

# THE TRUE *RHYNCHONELLA*

by D. V. AGER

**ABSTRACT.** The well-known brachiopod genus *Rhynchonella* was erected by Fischer de Waldheim in 1809. It was founded on a new species *R. loxia* from the Upper Jurassic of the Moscow region. On the basis of topotype material, this species is here revised and redescribed with details of internal structures not previously studied. Other species which may belong to *Rhynchonella* s.s. are also discussed.

## INTRODUCTION

A DISTINGUISHED palaeontologist recently commented in a discussion: 'There is a real need for palaeontology to return to the habit of calling a spade a spade and a *Rhynchonella* a *Rhynchonella*.' The present author agrees with the general sentiment of this remark, but not with the particular palaeontological example. It is the customary complaint of the specialist in one field of palaeontology that the genera in other fields are too finely subdivided. Let us, by all means, be content to call a rhynchonellid a rhynchonellid, but a generic name of the scope of *Rhynchonella sensu lato* no longer has any real value. In the widest sense, as generally recognized by non-specialists, it is a vast 'dust-bin' genus ranging from Ordovician to Holocene in age and including several thousand species. More than 150 genera have been defined within this group, and even though many of these may not be acceptable, there are certainly many more undescribed. The group as a whole is now variously regarded as a superfamily, a suborder, or even an order. This at least gives an indication of the complexity of the group, which is only obscured by 'lumping'. In view of the time-range and the number of species involved, to call all these forms by the one name '*Rhynchonella*' is even less desirable than to call all the Mesozoic ammonoids by the one name '*Ammonites*'.

A genus is, of course, merely a convenient fiction. Such fictions in the rhynchonelloids are valuable in that they enable us to distinguish the numerous lines of species that evolved, side by side, from the Ordovician onwards. Among the Mesozoic rhynchonellids, it is impossible to make any progress towards understanding the complex pattern of evolution within the group, until many of the vast number of described species are grouped together. The use of Buckman's often-derided generic names for brachiopods is not therefore so much a matter of futile 'splitting' as of useful 'lumping'. For all these reasons, it is considered highly desirable to place on record exactly what was meant by *Rhynchonella* when the name was first proposed.

*Special note.* Throughout this paper Russian place-names (apart from Moscow) are spelt according to the modern rules of transliteration now accepted in both Great Britain and the U.S.A. Many variants of these spellings are to be found in the literature and on museum labels.

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## SYSTEMATIC PALAEONTOLOGY

Suborder RHYNCHONELLOIDEA Moore 1952  
 Superfamily RHYNCHONELLACEA Schuchert 1896  
 Family RHYNCHONELLIDAE Gray 1848  
 Subfamily RHYNCHONELLINAE Gill 1871

Genus RHYNCHONELLA Fischer 1809

- Rhynchonella* Fischer 1809, p. 35.  
*Rhynchonellis* Fischer, Keferstein 1829, p. 50.  
*Rhynyonella* Fischer 1843, p. 117.  
*Rhynchonella* Fischer, Rouillier and Vossinsky 1847, p. 394.  
*Rhynchonella* Fischer, Hall and Clarke 1894, p. 823.  
*Rhynchonella* Fischer, Buckman 1918, p. 57.  
*Eurhynchonella* Leidhold 1920, p. 352.  
*Rhynchonella* Fischer, Wisniewska 1932, p. 13.  
*Rhynchonella* Fischer, Gerasimov 1955, p. 217.

*Type species* (by original definition). *Rhynchonella loxia* Fischer.

*Emended diagnosis.* Small to medium-sized, everted rhynchonellids. Subtrigonal in outline, gibbous or convexi-planate and cynocephalous in lateral view. Subcircular, depressed and biconvex in neanic stage. Usually a high fold in dorsal valve, and strong, sharp uniplication in anterior commissure. Both valves smooth posteriorly, costae few and sharp, developing late. Fine radial striae on well-preserved specimens. Beak small, slightly incurved, hypothyrid to submesothyrid. Strong dental plates. No cardinal process. Shallow septalium between hinge-plates and short dorsal median septum. Crura short, radulifer type.

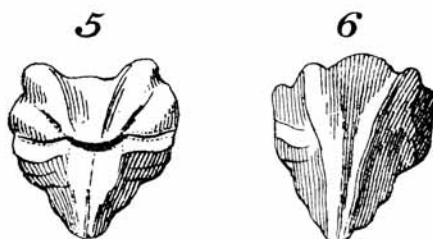
*Discussion.* Since *R. loxia* is almost the only species which can be attributed to *Rhynchonella* s.s. with any certainty, a generic description cannot be separated from that of the type species. Similarly, the generic diagnosis given above may require amendment if further species are confirmed.

Fischer de Waldheim (1809, p. 35) first proposed the name *Rhynchonella* in the course of describing some Jurassic fossils collected near Moscow. He distinguished the 'Rhynchonelles' as 'Térébratules à lobes intermédiaires si allongés qu'il en résulte la forme d'un bec. La pointe du bec est avec le trou du sommet dans le même plan.' He went on to define his new genus by the following characters, most of which are found in the majority of brachiopods: 'Coquille bivalve, régulière, à valves inégales, se fixant par un ligament ou un tube court; la plus petite valve perforée a son sommet peu proéminent, non recourbé; charnière à . . . dents.'

He clearly regarded his new species '*R. Loxiae*' (see text-fig. 1) as exemplifying his new genus. Fischer referred to *Rhynchonella* again in later publications (1825, 1830, 1837). In the last of these, however, he rejected what he then called his 'sous-genre de Térébratule' and reverted to Schlotheim's ubiquitous name '*Terebratula variabilis*' for his type species.

Keferstein gave '*Rhynchonellis*' as a genus in his catalogue (1829), apparently as a misreading of the Gallicized 'Rhynchonelles' in Fischer's later paper (1825, p. 6).

Later still Fischer (1843) changed his mind again and referred his Moscow form (which he misspelt '*Rhyngonella*') to Sowerby's species *Terebratula acuta*. This was followed by a long series of papers by Rouillier (1844, 1846, 1849) and Rouillier and Vossinsky (1847-8) in which the variations of Fischer's species and its relations were examined at length. In the last of these, the genus *Rhynchonella* may be said to have been discussed for the first time, and compared with *Terebratula*.



TEXT-FIG. 1. *Rhynchonella loxia* Fischer. Upper Jurassic, Tatarovop, near Moscow. Reproduction of original figures published by Fischer de Waldheim (1809, pl. 2, figs. 5, 6). 5 is the posterior view, 6 the anterior view, the ventral valve is uppermost in both cases,  $\times 2$  approximately.

The name *Rhynchonella* only crept into the non-Russian literature very slowly. It did not reach the French literature until it was accepted by d'Orbigny in 1847. It was brought to the notice of British palaeontologists by Davidson (1852, p. 65 and elsewhere) who provided a translation of Fischer's original remarks. The great German workers of the last century continued to use the name *Terebratula* for the rhynchonellids, though Quenstedt did use '*Rhynchonella*' for a few American Palaeozoic forms (1885, pl. 54) whilst curiously retaining *Terebratula* for a topotype specimen of Fischer's type species (ibid., pl. 53, fig. 54).

Rothpletz (1886) appears to have been the first to realize the need for finer definition within the great concourse of species that had gathered around the generic name *Rhynchonella*. He proposed thirty-five divisions which would be genera in the modern sense, though he did not give them generic names. Similarly, Buckman and Walker (1889) proposed eight groups among the Jurassic rhynchonellids and suggested the desirability of erecting a number of new genera or subgenera.

The first useful redefinition of *Rhynchonella* s.s. was made by Hall and Clark (1894, p. 823), who recognized the need '. . . for closer discriminations in this great group of species . . .'. Buckman, in his 'Burma Memoir' (1918), erected most of the Jurassic rhynchonellid genera now in use and redefined *Rhynchonella* s.s. in his own distinctive way (op. cit., p. 57), excluding from it practically all the forms that had previously been included.

Leidhold (1920) independently expressed the need for some grouping of the many rhynchonellid species, but he concentrated on different characters from those used by Buckman. He favoured the retention of the name *Rhynchonella* in a general sense only,

and proposed the name *Eurhynchonella* for the acutely-folded forms typified by *R. loxia*. This, however, is quite unacceptable under the rules of nomenclature.

Wisniewska (1932, p. 13) revised the genus with the aid of topotype specimens of *R. loxia* and gave details of various internal structures not previously described. This is the most valuable account of *Rhynchonella* s.s. at present available. Recently, Gerasimov (1955, pp. 218 et seq.), in reviewing the Mesozoic fossils of the Moscow region, recognized *Rhynchonella* in its modern restricted sense. He redescribed it briefly and figured a topotype specimen of the type species.

*Rhynchonella loxia* Fischer

Plates 1 and 2; text-figs. 1-4

- Rhynchonella Loxiae* Fischer 1809, p. 35, pl. 2, figs. 5, 6.  
*Rhynchonella Loxiae* Fischer 1830, pl. 23, figs. 8a, b.  
*Terebratula variabilis* Schlotheim, Fischer 1837, p. 147, pl. 23, figs. 8a, b.  
*Terebratula acuta* Sowerby, Fischer 1843, p. 117.  
*Terebratula aptycha* Fischer 1843, p. 124, pl. 4, figs. 7-9.  
*Terebratula acuta* Sowerby, Rouillier 1844, p. 889, pl. 22, figs. 1-10.  
*Terebratula aptycha* Fischer, d'Orbigny in Murchison *et al.* 1845, p. 482, pl. 42, figs. 22-26.  
*Terebratula Loxiae* Fischer, Rouillier 1846, p. 441.  
*Terebratula acuta* Sowerby, Rouillier and Vossinsky 1847-8, p. 375, pl. F, figs. 2, 3.  
*Rhynchonella Loxiae* Fischer, Eichwald 1866, p. 320.  
*Terebratula acuta* Sowerby, Quenstedt 1885, p. 693, pl. 53, fig. 54.  
*Rhynchonella loxia* Fischer, Hall and Clarke 1894, p. 822, pl. 42, figs. 1-3.  
*Rhynchonella loxia* Fischer, Buckman 1918, p. 57, pl. 18, figs. 30, 31.  
*Rhynchonella Loxiae* Fischer, Lewinski 1923, p. 45, pl. 8, figs. 3a-d.  
*Rhynchonella loxia* Fischer, Wisniewska 1932, p. 14, pl. 6, figs. 19, 20.  
*Rhynchonella loxiae* Fischer, Gerasimov 1955, p. 219, pl. 43, figs. 8, 9.

*Emended diagnosis.* Small *Rhynchonella* up to about 17 mm. long, 18 mm. wide, and 16 mm. thick. Trigonal in outline, ventral valve flat. High, sharp uniplication and fold, characteristically containing only one costa. Ventral sinus deep, somewhat U-shaped, often with median groove. Usually two costae on either side of fold. Beak small, slightly incurved.

*Type specimen.* Professor A. N. Sokolskaya has informed the author that Fischer's type specimen is lost (personal communication, January 1956). It was presumably destroyed with the rest of Fischer's collection in the great fire of 1812 when Moscow was occupied by the army of Napoleon Buonaparte (*vide* Fischer 1830, p. viii). It is not considered desirable to propose a neotype for a species of foreign origin and authorship, and although the species is of great importance, there has never been any confusion over its identity.

*Material and distribution.* Only a limited number of specimens of *Rhynchonella loxia* are available in Britain. Fischer originally recorded the species from Tatarovo, on the south bank of Moscow River about 10½ km. west-north-west of the Russian capital. The sections here were described in English by Murchison, Verneuil, and Keyserling (1845). No specimens are known to the author from Tatarovo; the vast majority of those mentioned in literature and available in collections are from Khoroshevo on the opposite bank of the river. From the geological map and from stratigraphical accounts such as

that mentioned above, it would appear that the uppermost Jurassic rocks are restricted to this side of the river.

There are a number of Russian examples of *Rhynchonella loxia* in the British Museum (Natural History) and a few in the Geological Survey Museum and in the Sedgwick Museum at Cambridge. Almost all of these which have detailed labels come from Khoroshevo. This is also the locality mentioned by Gerasimov (1955, p. 219) and is the origin of a number of specimens which he very kindly gave to the present author. A few specimens in the British Museum (Natural History) came from Mnevniky, about 2 km. farther south.

The age of the deposit concerned is variously recorded on British Museum labels as 'Oxfordian', 'Kimeridgian', and 'Portlandian'. According to Gerasimov (loc. cit.) it belongs to the J<sub>3</sub>vlg.s.ct division in the Russian nomenclature, i.e. the zone of *Craspedites subditus*. He also recorded *R. loxia* from other localities in the Moscow region at higher and lower horizons (the zones of *Craspedites nodiger* and *Kachpurites fulgens* respectively). These three zones form the upper part of the Volgian, that is the post-Middle Kimeridgian Jurassic, which cannot be correlated accurately with the west European successions (Arkell 1956, p. 8).

Lewinski (1923) described and figured *R. loxia* from the 'Bononian' (i.e. Volgian) of Brzostowka in Poland. Wisniewska (1932, p. 16) noted that this species is very rare in the Polish Upper Jurassic and only occurs in the Volgian in the vicinity of Tomaszów. Rozycki (1948) listed this species from the 'Bononian' in his valuable paper on the Upper Jurassic rhynchonellids of the Cracow-Czestochowa chain in Poland, but he did not discuss it otherwise, and it would not appear therefore to be a very important member of the fauna. The present author does not know of any records of this species from elsewhere.

*Description. External characters.* *R. loxia* is a small to medium-sized rhynchonellid. Specimens examined by the author showed the following range in dimensions:

	Minimum (mm.)	Mode (mm.)	Maximum (mm.)
Length . . . . .	8.0	10.1-10.5	13.8
Width . . . . .	8.6	12.1-12.5	16.8
Thickness . . . . .	6.6	11.6-12.0	15.5

In its earliest growth-stages, the shell is biconvex, depressed and circular in outline, like most Mesozoic rhynchonellids. With growth, the dorsal valve continues to be convex, whilst the ventral becomes almost flat. In the adult, the shell is subtrigonal in outline with rounded antero-lateral angles. The apical angle ranges from about 85° to about 115°, but is usually close to 100°. The valves meet anteriorly at a fairly obtuse angle, and some large specimens show a sudden decrease in growth-rate shortly before the cessation of growth (e.g. Sedgwick Museum specimen F. 9. 678).

The most distinctive features of the shell are the very sharp uniplication in the anterior commissure, and the very strong, sharp dorsal fold which begins to develop when the shell reaches about one-third of its ultimate size. The linguiform extension is correspondingly long and sharply trigonal, but the sinus is curiously shallow, having a flat floor usually with a central groove anteriorly. This contrasts markedly with the deep, sharp

sinus of *Homoeorhynchia acuta* (J. Sowerby) which was recently redescribed by the present author (Ager 1956, p. 20) and which otherwise closely resembles the present species in shape. Occasional specimens show the sharp uniplication without a correspondingly strong fold (see Pl. 1, figs. 2*b*, *c*). This appears to have resulted from the early cessation of shell-growth in the middle of the dorsal valve, so that the linguiform extension is folded back to fill the resultant embayment. Such specimens may be merely pathological oddities.

In lateral view the shell is usually trigonal in outline. The line from the beak along the crest of the fold makes an angle with the lateral commissure which ranges from about 45° to more than 90°; in the majority it is between 60° and 80°. The variations in all the above external characters were well described and figured by Rouillier (1844), when dealing with what were almost certainly topotype specimens of this species. It would be most unwise to attempt a variation study here without the benefit of personally collected material.

There is normally only a single costa on the crest of the fold, the sides of which are smooth. One specimen examined in the course of this study (Sedgwick Museum specimen F. 9. 797) has a second costa faintly developed in the fold. This may be transitional to the bi- and tri-costate forms discussed below. There are almost invariably two costae on either side of the fold, though traces of a third can also sometimes be observed. These costae are fairly sharp (the *tetrahedra* type of Ager 1956, p. viii) and appear just after the fold. Faint growth-lines are often visible.

In well-preserved specimens, both valves bear faint radial striae extending from the beak to the anterior margin (see Pl. 1, fig. 3*b*). Buckman (1918) placed considerable emphasis on this character, which he referred to as capillation. The faint lines seen on *R. loxia*, however, appear not to be true capillae, but merely an effect produced in slightly worn specimens due to the exceptionally fibrous nature of the shell. The lines are seen at all levels in the shell, but are less marked when it is relatively unworn. The calcite fibres lie at a very oblique angle and the shell readily flakes away. Since almost all of the specimens seen come from a single locality—Khoroshevo—it is possible (but not likely) that the above character is merely a secondary feature of local preservation. The same fine striae were observed in specimens of *R. rouillieri* (see below) from the nearby Lower Volgian locality of Mnevniki. It is probable that this character, and others discussed

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EXPLANATION OF PLATE I

In each case (*a*) is the dorsal view, (*b*) the lateral view, (*c*) the anterior view, and (*d*) the posterior view. BM = British Museum (Natural History), London; SM = Sedgwick Museum, Cambridge.

Figs. 1–3. *Rhynchonella loxia* Fischer. 1*a–d*, BM BB. 17578, ×3. Zone of *Craspedites subditus*, Upper Volgian, Khoroshevo, near Moscow. Well-preserved specimen showing the typical appearance of the species. Gerasimov collection presented by the author to the British Museum (Natural History). 2*b*, *c*, SM F. 9. 801, ×4. Labelled 'Oxford Clay'—probably Upper Volgian—Khoroshevo, near Moscow. An unusual form in which the uniplication is strongly developed but there is scarcely any dorsal fold. As a result there is a deep embayment in the dorsal valve, the lateral parts of which are half as long again as the centre part. 3*b*, *c*, SM F. 9. 674, ×4½. Labelled 'Portlandian'—probably Upper Volgian—Khoroshevo, near Moscow. A large well-preserved specimen in which the fold is developed to an exceptional degree. The fine radial striae or 'capillae' are clearly visible.

Figs. 4*a*, *c*. *Rhynchonella rouillieri* Eichwald. BM B. 2183, ×3. Labelled 'Kimmeridgian'—probably Lower Volgian—Mnevniki, near Moscow. An example of what is probably a closely related species with bi-costate fold, more upright beak and more depressed lateral profile.

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below, are seen because of the exceptionally good preservation of fossils in this neighbourhood, which often have the opalescent outer nacreous layer intact. This has been noted by several authors, including Fischer (1809, p. 35), Murchison *et al.* (1845, p. 236), and Arkell (1956, p. 492).

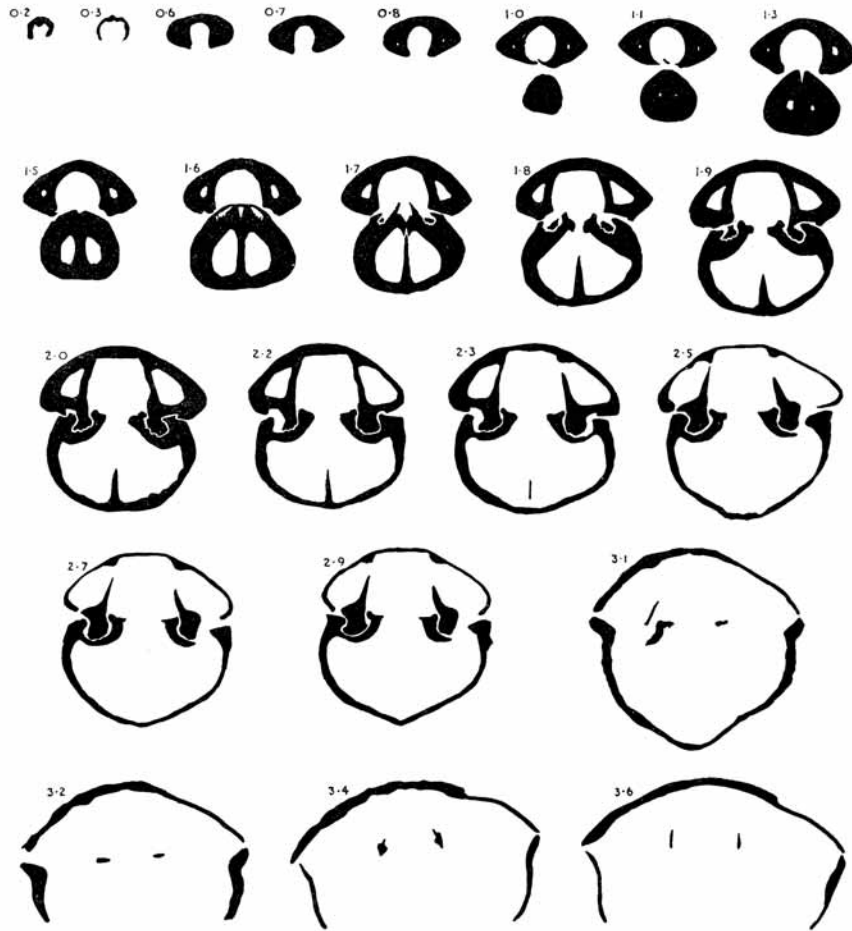
The beak is small and slightly incurved, with faint beak-ridges delimiting a wide, low interarea. The pedicle-opening is small, circular to elliptical and hypothyrid to submesothyrid. The deltidial plates are narrow, trigonal, and just conjunct.

*Internal characters.* Before describing the internal characters of the separate valves, it is necessary to mention a shell feature which is observable on the inner surface of both valves and on internal moulds. This is a *Schuppenpanzerstruktur* or 'shell-mosaic' produced by the proximal ends of the calcite fibres forming the shell wall (see Pl. 2, fig. 1). This was first described by Blochmann (1908) in three living rhynchonellid species; he did not think that it would preserve in fossils. Leidhold (1920) found it in a few Jurassic rhynchonellids from Germany. He argued that this character—in its various forms—was potentially of very great importance in the classification of fossil rhynchonellids. It therefore seems desirable to place on record the form of the scales in the type species of *Rhynchonella*. The 'scales' appear to be arranged in a somewhat haphazard pattern, but are constant in shape. Their outlines are much more pointed distally than in any of those figured by Blochmann (*op. cit.*, pl. 37) and Leidhold (*op. cit.*, pl. 4). It is doubtful if this character will ever be of any practical value in unravelling relationships, as it is only preserved in exceptional circumstances.

Owing to the limited number of specimens available in Britain, it was not possible to section many to study internal structures. Two specimens were ground following the techniques developed by Dr. H. M. Muir-Wood, and recently summarized by the present author (Ager 1956, p. iii). These are shown in text-figs. 2 and 3. Cellulose peels and photographs were taken of the sections as they were exposed, to act as a permanent record. It was also possible, through the kindness of Dr. Muir-Wood, to study a set of sections made under her direction at the British Museum (Natural History).

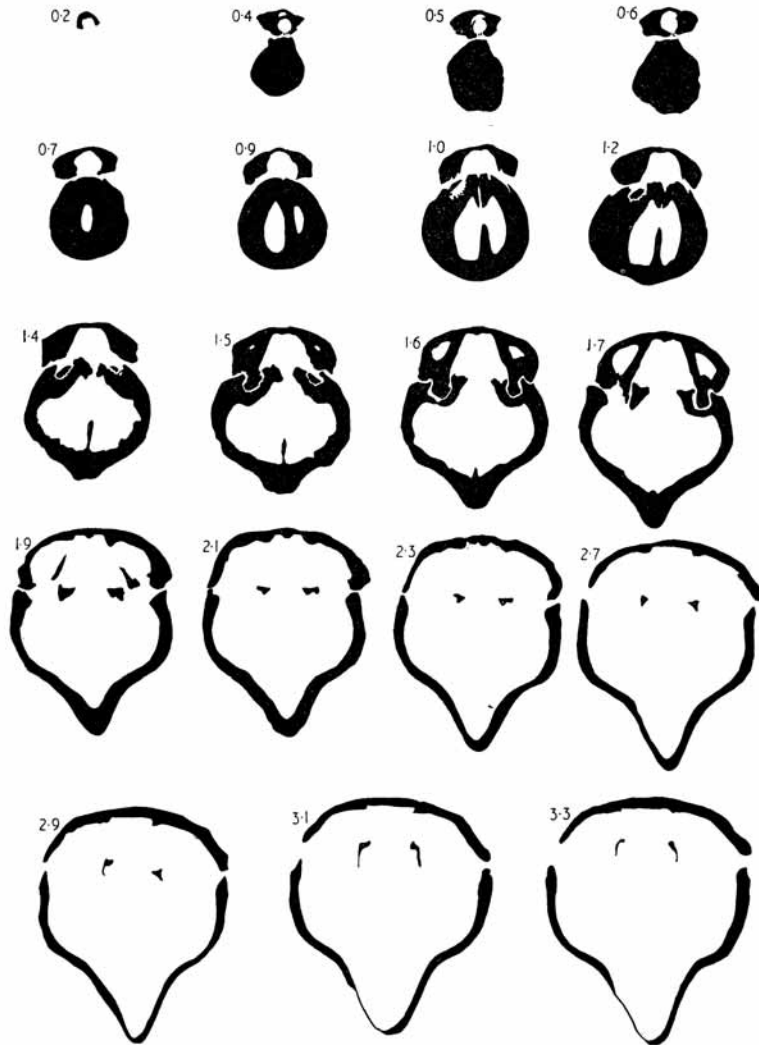
*Ventral valve.* A small pedicle-collar was observed in one specimen (see text-fig. 3). There are strong dental plates which diverge slightly both dorsally and anteriorly. Their forward edges are slightly inclined, so that in transverse sections they are seen to break away at, or just beyond, the plane of articulation (as defined by Ager, *op. cit.*, p. vii). The dental plates directly support strong, crenulated teeth. Short, blunt denticula are developed laterally. No septa or ridges have been observed in the ventral valve. The ventral muscle-scars are usually difficult to observe. The diductor muscle-scars form a somewhat elongated oval area, extending about one-third of the length of the valve in adult specimens. They completely surround the rather small impressions of the adductor muscles (see text-fig. 4). Small adjustor muscle impressions are sometimes visible laterally, and the muscle area as a whole is often surrounded laterally and posteriorly by ovarian impressions.

*Dorsal valve.* There is no cardinal process. The stout median septum breaks away from the septalial plates at an early stage and does not extend beyond the plane of articulation. A shallow septalium is developed between short hinge-plates. Both inner and outer socket-ridges are short, blunt, and fairly clearly demarcated. The main sockets are deep and crenulated; the accessory sockets are shallow and poorly defined. There are no distinct crural bases. The crura are of the radulifer type, short and flattened in the

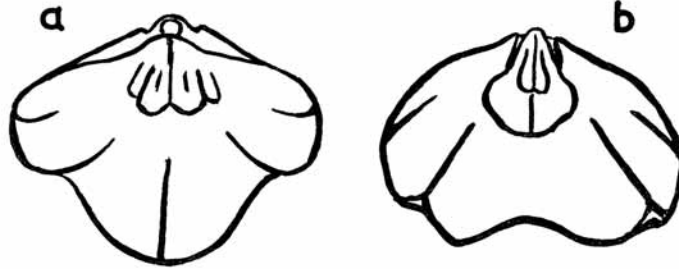


TEXT-FIG. 2. Camera lucida drawings of twenty-three transverse sections through the posterior part of a specimen of *Rhynchonella loxia* Fischer from the Upper Volgian of Khoroshevo, near Moscow. The top three rows show the form of the delthyrial and umbonal cavities in the ventral valve and the nature of the articulation. The bottom two rows show the form of the crura. The last three sections show part only of the dorsal valve. It is possible that much of the umbonal cavities and part of the delthyrial cavity may be filled anteriorly with secondary calcite or callus. Original length of the specimen 10.5 mm. The small figures refer to the distances in millimetres from the anterior point at which grinding was commenced. The crura finally disappeared at 3.8 mm. from this point. BM (B. 1325). All  $\times 4\frac{2}{3}$  approximately.





TEXT-FIG. 3. *Rhynchonella loxia* Fischer. Upper Volgian, Khoroshevo, near Moscow. A confirmatory set of transverse sections, comparable to those seen in text-fig. 2 but with some additional features. The pedicle-collar and deltidial plates are seen in the second, third, and fourth sections; the seventh and eighth sections show the form of the crura, which are distally expanded and which finally disappeared at 3.6 mm. from the posterior end. Author's collection J. 1067/1, presented by Dr. P. A. Gerasimov. All  $\times 4\frac{2}{3}$  approximately.



TEXT-FIG. 4. *Rhynchonella loxia* Fischer. Camera lucida drawings of an internal mould from the Upper Volgian, near Moscow, showing the arrangement of the muscle-scars. (a) dorsal valve, (b) ventral valve. Specimen in the Geological Survey Museum (register number FOR. 454), figured by Buckman (1918, pl. 18, fig. 30),  $\times 3$  approximately.

dorso-ventral plane; they curve sharply towards the ventral valve and are expanded distally. The dorsal muscle-scars take the form of narrow parallelograms set well forward. The anterior adductor scars are larger than the others and are placed on either side of the end of the median septum. Ovarian impressions are sometimes seen around the muscle area.

*Discussion.* Fischer's original description of this species (1809, p. 35) reads as follows: *Rhynchonella Loxiae*, mihi; valva major bidentata, margine terminali incurvo. . . . L'espèce de Tataroba que je décris, et qui a encore tout son nacre de perle, est petite, mais très distincte. Elle a 5 lignes de hauteur, et son bec courbé presque 7 lignes de largeur. Elle est bombée à côté du sommet, de sorte qu'elle représente parfaitement bien la tête d'un oiseau.

Fischer's original figures are reproduced in text-fig. 1. For the last sixty years the specific name has usually been spelt '*loxia*'. There is no indication in Fischer's papers of the origin of the name, unless it be intended to refer to the unusual beak of a genus of finches which includes the Crossbill (*Loxia curvirostra curvirostra* Linnaeus). Without any definite suggestion of a feminine attribution, the masculine ending is to be preferred, so the modern usage is adopted here.

The transverse sections published by Wisniewska (op. cit., fig. 3) look very different from those shown in text-figs. 2 and 3. This is because they appear to have been taken at right angles to the maximum length of the shell (i.e. the line from the beak to the highest point of the fold). The resultant plane is likely to be as much as  $45^\circ$  different from that shown here, and the effect is to give the appearance of a very small dorsal valve and low median septum, besides altering the shape of other structures. The present author has

#### EXPLANATION OF PLATE 2

Figs. 1-3. *Rhynchonella loxia* Fischer. 1, BM, BB. 17579. Zone of *Craspedites subditus*, Upper Volgian, Khoroshevo, near Moscow. *Schuppenpanzerstruktur* or 'shell-mosaic' on inner surface of dorsal valve near the hinge-line, showing the form of the scales. The black line at the top represents one-tenth of a millimetre. 2, BM B. 1325,  $\times c. 14\frac{1}{2}$ . Labelled 'Oxfordian?'—probably Upper Volgian—Khoroshevo, near Moscow. Cellulose peel of a ground specimen, 1.5 mm. from the posterior end showing the microscopic structure of the shell. 3, as fig. 2, but 1.6 mm. from the posterior end, showing the development of the septalium and sockets in the dorsal valve.

discussed elsewhere (Ager 1956, p. iv) his reasons for preferring the orientation used here. It should be remembered that Wisniewska's paper was published before Dr. H. M. Muir-Wood introduced the serial grinding technique to British Mesozoic brachiopod literature.

It is not possible to discuss in detail the relationships of this species to other members of the genus *Rhynchonella* s.s., since the majority of the latter are quite unknown in Britain. The distinctiveness of *R. loxia* would seem to lie particularly in its sharp, unicostate fold.

In general it may be said that *R. loxia* is unusual, but by no means unique, in its external appearance. In this it is perhaps somewhat unfortunate as the type species of a major group of brachiopods. Internally, however, it is very much the 'average' rhynchonellid. It is probably close to the main stock of rhynchonellids which persisted from the Silurian to the present day with very little change in the essentials of their shell structure. These are all impunctate, everted forms with short, radulifer-type crura and divided hinge-plates separated by a septalium (or cruralium) which is supported by a short median septum. There is no cardinal process and no median septum in the ventral valve. Such forms may be regarded as belonging to the subfamily Rhynchonellinae. Other forms, with features such as inverted shells (e.g. *Rhynchonellina*), cardinal processes (e.g. *Hemithyris*), fused hinge-plates (e.g. *Prionorhynchia*) or more complex crura (e.g. *Orbirhynchia*) may require new subfamilies. However, the classification of the rhynchonelloids is at the moment extremely incomplete and illogical, and much work needs to be done before it is desirable to erect further categories.

*Rhynchonella* s.s. may be regarded as a slightly specialized offshoot of the main stock of rhynchonelloids, its specialization taking the form of a paucicostate, cynocephalous shell, homoeomorphic with those belonging to *Pugnax*, *Homoeorhynchia*, and other genera.

#### POSSIBLY RELATED SPECIES

The following nominal species and subspecies have been associated with *R. loxia* by various authors and require individual consideration. Those marked with an asterisk are regarded by the author as probably belonging to *Rhynchonella* s.s., though it is by no means certain that they are all specifically distinct, and their internal characters have not been studied.

##### *Homoeorhynchia acuta* (J. Sowerby)

This species, which belongs to the Upper Pliensbachian (Middle Lias) of western Europe, has often been confused with *R. loxia*, as it was by Fischer himself (1843), Rouillier (1844), and Quenstedt (1885). The genus *Homoeorhynchia* has recently been revised (Ager 1956, p. 26) and its separation from *Rhynchonella* was there discussed. It is clear that, whatever may be the relationship between the two genera, the two species are quite distinct, though homoeomorphic in generalities. Similar homoeomorphs can be found among Palaeozoic rhynchonellids of the *Pugnax* group.

##### \**Rhynchonella* *bidens* and \**R. triplicata* (Phillips)

These names have been used by many authors for any sharply folded rhynchonellids with bi- or tri-costate folds respectively. They have recently been shown by the present

author (op. cit., p. 40) to be synonyms of the west European Lower Jurassic form *Rhynchonelloidea lineata* (Young and Bird). Rouillier and Vossinsky (1847) used the above names for Upper Jurassic rhynchonellids near Moscow associated with *R. loxia*. They recognized that the bi-costate form was merely a variant of the tri-costate one and suggested, as an alternative to 'bidens' the name *Terebratula triplicata subacuta* (op. cit., p. 376). There is, however, no more than a superficial resemblance to Phillips's Middle Liassic brachiopods from Yorkshire, and these Russian forms may be referred to the next species.

\**Rhynchonella rouillieri* Eichwald

This name was proposed by Eichwald (1868) for the Russian Upper Jurassic forms which Rouillier and Vossinsky had referred to *T. bidens* Phillips. Later (1869, p. 1286) he came to the conclusion that the tri-costate forms called *T. triplicata* by Rouillier also belonged here.

Wisniewska (1932, p. 16) revised *R. rouillieri* and included it in *Rhynchonella* s.s. Gerasimov (1955, p. 218) also did this and showed it to be a close relation of *R. loxia*, with *R. rouillieri* var. *subacuta* Rouillier (see above) as the immediate predecessor of the type species. He also proposed a new name for the tri-costate variants—*R. rouillieri* var. *biplicata*.

Morphologically, *R. rouillieri* would seem to graduate into *R. loxia*, but Gerasimov has shown that it preceded the type species in time, being recorded from various levels in the Lower Volgian, whereas Fischer's species is strictly Upper Volgian. It differs from *R. loxia* in its larger size, more upright beak, and (most obviously) in the presence of two or three costae on its pronounced fold. The relationship between the two species may be compared with that between *Homoeorhynchia acuta* (see above) and *H. cynocephala* (Richard) (see Ager 1956), but whereas in *Rhynchonella* the forms with bi- and tri-costate folds preceded the uncostate type, in *Homoeorhynchia* the relationship was the other way round. Radial striae have been observed in examples of this species from Mnevniki and there can be no doubt at all that it belongs to *Rhynchonella* s.s. A typical example is shown on Pl. 1, figs. 4a, c.

\**Rhynchonella malbosi* Pictet

Gerasimov observed (1955, p. 218) that *R. rouillieri* var. *biplicata* appeared to be very like *R. malbosi* var. *chomeracensis* Jacob and Fallot of the French Portlandian. He also compared the latter with *R. loxia*. In the absence of more evidence, it is impossible to be certain on the point, but this species may well be a contemporary western relation of the Russian forms and may also be related to *R. portlandica* Blake (see below).

\**Rhynchonella lewinski* Wisniewska

This is another bi-costate, sharply folded form which can reasonably be regarded as belonging to *Rhynchonella* s.s., though Wisniewska (1932, p. 18) expressed doubts about this when she first described it, because of her lack of well-preserved specimens. She recorded it from the Volgian (Bononian) of Poland.

*\*Rhynchonella aptycha* (Fischer)

This form was named by Fischer in 1843 (p. 124). He referred to it as a small version of 'acuta' (that being the name he was then using for *R. loxia*). It is obvious from his figures (op. cit., pl. 4, figs. 7-9) that it is merely a juvenile version of the type species, as was recognized by Rouillier (1844). D'Orbigny (in Murchison *et al.* 1845) used this name instead of *R. loxia*, apparently having overlooked Fischer's earlier paper.

*\*Rhynchonella canard* Fischer

In his 1809 paper Fischer distinguished *R. loxia* from two other species which had been figured by Bruguière (1797). Both of these Fischer included in *Rhynchonella*, but they appear to have been overlooked by later workers. The name *R. canard* was given to a rhynchonellid with a sharp, bi-costate fold. Bruguière has listed this as undetermined (op. cit., pl. 245, figs. 6a-c). This might possibly be conspecific with *R. rouillieri* but this is now impossible to prove.

*\*Rhynchonella aigle* Fischer

This is the second of the two forms named by Fischer from Bruguière's figures. It has a sharp, simple fold comparable to that of *R. loxia*. Fischer may have made a mistake here, for the figures he quotes (Bruguière, pl. 246, figs. 1a, b) are clearly identified by Bruguière (op. cit., p. 151) as *Terebratula spirifera* Lamarck. Fischer may have intended to refer to pl. 245, figs. 7a, b (i.e. the previous figures) which show a similar form, but which were noted by Bruguière as undetermined, like its predecessor discussed above. Again this form may be conspecific with some well-known species.

'*Terebratula*' *variabilis* Schlotheim

This is the most ubiquitous of all names in Mesozoic brachiopod studies. It was used by Fischer (1837, p. 147) to replace his own taxon *Rhynchonella loxia* and was subsequently used by other authors in this context. The original figures bear no resemblance whatever to *Rhynchonella* s.s. and the only specimens remaining in Schlotheim's collection with this name appear to belong to the genus *Gibbirhynchia* Buckman. The present author proposes to discuss this name further in the second part of his monograph of Liassic rhynchonellids.

'*Rhynchonella*' *subvariabilis* Davidson

This is the only species, apart from *R. loxia*, which Buckman (1918, p. 57) included in *Rhynchonella* s.s. This was founded chiefly, it would seem, on Davidson's remark (1852, p. 81) that its surface is '... minutely longitudinally striated'. Apart from this one character (which may not in fact be homologous), *R. subvariabilis* is a multicostate form quite unlike *R. loxia* in general appearance. Its inclusion in *Rhynchonella* is probably therefore quite unjustified.

*\*Rhynchonella portlandica* Blake

This is the only rhynchonellid known to the author in British strata comparable in age to the Volgian, and probably the only British rhynchonellid referable to *Rhynchonella* s.s. It was described by Blake (1880, p. 234) from the Portland Sand of the Dorset coast.

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and his figured specimens are preserved in the British Museum (Natural History) (register numbers B. 52283-5). It is very much like *R. loxia* in general shape, being smooth with a strong, sharp dorsal fold and uniplication, and a flat-bottomed ventral sinus. Buckman (1918, p. 57) rejected it as a member of the genus *Rhynchonella* because of the absence of what he regarded as the all-important radial striae. This may be merely a matter of preservation. The syntypes differ from *R. loxia* in having a more convex ventral valve, a larger and more incurved beak, and usually three or four lateral costae on each side. Like other rhynchonellids of this form, *R. portlandica* includes variants having two or three costae in the fold. It is perhaps noteworthy that this species is associated on the Dorset coast with the ammonite *Zaraiskites*, which occurs also in the Lower Volgian of Mnevniki, near Khoroshevo.

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This paper is a 'pre-Treatise' publication in connexion with the author's contribution on the Mesozoic and Cainozoic rhynchonelloids for the 'Treatise on Invertebrate Paleontology' at present being published in the U.S.A.

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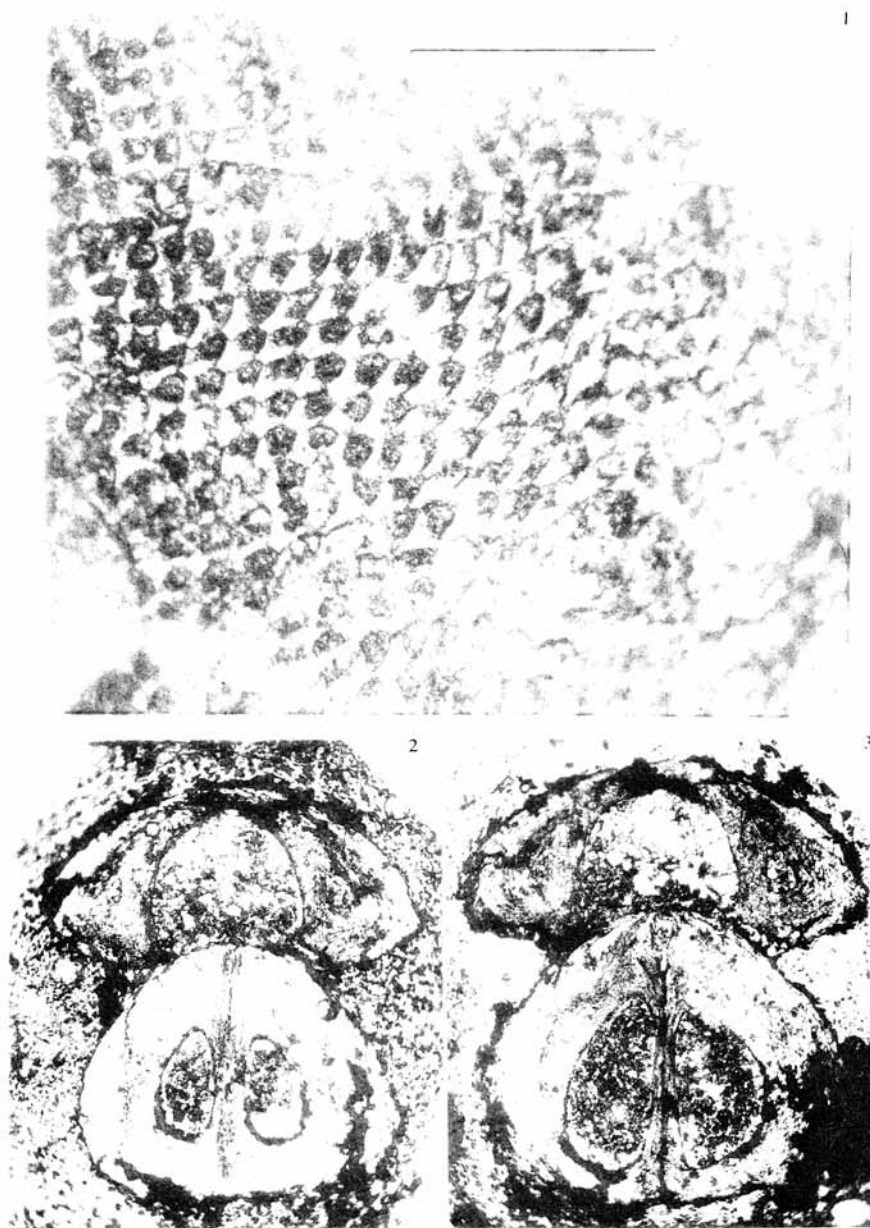
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