1a–c, dorsal, side, and anterior views, $\times 1$, USNM 429360. Inferior Oolite (Clypeus Grit, Upper Bajocian), Birdlip Hill, Gloucestershire, England.

FIGURE 2.—*Kallirhynchia yaxleyensis* (Davidson): 2a–c, dorsal, side, and anterior views, $\times 1$, USNM 123765a. Upper Bathonian, Lorraine, France.

FIGURES 3–8.—*Rhactorhynchia hampenensis* (Buckman): 3a–c, dorsal, side, and anterior views, $\times 1$, USNM 75579; 4a–c, dorsal, side, and anterior views, $\times 1$, USNM 104759; 5a–c, dorsal, side, and anterior views, $\times 1$, USNM 88742; 6a–c, dorsal, side, and anterior views, $\times 1$, USNM 92019; 7a–c, dorsal, side, and anterior views, $\times 1$, USNM 64406; 8a–c, dorsal, side, and anterior views, $\times 1$, USNM 89082. Inferior Oolite (Upper Bajocian); 3, from Selsley Hill, Stroud, Gloucestershire, England; 4, from Vesulian, Doultling, Somersetshire, England; 5, from Rodborough Hill, Gloucestershire, England; 6, from Cotswolds, England; 7, Calcairi Oolite, Calvados, France; 8, Upper *Trigonia* Grit, Buckholt Wood, Cranham, Painswick, England.

FIGURES 9–12.—*Burmishynchia* (*Hopkinsirhynchia*)? *oxoniensis* (Buckman): 9a–c, dorsal, side, and anterior views, $\times 1$, USNM 429254; 10a–c, dorsal, side, and anterior views, $\times 1$, USNM 429257; 11a–c, dorsal, side, and anterior views, $\times 1$, USNM 429253; 12a–c, dorsal, side, and anterior views, $\times 1$, USNM 429252. Jurassic Homomyenmergel (Bathonian), Liesberg, Switzerland.

FIGURES 13–18.—*Cryptorhynchia pulcherrima* (Kitchin): 13a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 76009a; 14, dorsal view, $\times 1$, topotype, USNM 76009b; 15a,c, dorsal and anterior views, $\times 1$, (sectioned) 16a,c, dorsal and anterior views, $\times 1.8$, topotype, USNM 76009c (sectioned); 17a–c, dorsal, side, and anterior views, $\times 1.8$, topotype, USNM 76009a; 18, dorsal view, $\times 1.8$, topotype, USNM 76009b. Putchum Group (Upper Beds, Bathonian), Jumara, Kutch, India.

FIGURES 19–21.—*Prionorhynchia belemnitica* (Quenstedt): 19a–c, dorsal, side, and anterior views, $\times 1$, USNM 75857; 20a–c, dorsal, side, and anterior views, $\times 1$, USNM 429116; 21a–c, dorsal, side, and anterior views, $\times 1$, USNM 429115. Lower Lias; 19, 21, from Hirschberg, Hindelang, Germany; 20, from Arzo (Tessin), Switzerland.

PLATE 14

FIGURES 1–6.—*Globirhynchia subobsoleta* (Davidson): 1a–c, dorsal, side, and anterior views, $\times 1$, USNM 429418; 2a–c, dorsal, side, and anterior views, $\times 1$, USNM 104778; 3a–c, dorsal, side, and anterior views, $\times 1$, USNM 75580a; 4a–c, dorsal, side, and anterior views, $\times 1$, USNM 429417; 5a–c, dorsal, side, and anterior views, $\times 1$, USNM 75580b; 6a–c, dorsal, side, and anterior views, $\times 1$, USNM 429416. Inferior Oolite (Oolite Marl, Aalenian); 1, 4, 6, from Notgrove, near Cheltenham; 2, from Minchinhampton, Gloucestershire; 3, 5, from Wall's Quarry, Brimscombe, Stroud, England.

FIGURES 7–10.—*Granulirhynchia granula* (Upton): 7a–c, dorsal, side, and anterior views, $\times 1$, USNM 64420; 8a–c, dorsal, side, and anterior views, $\times 1$, USNM 429449; 9a–c, dorsal, side, and anterior views, $\times 1$, USNM 75603a; 10, dorsal view, $\times 1$, USNM 75603b. Inferior Oolite (lower part, Aalenian); 7, from Cheltenham; 8, from Stanley Hill; 9, 10, from Leckhampton Hill, Gloucestershire, England.

FIGURES 11–13.—*Flabellirhynchia lycetti* (Davidson): 11a–c, dorsal, side, and anterior views, $\times 1$, USNM 75591; 12a–c, dorsal, side, and anterior views, $\times 1$, USNM 123684; 13a–c, dorsal, side, and anterior views, $\times 1$, USNM 429422. Inferior Oolite (Oolite Marl, Aalenian); 11, from Notgrove, Gloucestershire; 12, from Leckhampton Hill, Gloucestershire; 13, from Minchinhampton, Gloucestershire, England.

FIGURES 14, 15.—*Burmishrhynchia* (*Hopkinsirhynchia*) *latiscensis* (Laurin): 14a–c, ventral, side, and anterior views of a dorsal valve, showing radulifer crura and septum, $\times 1.8$, topotype, USNM 429243; 15a,b, interior of a specimen, showing radulifer crura and septum, $\times 1.8$, topotype, USNM 429241. Lower Callovian, Chatillon-Sur-Seine, Cote d'Or, France.

FIGURE 16.—*Rhynchonelloidea subangulata* (Davidson): 16a,b, a dorsal valve eacavated to show interior, $\times 1.8$, USNM 429153. Inferior Oolite (Pea Grit, Aalenian), Crickley Hill, Cheltenham, England.

FIGURE 17.—*Burmishrhynchia* (*Hopkinsirhynchia*) *latiscensis* (Laurin): 17a–e, interior of a specimen, $\times 1.8$, topotype, USNM 429242. Lower Callovian, Chatillon-Sur-Seine, Cote d'Or, France.

PLATE 15

FIGURE 1.—*Septaliphoria arduennensis* (Oppel): 1a–c, dorsal, side, and anterior views, $\times 1$, USNM 429575. Oxfordian, from England.

FIGURES 2, 3.—*Septaliphoria? mourdoni* Laurin: 2a–c, dorsal, side, and anterior views, $\times 1$, USNM 429582; 3a–c, dorsal, side, and anterior views, $\times 1$, USNM 429583. Lower Callovian, Argences, Calvados, France.

FIGURE 4.—*Septaliphoria arduennensis* (Oppel): 4a–c, dorsal, side, and anterior views, $\times 1$, USNM 429572. Oxfordian, from Bourges (Cher), France.

FIGURES 5, 6.—*Septaliphoria astieriformis* Wisniewska: 5a–c, dorsal, side, and anterior views, $\times 1$, USNM 429579; 6a,b, dorsal and anterior views, $\times 1$, USNM 429580. Oxfordian, Kodrqb Koto, Czystochowy, Poland.

FIGURES 7, 8.—*Septaliphoria pinguis* (Roemer): 7a–c, dorsal, side, and anterior views, $\times 1$, USNM 429576; 8a–c, dorsal, side, and anterior views, $\times 1$, USNM 87228a. Astartien (Upper Oxfordian); 7, from Sobkow Kielc; 8, from Sulejow, Poland.

FIGURES 9–16.—*Burmishynchia (Hopkinsirynchia) latiscensis* (Laurin): eight dorsal valves showing variations of septalium and radulifer crura; all $\times 4.0$, topotypes; 9, USNM 429244; 10, USNM 429245; 11, USNM 429246; 12, USNM 429247; 13, USNM 429248; 14, USNM 429249a; 15, USNM 429249b; 16, USNM 429249c. Lower Callovian, Chatillon-Sur-Seine, Cote d'Or, France.

FIGURES 17, 18.—*Thurmannella obtrita* (Defrance): 17, side view of an excavated specimen, showing calcarifer crura, $\times 1.6$, USNM 306011f; 18a–e, another specimen excavated to show calcarifer crura, $\times 1.6$, USNM 306011g. Lower Oxfordian, Park on south side Ft. Benoit of Besoncon, France.

FIGURE 19.—*Pycnoria magna* Cooper: specimen excavated to show strongly secondary thickenings and very short septalium, $\times 1.8$, USNM 429467. Zohar Shales (Upper Bathonian to Lower Callovian, near base), NW side Hamaktesh Hagadol, southern Israel.

PLATE 16

FIGURES 1, 2.—*Bradfordirhynchia bradfordensis* (Buckman): 1a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429130; 2a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429131. Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England.

FIGURES 3–6.—*Cryptorhynchia pulcherrina* (Kitchin): 3a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429604; 4, dorsal view, $\times 1$, topotype, USNM 429605; 5, dorsal view, $\times 1.8$, topotype, USNM 429604; 6a,b, dorsal and anterior views, $\times 2$, topotype, USNM 429605. Putchum Group (Upper Beds), Jumara, Kutch, India.

FIGURE 7.—*Septaliphoria? mourdoni* Laurin: dorsal, side, and anterior views, $\times 1$, USNM 429584. Lower Callovian, Argences, Calvados, France.

FIGURES 8–10.—*Prionorhynchia belemnica* (Questedt): 8a–c, dorsal, anterior, and posterior views, $\times 1$, USNM 429118; 9a–c, dorsal, anterior, and posterior views, $\times 1$, USNM 429114; 10a–c, dorsal, anterior, and posterior views, $\times 1$, USNM 31055a. Lower Lias; 8, from Arzo (Tessin), Switzerland; 9, from Hindelang, Bavaria, Germany; 10, from Wuttenburg, Germany.

FIGURES 11–13.—*Burmihynchia (Burmihynchia) gutta* Buckman: 11a–c, dorsal, side, and anterior views, $\times 1$, H244333; 12a–c, dorsal, side, and anterior views, $\times 1$, H244610a; 13a–c, dorsal, side, and anterior views, $\times 1$, H244610b. Lower Bathonian, West Mount, Nardigangre, Northern Tibet, China.

FIGURES 14–16.—*Daghanirhynchia daghaniensis* Muir-Wood: 14a–c, dorsal, side, and anterior views, $\times 1$, USNM 429281; 15a–c, dorsal, side, and anterior views, $\times 1$, USNM 75665a; 16a–c, dorsal, side, and anterior views, $\times 1$, USNM 75665b. Lower Callovian; 14, from Bihendula; 15, 16, from Madashon, Somaliland (Somalia).

FIGURES 17, 18.—*Bradfordirhynchia bradfordensis* (Buckman): 17a,b, dorsal and anterior views, $\times 2$, topotype, USNM 429130; 18a,b, dorsal and anterior views, $\times 2$, topotype, USNM 429131. Bradford Clay (Upper Bathonian), Bradford-on-Avon, Wiltshire, England.

FIGURES 19, 20.—*Obsoletirhynchia diducta* (Buckman): 19a–c, dorsal, side, and anterior views, $\times 1$, USNM 31414a; 20a–c, dorsal, side, and anterior views, $\times 1$, USNM 31414b. Upper Bathonian, Ranville, France.

PLATE 17

FIGURES 1–5.—*Rhactorhynchia turgidula* Buckman: 1a–c, dorsal, side, and anterior views, ×1, USNM 268928a; 2a–c, dorsal, side, and anterior views, ×1, USNM 429369; 3a–c, dorsal, side, and anterior views, ×1, USNM 268928b; 4a–c, dorsal, side, and anterior views, ×1, USNM 268928c; 5a–c, dorsal, side, and anterior views, ×1, USNM 429370. Inferior Oolite (Upper *Trigonia* Grit, Upper Bajocian), Leckhampton Hill, near Cheltenham, Gloucestershire, England.

FIGURES 6, 7.—*Obsoletirhynchia rostrata* (Sowerby): 6a–c, dorsal, side, and anterior views, ×1, USNM 429357; 7a–c, dorsal, side, and anterior views, ×1, USNM 429356. Upper Bathonian, Campagnette Quarry, Ranville, France.

FIGURES 8–10.—*Obsoletirhynchia obsoleta* (Sowerby): 8a–c, dorsal, side, and anterior views, ×1, USNM 429332; 9a–c, dorsal, side, and anterior views of a juvenile specimen, ×1, USNM 75577b; 10a–c, dorsal, side, and anterior views of a very large specimen, ×1, USNM 429345. Upper Bathonian (*Eudesia cardium* zone); 8, from Amfreville, Calvados; 9, from Ranville; 10, Selongey, Cote d'Or, France.

FIGURES 11–13.—*Rhactorhynchia tumefacta* Buckman: 11a–c, dorsal, side, and anterior views, ×1, USNM 429387; 12a–c, dorsal, side, and anterior views, ×1, USNM 429386; 13a–c, dorsal, side, and anterior views, ×1, USNM 429385. Inferior Oolite (Upper *Trigonia* Grit, Upper Bajocian), Leckhampton Hill, Gloucestershire, England.

FIGURE 14.—*Aalenirhynchia walkeri* (Rollier): 14a–c, dorsal, side, and anterior views, ×1, USNM 429165. Inferior Oolite (Pea Grit, Aalenian), Leckhampton Hill, Gloucestershire, England.

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FIGURES 1–4.—*Globirhynchia tatei* (Davidson): 1a–c, dorsal, side, and anterior views, $\times 1$, USNM 429440; 2a–c, dorsal, side, and anterior views, $\times 1$, USNM 89801a; 3a–c, dorsal, side, and anterior views, $\times 1$, USNM 89801b; 4a–c, dorsal, side, and anterior views, $\times 1$, USNM 429441. Inferior Oolite; 1, 4, from the Oolite Marl (Aalenian), Frith Quarry, Painswick, Stroud; 2, 3, from the Gryphite Grit (Middle Bajocian), Scottsquar Hill, Painswick, Gloucestershire, England.

FIGURES 5, 6.—*Globirhynchia subobsoleta* (Davidson): 5a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429424; 6a–c, dorsal, side, and anterior views, $\times 1$, topotype, USNM 429425. Inferior Oolite (Oolite Marl, Aalenian), Cleeve Hill, Gloucestershire, England.

FIGURES 7–10.—*Globirhynchia tatei* (Davidson): 7a–c, dorsal, side, and anterior views, $\times 2$, USNM 429440; 8a–c, dorsal, side, and anterior views, $\times 2$, USNM 429441; 9a–c, dorsal, side, and anterior views, $\times 2$, USNM 89801b; 10a–c, dorsal, side, and anterior views, $\times 2$, USNM 89801a. Inferior Oolite; 7, 8, from the Oolite Marl (Aalenian), Frith Quarry, Painswick, Stroud; 9, 10, from the Gryphite Grit (Middle Bajocian), Scottsquar Hill, Painswick, Gloucestershire, England.

FIGURES 11–14.—*Pycnoria depressa*, new species: 11a–c, dorsal, side, and anterior views, $\times 1$, USNM 429551; 12a–c, dorsal, side, and anterior views, $\times 1$, USNM 429557; 13a–c, dorsal, side, and anterior views, $\times 1$, USNM 429558; 14a–c, dorsal, side, and anterior views, $\times 1$, USNM 429552. Upper Bathonian, Gebel Maghara, northern Sinai, Egypt.

FIGURES 15–18.—*Pycnoria magna* Cooper: 15a–c, dorsal, side, and anterior views, $\times 1$, USNM 429490; 16a–c, dorsal, side, and anterior views, $\times 1$, USNM 429491; 17a–c, dorsal, side, and anterior views, $\times 1$, USNM 429489; 18a–b, dorsal and side views, $\times 1$, USNM 429492. Upper Bathonian, Gebel Maghara, northern Sinai, Egypt.

FIGURE 19.—*Septaliphoria? mourdoni* Laurin: dorsal view, showing conjunct deltidial plates with rims around foramen and fine growth lines on shell, $\times 2$, USNM 429582. Lower Callovian, Argences, Calvados, France.

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