

RHAETIAN ARTICULATE BRACHIOPODS OF EUROPE

BY

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ABSTRACT

With the exception of the extremely rare thecideids and thecospirids, all the articulate brachiopods from the Rhaetian of the Western Alps of France and Switzerland, the Northern Alps of Austria and Bavaria, the Lombardy Alps of northern Italy, the Carpathians of Slovakia, the Tatra of Poland and the Persani Mts. of northern Rumania are revised in this thesis. The work has been based on collections made by the writer from the whole of this area with the exception of the Western Alps. From eight superfamilies, thirty four species are described. Their relationship to those from the Norian of Slovakia and eastern Bulgaria is discussed, also using collections made by the writer, and the recently revised Norian fauna of the southern Soviet Union is considered throughout. New taxa comprise seven species, four genera and one subfamily.

The composition and status of all families, subfamilies and genera is discussed in detail. In particular the content of the rhynchonellid subfamilies, Cirpinae, Rhynchonellinae and Tetrarhynchiinae is considered at length and several subfamilial divisions are suggested.

Serial transverse grinding has been used to study the internal structure of all but the rarest species and photomicrographs accompany detailed drawings made from acetate peels.

The ecology of many of the species is discussed and the adaptation of Austrirhynchia cornigera to orientation in currents is proposed.

As a preliminary to the palaeontological study, the stratigraphy and status of the Rhaetian stage itself is discussed in detail. It is considered that the lower boundary may be usefully lowered to coincide with the disappearance of Monotis.

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INTRODUCTION

PREVIOUS RESEARCH

It is now well over a century since PETZHOLDT (1843) published the first figures of a Rhaetian brachiopod, Spiriferina jungbrunnensis (now a nomen oblitum of Zugmayerella uncinata). Since then, although almost all the first descriptions have appeared in only two monographs, they have involved the first application of techniques which have revolutionised brachiopod systematics.

ZUGMAYER, in 1880, described in detail how transverse parallel sections could be made using guide lines on the ventral and dorsal valves. His five transverse serial sections of Oxycolpella oxycolpos are the first known and together with those published by BITTNER (1898) of another Rhaetian species, Carapezzia geyeri (see plate A herein), were not to be excelled in quality for several tens of years. ZUGMAYER illustrated the internal structure of each of the species he described with what he termed a 'Cardinal-Schliff'. This constantly oriented section lies close to the plane of articulation and was carefully chosen to reveal the maximum internal detail. The results he obtained enabled ZUGMAYER to make the first divisions of the catch-all genera Terebratula and Spiriferina.

Similarly, calcination of the shell by burning, a technique commonly attributed to BUCKMAN (1918), who employed it to reveal muscle scars, was used to considerably better purpose by ZUGMAYER (1880) to accentuate the contrast of the internal elements of his ground specimens (see plate 8, fig.3 herein).

However, it was SUESS, professor of geology in the University of Vienna and one of the leading scientists of the nineteenth century, who laid the foundation for the study of the alpine Rhaetian and its brachiopod fauna. Born in London, SUESS published his 'Brachiopoden der Küssener Schichten' (1854) at the age of twenty three. His later papers with OPPEL (1856) on the equivalence of the intra and extra-alpine Rhaetian beds, and with MOJSISOVICS (1868) on the litho-faunal facies of the Rhaetian, are fundamental. Remarkably, SUESS's wider interests led him to initiate the scheme

whereby Vienna today receives her water supply from the Alps, and to become a leading Liberal member of the Austrian Parliament (see GREGORY 1915).

Prior to SUESS's monograph only three Rhaetian species had been described: Austrirhynchia cornigera and Calcirhynchia subrimosa by SCHAFHAUTL (1851), and Zugmayerella uncinata by the same author two years later. No further original descriptions followed for twenty six years until ZUGMAYER (1880) published the results of his work in the Piesting Tal region near Vienna. This area has a remarkably rich and diverse Rhaetian fauna and must inevitably have become a keystone in its study. ZUGMAYER, living in the Piesting Tal, was able to devote considerable time to collecting. This coupled with his advanced technique, discussed above, and the work of SUESS and MOJSISOVICS (1868) on the facies of the Rhaetian, enabled ZUGMAYER to produce a monograph including not only ten new species but in addition, a table of the facies distribution of the twenty six species then known.

As a consequence of ZUGMAYER'S thorough study BITTNER felt able to leave the Rhaetian fauna out of his 'Brachiopoden der alpinen Trias' (1890). However, he included short descriptions and figures of specimens from the late Norian of Drnava (south Slovakia), which may be attributed to Rhaetian species. Similarly BITTNER's several papers on the Norian fauna of north east Turkey (1891, 1892a, 1895) involve Rhaetian species.

Some seventy years after ZESJSZNER (1845) figured Rhaetina gregaria as SOWERBY'S Terebratula biplicata, GOMTEL (1917) produced his monograph covering the entire Rhaetian invertebrate fauna of the Slovakian Carpathians and the Polish Tatra. However, despite lengthy collecting, he was unable to add any further species to those recognised by SUESS and ZUGMAYER (Spirifer - ina nov.sp. = Zugmayerella koessenensis herein). His work, like that of PALFY (1925) who listed the Rhaetian fauna of the Apuseni mts. in north west Rumania, PREDA (1962) who gave brief descriptions of a few species, and DOUGLAS'S description (1929) of an apparently Rhaetian fauna in Iran, is most valuable in providing evidence of the constant character of the fauna.

Many Rhaetian species have also been described by two Soviet authors, MOISSEIEV (1927, 1932, 1947) and DAGIS (1963) from the Upper Triassic of the Caucasus, Crimea and Pamirs, and by MAHEL (1958) from central Slovakia.

Some controversy exists over the age of the faunas described by these authors but according to the interpretation held here (see Stratigraphy), the highest beds they deal with are Norian. However, many of the genera erected by DAGIS are applicable to Rhaetian species. DAGIS has also monographed the brachiopod fauna from the Upper Triassic of Siberia (1965) and his are the pioneering works of a modern revision of the Triassic brachiopods.

OBJECT OF STUDY

During the greater part of Triassic time marine sedimentation in Europe was restricted to the area now represented by the Alpine chain and the Alps of the Dinarides. Northern Europe, later to be covered by the shallow sea of the Jurassic, was desert. As a result, from the early days of palaeontology attention has been concentrated on the prolific and easily collected Jurassic fauna occurring in tectonically undisturbed areas, whilst the Triassic fauna, found only in discontinuous outcrops in difficult terrain, has been neglected.

That the fauna is rich is clear from the work of BITTNER (1890, 1892 etc.) who described over a thousand species in the last years of the nineteenth century. As the brachiopod specialist of the Austro-Hungarian Survey, BITTNER was fortunate in receiving collections made by geologists mapping over the whole of alpine Europe. However, although he was familiar with the technique of serial grinding, unsuitable preservation and lack of time only allowed him to apply it to a few of the species he described. Therefore the classification of Mesozoic brachiopods, now based on internal structure, has been guided by groupings of Jurassic genera with little regard for their Triassic ancestors. The lines of descent of even the most important Jurassic stocks are hazardously speculative, and differences of approach and nomenclature have grown up between Mesozoic and Palaeozoic workers.

Although the necessity of modern work on Triassic forms has often been commented on (e.g. STEHLI, 1956a, 1965, and AGER, 1965) it was only when DAGIS (1963, 1965) described the Norian faunas of both ^{the} south west and north east Soviet Union that such work began to appear. In providing a revision

of the alpine Rhaetian fauna the aim of this thesis is to make a link to the Jurassic and to help in building a well defined base for further revision in the Triassic.

FIELD PROGRAMME

During the first winter of this study the whole of the Rhaetian outcrop as it appeared on the 1:75,000 Geologische Spezialkarte der Republik Österreich (formerly - der Österreichisch-ungarischen Monarchie): geol. Bundesanst., Wien, 1898, was drawn onto 1:50,000 topographic maps (Wanderkarte, Bundesamt für Eich- u. Vermessungswesen, Wien). This covered the Rhaetian of present day Austria, Slovakia and Poland. Maps of various scales accompanying papers on aspects of the geology of Bavaria were similarly used for tracing the Rhaetian in Bavaria (topographic maps - 1:25,000, Bayer. Landesvermessungsamt Munich, 1959). Extensive notes were also made from a large number of papers which cited Rhaetian brachiopods in their faunal lists. These, together with the information gained during an early, preliminary examination of localities in Austria and museum collections in Vienna and the B.M.N.H., enabled a field programme covering the richest and most interesting localities to be planned for the following summer.

In the course of five months field work, with additional help from members of Institutes and Universities, a basic collection was amassed from the Rhaetian of the Northern Alps of Austria and Bavaria, the Southern Alps, the Carpathians of Slovakia and the Tatra of Poland, together with important comparative material from the late Norian of Drnava in Slovakia.

During the following winter contact was made with members of institutes and Universities in Italy, Rumania and Bulgaria. As a result field work was carried out in these countries in the summer of 1965, in addition to further investigation in the Northern Alps, particularly of type localities in the Vienna region.

DEVELOPMENT AND DISTRIBUTION OF THE MARINE RHAETIAN IN EUROPE.

NOTE

The map (enclosure 1) to accompany this discussion was prepared from the Carte géologique de l'Europe (Int.Geol.Congr., 1st. edn., 1881-1913, Berlin:Dietrich Riemer; and 2nd.edn., 1933, Pruessische Geol.Landes.) and shows the whole of the Upper Triassic. The Rhaetian alone is too restricted to be drawn on this scale but follows essentially the same distribution pattern. The outcrops indicated near Pisa and Perugia are marked as 'Rhaetic' on maps of the first edn. but as middle Triassic on the second. They are included here since they are probably the site of supposed Rhaetian species mentioned in the text. The Upper Triassic of Yugoslavia, unimportant for Rhaetian brachiopods, is drawn from the second edition on which the bulk of the Triassic is undivided. Certainly the Upper Triassic of Yugoslavia is more extensive.

The terminology of the Alps used here and throughout this thesis is that employed by German geologists : the French and Swiss Alps are referred to as the Western Alps; the Austro-Bavarian Alps as the Northern Alps (i.e. the Northern Calcareous Alps = the Eastern Alps of French geologists), and the Gailtaler Alps and the Karawanken of S.Austria as the Southern Alps (i.e. the Southern Calcareous Alps). The Southern Alps sensu van BEMMELLEN (1957) are here termed the Dinarides.

The Transylvanian Alps are equivalent to the Southern Carpathians of some authors.

The palaeogeography of Mesozoic sedimentation in alpine Europe is difficult to disentangle from the complications of tectonics. The Northern Alps of Austria and Bavaria have been the principal area studied for this thesis and two views of their history prevail: according to the ultra-nappist theory, now the most favoured, they have their roots adjacent to the Southern Alps and have been thrust over the alpine core to their present position. The tectonic windows of the Engadine and Tauern thus represent the Western Alps of Switzerland and France. On the other hand the autoch -

tonists argue that the Mesozoic of the Alps accumulated north of the alpine core in a broad basin which has since only been narrowed by thrusting.

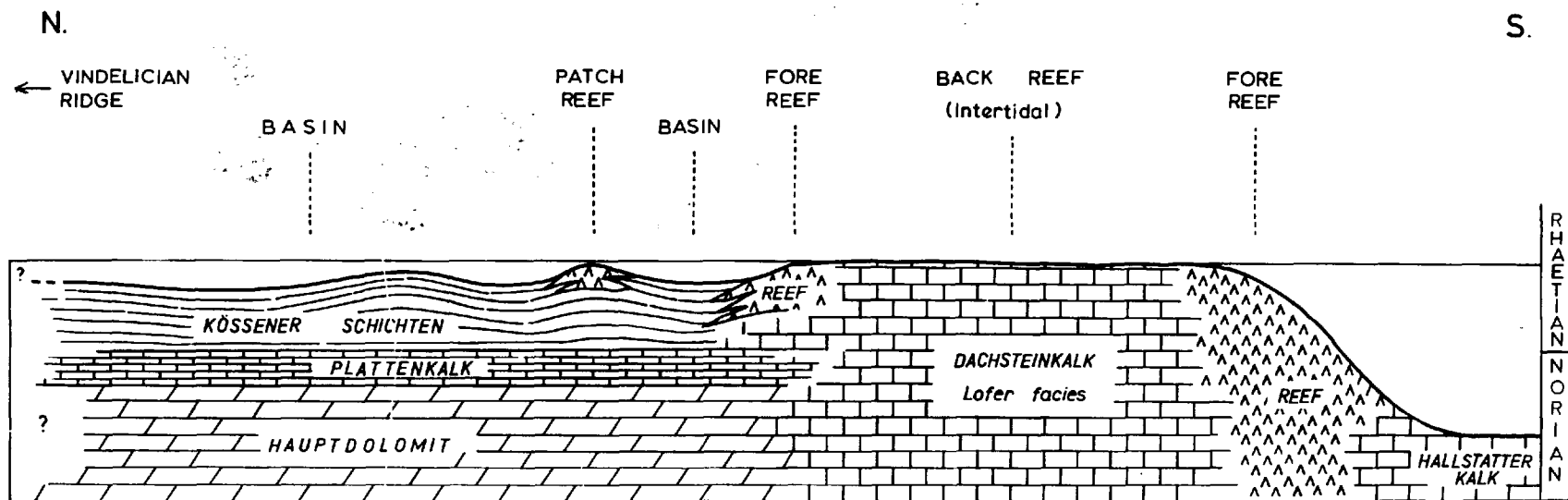
Despite these widely differing hypotheses the essential pattern of Triassic sedimentation in Europe is not difficult to recognise.

To the north of the Alps desert conditions prevailed during Triassic time and the red sandstones and marls of the Lower and Upper Triassic are broken only by the widespread transgression of the Muschelkalk. In the Alps and to the south occur the thick deposits of the Tethyan geosyncline. One of GÜMBEL's major contributions to alpine geology was to explain these contrasting areas of deposition through the hypothesis that the Alpine and extra-Alpine regions were separated by an emergent zone now commonly termed the Vindelician Swell. This belt lies to the north of the present Alps, extending westward through Bavaria from the Bohemian massif, through the external massifs of the Swiss and French Alps, Corsica and possibly represented in Spain by the coastal massifs (CAREY 1958).

The late Triassic was marked in Northern Europe by a transgression during the Rhaetian which introduced the marine régime of the Jurassic. The deposits of this age in central and northern Germany, France, Britain, Poland and Scandinavia are thin and remarkably poor in such fossils as corals and brachiopods which characterize most Mesozoic marine deposits. ELLIOTT (1953) interpreted this Swabian facies of the Rhaetian as the sediments of a shallow landlocked sea of diminished salinity.

Facing the Tethys to the south at this time was a massive barrier-reef (text-fig. 1), the Dachstein Riffkalk or Hochgebirge-Korallenkalk, and its fore-reef deposits interfinger with the red ammonite bearing Hallstatt limestones. Opinion differs over the nature of the environment in which these limestones were deposited and ZAPPE (1959) summarized several of the arguments. FISCHER (1964) believed them to be the sediments of a deep, starved basin.

Northward in the backreef area occur the Dachstein limestones. FISCHER (1964) investigated this facies in detail in the Salzburg area. Recognising shrinkage phenomena, algal mats and weathering mantles FISCHER interpreted these limestones as cyclothemic lagoonal deposits periodically



Diagrammatic cross-section through late Triassic facies in the Northern Alps (Salzburg region). After FISCHER (1964).

exposed to erosion. The fauna of this region was restricted and consisted mainly of megalodont lamellibranchs. In two places FISCHER reported Norian brachiopods in neptunian dykes which probably indicate tidal channels of near normal salinity. In the Norian part of the Dachsteinkalk the limestones, forming a zone 20 or 30kms. broad, pass gradually into the massive Hauptdolomit and thence to the shore of the Vindelician Swell. Mr. D. J. SHEARMAN (verbal communication 1966) is of the opinion that the conditions of sedimentation in the late Triassic in this area may have been similar to those on the shores of the Persian Gulf at present.

In the late Norian the Hauptdolomit was superseded by the Plattenkalk, a variably dolomitic or calcareous sequence of platy limestones interspersed with shaley partings. The Rhaetian is then marked by the development of a shallow basin and the Plattenkalk is overlain by marly limestones of the Küssener Schichten.

In the middle and late part of the Rhaetian the southern edge of the basin was rimmed by small reefs dividing it from the Dachsteinkalk intertidal zone, and small patch reefs occur on local swells within the basin. It is in this basinal region commonly in the neighbourhood of the reefs that the brachiopod fauna occurs. Text-plates 1-5 show the beds as they appear in the field.

The sedimentation pattern outlined above is reflected in the type region of the Rhaetian in the Rhätikon at the extreme western tip of the Northern Alps. PUGIN (1964) considered the succession and fauna there in detail and the following is a summary:

Above the massive Hauptdolomit of the Norian occurs some 500-700ms. of thin bedded, partly calcareous, partly dolomitic Plattenkalk. This is conventionally assigned to the Norian as it was by GÜMBEL (1861).

Transitionally superseding the Plattenkalk is a series of dark shales, limestones and occasional coral beds of the Rhaetian Küssener Schichten. Its thickness is variable between 150 and 600ms. and here, like everywhere else in the Alps, it is tectonically plastic and difficult to measure.

Succeeding the Küssener Schichten are 0-100ms. of massive bedded, light

Text-plate 1.



200 m

The arrow indicates collection point Stp.1 and the site of text-plate 2.

The west side of the Steinplatte reef from Grünwaldspitz, showing the massive reef and the bedded fore-reef limestones.

Text-plate 2

Medium bedded calcarenites at point Stp.1 on text-plate

1. Certain of these beds are rich in Rhaetina pyriformis with occasional Austrirhynchia cornigera and Fissirhynchia fissicostata.

Text-plate 3

Medium bedded calcarenites some 6 kms. to the north of the Steinplatte reef, also notable for Rhaetina pyriformis.

2



3



Text-plate 4

Flaggy to medium bedded calcilutites intercalated with shale in the Lofer Graben, between Kössen and Reit im Winkl, about 10 kms. north west of the Steinplatte reef. These beds are notable for burrowing and aligned pelecypods.

Text-plate 5

Incursion of calcarenites into the shale - calcilutite sequence of text-plate 4. Associated with these beds are the brachiopods Fissirhynchia fissicostata, Oxycolpella oxycolpos and Austriirhynchia cornigera. Above the upper - most limestone bed colonies of Calcirhynchia subrimosa occur.

4



5



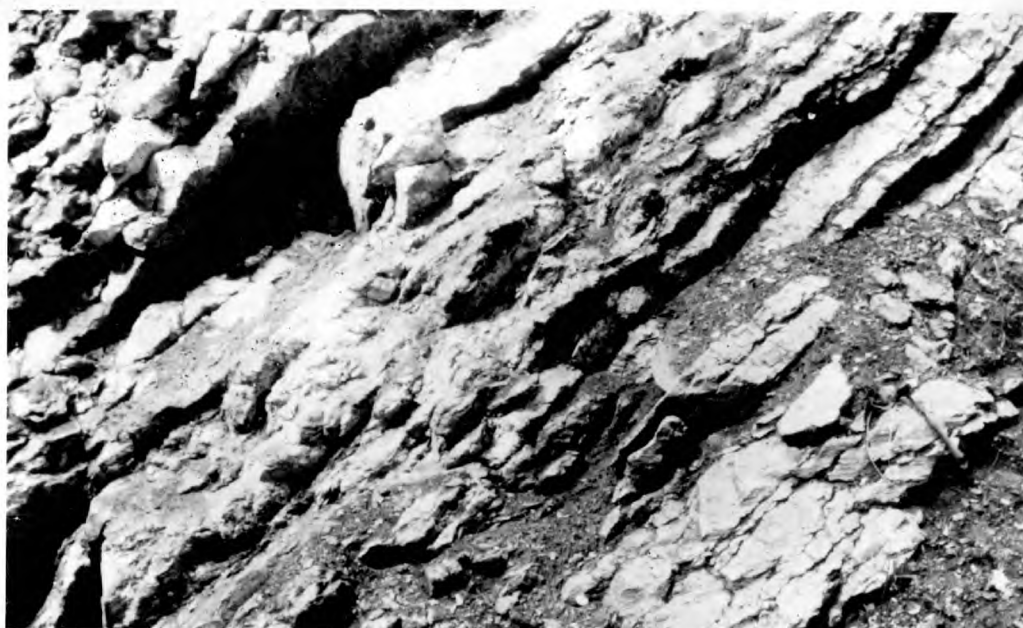
Text-plate 6

Thecosmilia coralline limestone and shale at Ampelsbach, Bavaria. Rhaetina gregaria ?ssp.nov. occurs very abundantly in association with fragmented corals but not with corals in position of growth or in the shales.

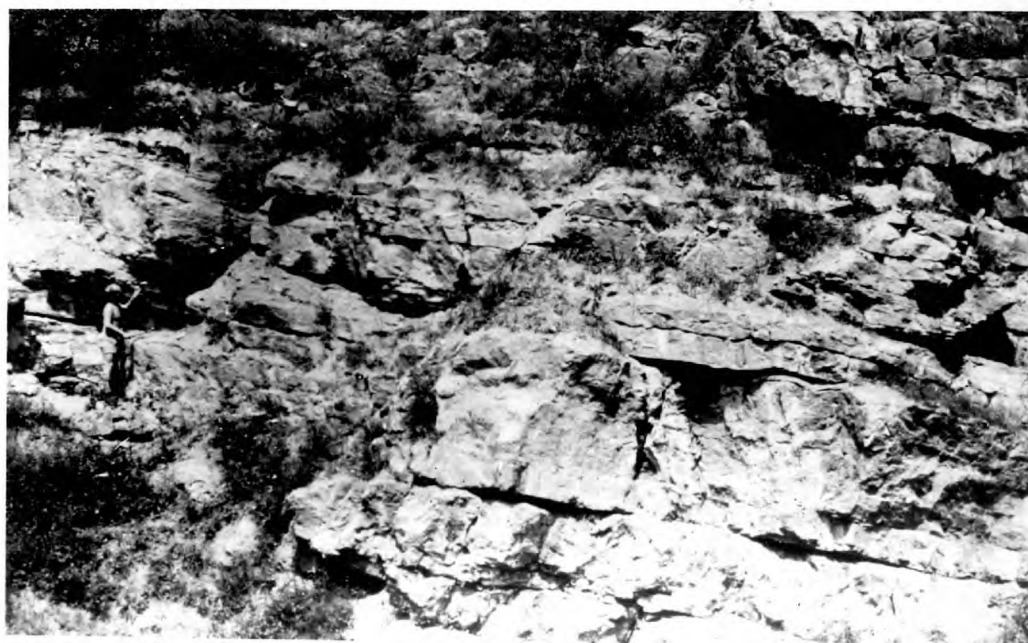
Text-plate 7

Faulted thick bedded limestone at Bystry potok, Slovakia. Certain bedding planes are very rich in Zugmayerella uncinata and Rhaetina gregaria.

6



7



coloured limestones, often a little oolitic and with horizons of red marls to the north.

This profile illustrates the essential character of the Rhaetian in the Northern Alps but considerable variations in detail occur. Towards the south reef development is prevalent in the late Rhaetian and may be extremely massive as in the Sonwendgebirge described by WÄHNER (1903). Reefs may also occur in the lower part of the Rhaetian and FABRICIUS (1959) following a thorough study in Bavaria, named it the 'Rhäto-Lias Riffkalk' after he had found evidence that it continued into the Liassic. On the other hand an upper reef stratum may be missing as in the profile in the Ostrohorn Group used by SUESS and MOJSISOVICS (1868) in recognising the classic fauno - lithological facies of the Rhaetian. At this level they found instead Choristoceras marshi in beds of grey limestone, and QUENSTEDT (1951) found this to be of regional validity.

In the more northerly region of the basin, lying closer to the Vindelician shoreline, reefs are uncommon and small e.g. the Axelstein reef described by LUTYJ-LUTENKO (1951).

In the Vienna area the Plattenkalk is missing and the Kössener Schichten lie directly on the Hauptdolomit. Algal Dachsteinkalk with megalodonts, is dominant in this region and appears to have been interspersed with shallow lagoons and channels in which rich brachiopod faunas flourished.

Further discussion of the variation of the Rhaetian in the Northern Alps can be found in von ARTHABER (1905) and HERITSCH (1915). HAHN (1910) described the facies variation in the Berchtesgarden area, and OHLEN (1959) studied the Steinplatte reef in more detail. FABRICIUS (1959, 1960 and in press) discussed the facies and sedimentation in Bavaria and the Tirol.

In the Western Alps of France and Switzerland the Rhaetian occurs in both the internal and external zones and represents deposits on the very boundary of the Vindelician Swell. They are described in detail by KILLIAN and REVIL (1912). In the external zone the Rhaetian is of the Germanic Swabian type but in the Pas du Roc nappe of the internal zone is found the most westerly development of proven marine Rhaetian. The limestones are dark, thin bedded, intercalated with much shale and rest on Keuper marl.

The same tectonic units and similar sediments are found in the Alps of the Haute Savoie and northern Switzerland.

In Czechoslovakia the Rhaetian follows the Carpathian chain with minor exposures on the northern edge of the Little Carpathians. In the west Slovakian Carpathians and the Tatra of southern Poland it is present in a variety of tectonic units and sedimentary facies representing differing proximity to the continuation of the Vindelician chain - the Vindelizisch - Beskidische Schwelle of ANDRUSOV (1965), - and miniaturising several structural units of the Northern Alps. The Triassic of Slovakia is discussed in detail by ANDRUSOV (1965) and of Poland by KOTANSKI (1959, 1963).

In the High-Tatric Series of north Slovakia and southern Poland the Rhaetian is almost wholly continental with only minor marine developments, but in the Sub-Tatric Series, extensive in Slovakia, a rich marine fauna is present and was monographed by GOETEL (1917). In Poland and in the Krizna nappe of Slovakia the marine limestones of this Series lie on continental Keuper. The well known locality of Bystry potok in the Vah valley, is in the Krizna nappe.

Hybe, which yielded the bulk of GOETEL's material, lies in the more southerly Choc nappe in which the Hauptdolomit is present and the Upper Triassic is fully marine. This unit was correlated by TOLLMAN (1963) with the upper North-Alpine nappe and therefore parallels the Austro-Bavarian Rhaetian in its tectonic position as well as its fauna. The limestones of Hybe are dark, very thick bedded and lie on Norian Dachsteinkalk. There is no sign of an upper reef development in Slovakia and Hybe, at least, resembles localities in the Vienna area.

In the Norian Dachsteinkalk development of the southernmost tectonic unit, the Gemerides, lie both Drnava and the Stratenska hornatina Mts. with their so-called 'mixed Norian-Rhaetian' fauna.

In Hungary and Yugoslavia the late Triassic is developed as massive Dachsteinkalk with Megalodon and brachiopods are unknown. However a rich fauna, listed by PALFY (1925) and briefly discussed by PREDA (1962), is found in the Apuseni Mts. of north-west Rumania. Here the Rhaetian lies conformably,

or with a slight disconformity, on Dachsteinkalk and comprises dark limestone with Megalodon, occasional corals and a rich fauna of wholly typical alpine Rhaetian brachiopods (see BLEMMHU and MANTEA 1964). Dark limestones with Megalodon are also present in the Persani Mts. of the Carpathians (PATRULIUS 1964). The immediate proximity of a rich Norian fauna discovered recently by Dr.D.PATRULIUS (verbal communication 1965) which is faunally and lithologically analogous to the Norian of the E.Bulgarian Balkans, described by GANEV (1961) and the Caucasus (DAGIS, 1963) is here thought to indicate strongly the stratigraphical separation rather than the mere facial equivalence of the Norian and Rhaetian suggested by some authors (see Stratigraphy).

The Rhaetian in the Southern Alps is of a similar character to the Northern Alps: Norian Hauptdolomit is overlain by Plattenkalk and that in turn by Rhaetian shales, marls, and subordinate limestones. The fauna, though not rich, contains typical Rhaetian lamellibranchs and a few brachiopods and corals. SCHLAGER (1962) and van BEMMELLEN (1957 and 1961) described the succession in detail.

In the Lombardy Alps of northern Italy BERNOULLI (1964) distinguished three facies in the Rhaetian: east of Lake Garda both the Norian and the Rhaetian are developed as Hauptdolomit and are inseparable. It is these massive beds which form the Dolomites. Between Lakes Garda and Lugano is found the basinal Lombardy facies in which 1000ms. of Rhaetian beds are divisible into three well marked divisions - a lower shaley unit; a middle limestone unit, in which corals and rare brachiopods occur; finally an upper unit of massive dolomite, the Conchodon Dolomite. West of lake Lugano on the Lugano Swell, the whole of the Rhaetian is very reduced and represented by littoral Bahama bank like (WIEDENMAYER 1963) deposits transgressive on Hauptdolomit.

ALLASINAZ (1962) and GNACCOLINI (1965) consider the Rhaetian of important parts of the Lombardy Alps in detail.

With regard to the Rhaetian, the writer agrees with van BEMMELLEN (1957) that the facies of the Southern Alps can be considered as transitional between that of the Northern Alps and the Dinarides. There is certainly not the abrupt change in facies which might be expected if the Alps and Dinarides lay on opposite sides of the Tethys as suggested by CAREY (1958).

HISTORY AND PROBLEMS OF RHAETIAN STRATIGRAPHY

Beds later to be included in the Rhaetian were first distinguished by von BUCH in 1828 in the neighbourhood of the Tegernsee in Bavaria, and their subsequent study engaged the attention of some of the finest of the early Alpine geologists. A resume of the early work and terminology can be found in STOPPANI (1861) and the distribution and palaeontology in DITTMAR (1864).

Only a few years after von BUCH's work ALBERTI (1834) proposed the tripartite division of the Triassic and recognised a vertebrate bearing sandstone - the Tübingen sandstone - lying conformably above the red Keuper marls. This formation was soon correlated with the bone bed found in Britain and its position between the Keuper and the Psiloceras planorbis zone of the Liassic became well established.

Simultaneously with the research on the Tübingen sandstone and its equivalents in Northern Europe, the Küssener Schichten had become widely recognised in the Alps. In 1854 SUESS published his monograph 'Über die Brachiopoden der Küssener Schichten' and two years later he and OPPEL (1856) produced their classic memoir 'Über die mutmasslichen Äquivalente der küssener Schichten in Schwaben'. Through the common presence of Rhaetavicula contorta and other lamellibranchs SUESS and OPPEL were able to demonstrate the coevality of the Alpine Küssen beds and the Swabian vertebrate deposits.

Up to this time the only means of comparing the Alpine and extra-Alpine Trias had been afforded by the few species recognised as common to the diverse developments of the Muschelkalk, and this additional reference level determining the upper boundary of the Triassic provided a new tool for the solution of the structure and stratigraphy of the Alps.

Opinions varied over whether the Küssener Schichten had an affinity with the Triassic or the Jurassic. LEYMERIE (1839) had laid the foundation of a French opinion which still persists, in placing the

equivalents of the Tübingen Sandstone in the Liassic and coining the term 'infraliasique'. Many English geologists followed him, but the Germans and Austrians after initial uncertainty were more impressed by the opinion of OPPEL (1859) who followed the 'Contorta Zone' through France and Luxemburg and came to the conclusion that the boundary between the Triassic and Jurassic should be placed above it and below the zone of Psiloceras planorbis.

In 1861 GÜMBEL published his compendious work on the geology of Bavaria and produced an entirely new nomenclature for the Alpine Triassic. He adopted the extra-Alpine divisions of Bunter, Muschelkalk and Keuper and following the example of OPPEL and SUESS correlated them with the marine strata of the Alps. It was in this work that the Rhaetian was named.

In the Keuper GÜMBEL distinguished Lower, Middle and Upper 'Abtheilungen' or 'Gruppen' comprising seven minor 'Glieder', in which he listed the current formation synonyms. He tabulated the 'Obere Abtheilung' as follows:-

Lias

1. Obere Abtheilung (rhaetische Gruppe).

1. Oberes Glied: Dachsteinkalk.

Hauptlager des Megalodus triqueter.

Oberster Keuperkalk der Alpen.

Megalodus - und Lithodendronkalk.

Banco madreporico.

2. Unteres Glied: Oberer Muschelkeuper.

Schichten der Avicula contorta.

Kössener-Schichten.

Gervillien-Schichten.

Oberes St. Cassian.

Deposito dell'Azzarola.

2. Mittlere Abtheilung (Hauptdolomit-Gruppe)

3. Oberes Glied: Plattenkalk.

Having discussed the distribution and development of the Triassic he summarized his conclusions regarding the distinctness of the upper part (p.214) :-

'.... Es wäre nach den in den Alpen herrschenden Verhältnissen nicht unnatürlich, aus den oberen Schichten des Alpenkeupers, den Küssener-Schichten und den Dachsteine eine eigene, zwischen Keuper und Lias stehende, selbstständigere Schichtengruppe oder Formation zu bilden, welcher man den Namen rhaetische Formation von dem Haupt - gebiete ihrer Entwicklung in den rhaetischen Alpen beilegen könnte.'

GÜMBEL did not give the location of a type section and it is clear that he considered the Rhaetic Alps as a type region. PUGIN (1962) who quoted GÜMBEL at greater length than here, considered the problem of a stratotype in some detail and limited the area to the Rhätikon. A summary of the succession found there is included in the Distribution of the Marine Rhaetian herein.

Although GÜMBEL was able to use Rhaetavicula contorta as an index fossil of his 'rhaetische Gruppe' (see table) the scarcity of fauna in the Alpine development did not allow him to draw a palaeontologically precise lower boundary. He was thus forced to define it solely on lithology - 'Mit den aufgelagernden Mergelshiefer begegnen wir einer Bildung' (p.121). This unsatisfactory situation was complicated when MOJSISOVICS⁽¹⁸⁶⁹⁾ drew the upper boundary of the Norian on the basis of ammonite zonation in the Austrian Alps.

MOJSISOVICS distinguished three distinct ammonite faunas in the Hallstadt area of the Austrian Alps and as a result divided the upper Triassic into a lower 'Noric' and an upper 'Carnic' division, the boundary between them being drawn supposedly in the centre of the Hallstadt limestone, above the zone of Pinacoceras metternichi.

Unfortunately MOJSISOVICS's scheme contained several serious stratigraphical errors. These caused much controversy and ultimately gave rise to a fascinating, but unfortunately at times bitter polemic between himself and BITTNER who monographed the Triassic brachiopods in the last dozen years of the century. In 1902 MOJSISOVICS partially remedied the inadequacies of his first scheme by placing the Hallstadt

STRATIGRAPHICAL SCHEMES FOR THE RHAETIAN

AMMONITE ZONES after Kittl. 1903		THIS THESIS (general)	POPOV, 1961 (cf. Fromaget 1940) (general)	DAGIS, 1963 (cf. Fromaget 1940) (general)	SLAVIN, 1961 (general)	MULLER and FERGUSON 1939 (Nevada)	McLEARN 1960 (Br. Columbia)	TOZER, 1965 (Br. Columbia)	TUCHKOV 1962 (supposed)	TUCHKOV 1962 (actual)	
LIAS HETTANGIAN RHAETIAN NORIAN TRIASSIC	Psiloceras planorbis	Hettangian	Hettangian	Hettangian	Hettangian	Hettangian			Hettangian	Hettangian	P. planorbis
	Choristoceras marshi	Rhaetian (Austriptychidia cornigera)	Rhaetian	"Norian"	Swabian subst.	Rhaetian (C. marshi)	not recognised	not recognised	Rhaetian	Rhaetian	C. marshi
	Pinacoceras metternichi	favoured base		Rhaetian	Laba substage	P. metternichi	Rhaetian (C. cf. C. marshi)	Rhaetian (C. cf. C. marshi)			P. metternichi
	Cyrtopleurites bicrenatus	Norian (Monotis sp.)	Norian	Norian	Norian	Monotis subcircularis	Monotis subcircularis	Monotis subcircularis	Norian (Monotis ochotica)	Norian (Monotis ochotica)	C. bicrenatus

limestone below the Rhaetian. At the same time he recognised the Sirenites argonautae zone above that of P. metternichi. This upper zone was immediately disputed by KITTL (1903), later by DIENER (1925) and more recently by TOZER (1965). Accordingly it is not considered here and the zone of Pinacoceras metternichi is recognised as the terminal unit of the Norian.

The Rhaetian ammonite bearing continuation of the Hallstadt limestone - the Zlambach marl - is rarely exposed and the few ammonites it contains are all of Norian genera. Together with the tectonic and facies complications which caused MOJSISOVICS to misinterpret the field evidence, this has made it difficult to reconcile the palaeontological boundary of the Norian with the lithological boundary of the Rhaetian. Proposals have therefore been put forward to lower the boundary between the stages to a recognisable horizon in the present Norian. These schemes are separately discussed below.

The absence of ammonites in the dominant facies of the Rhaetian has also led to the brachiopods being regarded as index fossils. Their shortcomings in a role they can rarely fulfill have inevitably been exposed, since so-called index Rhaetian brachiopods have been found associated with ammonites of the Pinacoceras metternichi zone. Instead of the range of the brachiopods being extended as would normally be the case, it has caused the belief among several authors that GUMBEL's 'rhaetische Gruppe' is no more than a special facies of the Norian.

FROMMART (1940) has been the stimulus of much of the recent doubt over the separate existence of the Rhaetian stage. He re-examined the Napeng beds of Burma, first investigated by HEALEY (1908), and found the Norian ammonites Anatibetites and Paratibetites associated with Rhaetavicula contorta and other lamellibranchs commonly present in the European Rhaetian. FROMMART therefore concluded that 'the Rhaetian stage cannot be distinguished from the Norian on stratigraphic, tectonic or even palaeontological grounds, at least as regards the marine fauna', and that 'there is no reason to regard the Rhaetian as a separate stage: it is simply the highest zone of the Norian stage' (transln. of POPOV 1961).

DAGIS (1963) having monographed the upper Triassic brachiopods of the Caucasus, Crimea and Pamirs felt similarly and wrote that the Rhaetian is 'in some part (and perhaps in its entirety) only a special facies of the Norian stage' (NLL transln.)

In fact forty years before FROMMARGET, KITTL (1903) had drawn attention to the possibility that the Rhaetian Küssener Schichten may belong to the Norian - 'Es entsteht die Frage ob die Küssener Schichten nicht etwa nur eine besondere Facies der oberste norischen Schichten darstellen'. His doubts were raised by an investigation of the ammonite bearing Zlanbach marls in the Salzkammergut. These marls interdigitate at their base with Halorella-bearing Norian limestones and pass into lithologically identical Liassic beds with Psiloceras. In the lower part of the marls, ammonites are relatively rich and in what he termed the Cochloceras Schichten, KITTL lists ten well known Norian genera. In the upper part, the Choristoceras Mergel, only three genera, Choristoceras, Cladiscites and Megaphyllites are present. The fact that the latter pair also occur in the underlying beds led to KITTL's doubts over the characterisation of the Rhaetian, but he dismissed them on considering the singularity of the brachiopod and lamellibranch fauna of other facies of the stage.

A comparable ammonite bearing sequence in Nevada, continuous from the Triassic to the Liassic was described by MÜLLER and FERGUSON (1936 and 1939). Above beds containing Pinacoceras metternichi and other ammonites of that zone, including four species found by KITTL, these authors found Choristoceras marshi, C.cf.C.ammonitiforme and Arcestes sp. 'associated with Pteria contorta'. The conformable base of the Liassic is then marked by the appearance of Psiloceras planorbis (see also fig.2 of HALLAM 1965). REESIDE et al (1957) noted that SANBORN (1952 - unpub - lished) had found a similar sequence in California, and TOZIER (1965) recorded beds with Choristoceras cf. marshi at the summit of the Triassic in British Columbia.

Thus continuous ammonite bearing sequences in both Europe and North America contain beds at the top of the Triassic which are

recognisable only through the relative rarity of their ammonites. Although Choristoceras is commonly present, no ammonite genus is restricted to these beds, and POPOV recognising that they represented the Rhaetian concluded that it was an impracticable stage. Drawing additional evidence from north east Siberia he proposed that the lower boundary of the ultimate stage of the Triassic should be set at the base of the present Sevatian substage.

Prior to 1959 the upper boundary of the Norian in north east Asia was drawn at the highest occurrence of Monotis ochotica and the 500 - 1300m. of sandstones, shales and tuff between this and the Psiloceras bearing Hettangian were regarded as Rhaetian (e.g. TUCHKOV 1956 and 1959). However the known fauna of brachiopods, lamellibranchs and a single gastropod and ammonite was ambiguous, giving no firm support to the Rhaetian age of the beds. In an attempt to resolve the situation a detailed palaeontological survey was carried out in 1961 and 40 ammonites from above Monotis ochotica were identified and dated by POPOV as late Norian (Sevatian substage). POPOV⁽¹⁹⁶¹⁾ then concluded that the Rhaetian of the two investigated sections 'is certainly Norian'. DAGIS (1963) interpreted this to mean that the super-Monotis Norian strata 'occupy the entire stratigraphic gap between the strata with Monotis ochotica and the Liassic deposits with Psiloceras'. The field evidence as given by POPOV does not appear to support this.

In one section in which Norian ammonite bearing beds are overlain by others with Psiloceras, the Liassic consists of conglomerates and sandstones and may therefore be suspected as unconformable. In the second section, explicitly stated to be conformable, POPOV himself remarks that 'it remains possible that the Rhaetian may be found in the uppermost part of the upper Norian which has not yet yielded any fossils' (I.G.R. transl.). In view of the known rarity of ammonites at this level and recent information on the stratigraphy of Monotis (TOZER 1965, see also below), POPOV's afterthought may well be correct. Additional evidence that it is so appears in the brachiopod fauna of POPOV's sections investigated by DAGIS (1965) for it contains six genera not known in the Alpine Rhaetian and of the genera which are

there are no species in common. This is notable evidence contrary to any supposition that the deposits of the two areas are merely facies equivalents. However it is a geographically remote fauna and not as significant as that from the Caucasus also monographed by DAGIS (1963).

In the Caucasus, which serve as a model for the Crimea and Pamirs, DAGIS distinguished four 'series' -

- d - 'Norian-Rhaetian beds.
- c - Red limestones.
- b - Reef limestones.
- a - Basal series.

The lowest three contain *Monotis* species and are undoubtedly Norian. The 'Norian-Rhaetian' beds - the highest - occur directly above the last appearance of *Monotis* and contain a rich brachiopod fauna of fifty-one nominal species which includes ten of the seventeen in the Basal Series, giving the whole sequence a unified aspect. The ammonites in the 'Norian-Rhaetian' beds indicate the Late Norian.

Ten species of brachiopod commonly found in the Alpine Rhaetian were also described by DAGIS from the 'Norian-Rhaetian' beds but to regard them as 'characteristic index forms of the Rhaetian stage', as he does, and then to question the viability of the Rhaetian because of their association with Norian ammonites, is misleading. It ignores the impressive list of twelve accompanying genera which are wholly foreign to the Alpine Rhaetian, evidence which is supported in the Stratonka hornatina fauna monographed without generic revision by MAHEL (1958). Here nine of the same ten species occur with seventeen including *Halorella*, well known in the Norian. In the east Bulgarian Balkan mts. GANEV (1961) listed a number of localities as Rhaetian and DAGIS (personal communication 1966) regarded them as lithologically and faunally equivalent to the Caucasian upper Triassic, thus confirming the writers own view. However, collection and examination of material kindly lent by Dr. GANEV showed this fauna also contains many characteristic Norian species alongside its Rhaetian elements. The faunas described by BITTNER (1891,

1892a, and 1895) from north east Turkey, and reported by MERHART (1910) from northern Rumania, also contain recognisable Norian species and need not be thought of as comprising the Rhaetian.

Undoubtedly the Norian fauna providing the closest parallel to the Rhaetian is that which occurs at Drnava (formerly Derno) in South Slovakia, where the wide range of disparate Norian genera found in the Caucasus are absent. STURZENBAUM (1879) was the first to draw attention to this locality. The brachiopods were subsequently described by BITTNER (1890) and the ammonites by MOJSISOVICS (1896). There is no doubt whatever of the Norian age of the ammonites, nor of the dominance of Rhaetian species in the brachiopod fauna. Most suggestive however, is the presence of Pexidella strohmayeri, a small diplospirelliform athyrid which occurs in large numbers in the Norian Hallstadt Limestone but is quite unknown in the Rhaetian. A similarly suggestive absentee is the rhynchonellid Austrirhynchia cornigera. This species is easily dispersed by currents and is present in all the important Rhaetian brachiopod yielding localities in the Alps, Slovakia (Hybe, Bystry potok) southern Poland and Rumania, whilst it has never been recorded in the Norian. It seems in fact to be a true index species for the Rhaetian and its absence at Drnava may have the obvious significance.

Aulacothyris conspicua and Lobothyris hungarica found at Drnava also occur in the neighbouring Norian locality of Stratenska hornatina but are unknown in the European Rhaetian. However, this evidence of Norian age must be qualified by the fact that both genera are recorded in the Liassic and must therefore be expected in the Rhaetian somewhere, but possibly outside Europe. Finally further evidence for stratigraphical separation may lie in the slight differences in some of the Rhaetian species present - e.g. the marked flatness of the brachial valve of F.fissicostata, which is more comparable with Slovakian Norian than Alpine Rhaetian examples. These slight differences may, however, be due to geography or facies.

An abundant fauna of lamellibranchs also occurs at Drnava. Together with the ammonites it is being investigated under the direction of

Mme.W.ANDRUSOVA of the Slovakian Academy of Sciences, Bratislava, through whose kindness the writer was able to visit the exposure shortly after it was re-opened. It will be of great interest to learn the degree of affinity this part of the fauna shows to the Rhaetian.

An important point to be borne in mind when considering such 'mixed' faunas as Drnava and the possible stratigraphical equivalence of the Norian and Rhaetian, is the remarkable uniformity of the Rhaetian brachiopod fauna over the whole of its distribution in Europe even as far as Iran (DOUGLAS 1929). Yet prolific, distinct and proved Norian faunas are closely juxtaposed in parts of the Alps, and in the Carpathians of Slovakia and Rumania. The latter fauna has only recently been discovered in the Persani Mts. of West Rumania (by Dr.D.PATRULIUS, verbal communication 1965), and clearly illustrates the proximate development of typical Rhaetian and Norian faunas. A wide range of facies and therefore environments is encompassed within the Rhaetian, particularly in the Northern Alps providing ample opportunity for the appearance of many members of the brachiopod fauna of any supposed Norian facies equivalents. It is difficult to envisage any arrangement of palaeogeography or ecological regime strict enough to effect so drastic and constant a separation of brachiopod faunas over the whole of Alpine Europe.

Therefore the Rhaetian is here regarded as stratigraphically distinct from the Norian.

Distinct though the European Rhaetian brachiopod fauna is as a whole, it must be admitted that its character is negative. Only Austrirhynchia cornigera is a new form and the fauna is more notable for its lack of many Norian genera and species. This apparently holds true also for the ammonites, and despite the correction of many of the inadequacies of MOJSISOVIC'S zonal scheme for the upper Triassic by TOZER (1965) it has still not been possible to give any further precision to the lower boundary of the Rhaetian.

Because of these difficulties over the recognition of the Rhaetian POPOV (1961) proposed that the lower boundary of the ultimate stage of the Triassic be drawn below the zone of Pinacoceras metternichi. At this point POPOV recognised the disappearance of fourteen ammonite genera and the first occurrence of two others, but this sharp faunal division is almost certainly caused by discrepancies in the Alpine zonal scheme and remains to be proved by modern research.

Although it was not his intention, TUCHKOV (1962) also advocated the lowering of the base of the Rhaetian, in accepting the equivalence of the Monotis subcircularis zone proposed by McLEARN, with the Pinacoceras metternichi zone.

McLEARN recognised the Monotis subcircularis zone in the Triassic of British Columbia but even in 1960 when he summarized the results of his research he was unable to certainly correlate it with Alpine zones. In the Rapide-qui-ne-parle-pas section he found beds with Rhacophyllites above Monotis and in his stratigraphical table inserted them below the Rhaetian, thus indicating that the zones of M.subcircularis and P.metternichi were probably not fully equivalent. This was subsequently confirmed by TOZIER (1965) who identified Choristoceras above beds with Rhacophyllites and Rhabdoceras suessi in another British Columbian profile. However MÜLLER and FERGUSON (1939) regarded the P.metternichi and M.subcircularis zones as facies equivalents and this was schematically presented in REESIDE et al (1957) and by WESTERMANN (1962) who monographed the monotids from McLEARN's sections.

It was through MÜLLER and FERGUSON's correlation together with his field experience in north east Asia where Monotis ochotica is the last mappable horizon, that TUCHKOV (1964) was led to propose that Monotis could be used to define the boundary of the Rhaetian. The disregard of the Norian age of the ammonite fauna of Dnava, the 'Norian - Rhaetian' beds of the Caucasus and of north east Asia which was then forced on him, suggests that, in these areas at least, Norian beds supersede the last appearance of Monotis. This is wholly in accord with the situation revealed in British Columbia.

Acceptance of the disappearance of Monotis as marking the terminal stage of the Triassic is a practical move which the writer favours. Monotis has the world wide distribution usually associated with ammonites and, indeed, was thought by JEFFRIES and MINTON (1965) to be a pelagic genus. This boundary will, however be lower than the present one and not coincident with it as TUCHKOV believed.

SLAVIN (1961 and 1963) put forward an entirely different suggestion. He accepted the proposition that the Rhaetian is merely a facies of the Norian and included beds with a 'mixed Norian-Rhaetian' fauna together with the marine Alpine Rhaetian in a new substage of the Triassic, the Laba substage, taking as the type section the Caucasian 'Norian-Rhaetian' by the Laba river. He makes no precise statement regarding the position of the lower boundary and DAGIS (1963) assumed it to be above the Pinacoceras metternichi zone. Since ammonites of the metternichi zone are also found in the 'mixed' fauna e.g. Drnava, SLAVIN cannot have intended this and the first part of his proposals must involve a lowering of the present boundary in much the same manner as TUCHKOV or POPOV.

The novelty of SLAVIN's scheme lies in the isolation of the lamellibranch rich Swabian facies in a new substage, the Swabian substage, which he referred to the Jurassic. This was the first occasion on which the equivalence established by OPPEL and SULESS in 1861 and found valid by generations of Alpine geologists had been challenged. SLAVIN found his evidence for it in the apparently unconformable superposition of the lamellibranch bearing beds on the brachiopod rich facies in an unnamed profile in the Codru zone of the Apuseni mts. of north west Rumania. Several faunally rich sections in the area were visited by the writer but this situation was not seen. Furthermore it has not been found to be of any regional importance by geologists mapping in the area (Dr.G MANTEA and Dr.J.BORDEA, verbal communication 1965), and is in fact directly contrary to the relation of the faunas in the Frunza valley near Ferice (BLEAHU and MANTEA 1964). The field relations demanded by SLAVIN are also quite opposite to the common situation in

the Northern Alps where the most lamellibranch rich beds occur at the base of the Rhaetian (e.g. QUENSTEDT 1951). His proposal has already been strongly criticised by TRÜMPY (1963), DAGIS (1963), BERNOULLI (1964) and SOMOS (1965) and is not accepted here.

POPOV (1961) raised the technical point that even if the Rhaetian is stratigraphically distinct it cannot be of higher rank than a zone since only one - that of Choristoceras marshi - has ever been recognised within it. However the number of zones which can be recognised in a sequence is a reflection only of the nature and richness of the fauna, and the lack of ammonites in the Rhaetian should not be allowed to override the widespread geological importance which prompted its erection.

SLAVIN's proposal is the only one to have made any concession to the French point of view which sees the Rhaetian as the initial stage of the Jurassic. Ever since LEYMERIE (1839), French geologists, with progressively fewer allies have argued that since the Rhaetian transgression marks the amelioration of the aridity of the Triassic, the beginning of the marine régime of the Jurassic and accompanies the birth of such depositional areas as the Paris Basin, it is more suitable as a basal than an ultimate stage (e.g. RICOUR 1961 - opinion of French 'Colloque sur le Lias'; RICOUR 1963 - opinion of French 'Colloque sur le Trias'; ARKELL 1933). Opposed to this view have been the Mediterranean Mesozoic Committee of the International Stratigraphical Commission (AGER 1963; RICOUR and SIGAL 1964), the British Mesozoic Era Subcommittee (AGER 1964), and ARKELL (1956).

Argument contrary to the assignation of the Rhaetian to the Jurassic has centred on faunal evidence. German geologists with the benefit of marine as well as continental Triassic have always laid heavy emphasis on the strong Triassic character of the Rhaetian ammonites. All the genera are common to the Norian whereas the Hettangian is marked by the appearance of over twenty new genera (ARKELL 1957) one of which, Psiloceras is an excellent marker for its base.

For this pragmatic reason, if no other, the Rhaetian should be placed in the Triassic, for the Rhaetian - Hettangian boundary marked in Europe, North America and Asia by Psiloceras planorbis is unchallengably the most suitable major dividing line. Accordingly the Rhaetian is here regarded as the terminal stage of the Triassic.

GENERAL PALAEONTOLOGY

ECOLOGY I

Considerable importance has been attached during this study to field collecting, not only in order to supplement old collections but also to provide information on occurrence and association unobtainable from museum material. This information has been used throughout the systematic revision in order to judge the practicability of new or already established species. In addition much data has been gathered on the fossil communities long recognised in the Rhaetian.

These communities are outlined below. A more detailed discussion will be possible after the imminent publication of a review of the facies of the Rhaetian in Bavaria and the Tirol (FABRICIUS, in press).

Following his study of the brachiopods of the Küssener Schichten, and of the equivalence of the Swabian and alpine deposits, SUESS, together with MOJSISIVICS (1868) published details of a section from the Norian to the Liassic in the Kendelbachgraben near the Wolfgangsee, Salzburg. They divided the Rhaetian into four litho-faunal facies: the Swabian, Carpathian, Küssener and Salzburger Facies. These are now in need of revision. For instance, the Swabian lamellibranch bearing facies, far from being similar to the Rhaetian of Northern Europe as its name implies, probably represents relatively deep water. Its aligned and burrowing pelecypods together with the alternation of shale and dark, thin bedded limestone indicate muddy conditions with regular currents. The Küssener facies at its type locality in the Lofer Graben represents an incursion of a shallower peri-reefal environment with a varied brachiopod fauna. The Carpathian facies is faunally characterised by prolific Rhaetina gregaria and represents banks of that species accompanied by Zugmayerella uncinata. The Salzburger facies is the most unusual and is characterised by Choristoceras marshi.

These facies may be best recast as fossil community facies when their environments and relationships are better understood.

Summary of brachiopod associations and occurrence (see enclosure 2.)

Rhaetina gregaria and Zugmayerella uncinata are common and almost invariable associates. They occur together in the Pas du Roc nappe of the French Western Alps, in the Haut Savoie, and are found again in large numbers along the northern front of the Rhaetian basin in the Northern Alps, the Slovakian Carpathians and the Polish Tatra. Evidently R.gregaria thrived in dense banks in shallow water. It dominates its companion Z.uncinata in the ratio of about 50:1.

A probable subspecies of R.gregaria, also associated with Z.uncinata, occurs at Ampelsbach in Bavaria and apparently surrounded a flat field-like Thecosmilia reef. It rarely encroached on the reef and is now found only with broken coral fragments. In northern Italy a hint of the same association is seen, but here the corals are not fragmented and Rhaetina is very rare, too rare to be compared subspecifically with the Ampelsbach specimens.

The occurrence of many of the other common species is well illustrated by their distribution around the Steinplatte reef. Here the fore-reef and basinal facies of the Rhaetian are well exposed (text-plates 1-5). Extending for two or three kilometres from the immediate neighbourhood of the reef occur thin colonies of the large dielasmatic Rhaetina pyriformis. Rarely more than three or four individuals are concentrated together but exposures yield many specimens and local communities evidently existed.

Dense, monotypic colonies of dozens of individuals of Zugmayerella uncinata also occur in the fore-reef calcarenites. Such colonies are additionally found near the Axelstein reef and at Bystry potok in Slovakia (see ANDRUSOV 1965, pl.21). This latter locality also yields Rhaetina gregaria in large numbers.

A very few individuals of Calcirhynchia subrimosa accompany Z.uncinata near the Steinplatte reef but this small rhynchonellid is only found in large numbers in a dark limestone bed in the nearby Lofer Graben. Dark limestones alternate with shales (see text-plate 4) and conditions were evidently quieter with a muddy bottom and burrowing lamellibranchs. C.subrimosa occurs in closely packed colonies of 200-300 small, globose individuals

belonging to all growth stages. They were possibly attached to anchored algae in the same manner as AGER (1965a) suggested for the type of the genus, C. calcaria, well known in the Lower Liassic. Isolated individuals are larger and more variable in form (see description of C. subrimosa).

In the bed immediately below C. subrimosa two other well known species are found, Oxycolpella oxycolpos and Fissirhynchia fissicostata. This bed is a relatively thick calcarenite (see text-plate 5) containing shell detritus and indicates an incursion of peri-reefal conditions. It is this locality which gave the Küssener facies its name and the above two species were regarded by SUESS and MOJSISOVICS (1868) as characteristic.

F. fissicostata is also found in the fore-reef calcarenites. It is the most widely distributed of the Rhaetian rhynchonellids and commonly occurs sporadically. In the calm water of the Lofer Graben basin it is oval in form with a small pedicle opening and relatively shallow ribs (e.g. plate 1, fig.1). In coarser sediment of a rougher environment, more triangular specimens with sharper, deeper ribs are found (e.g. plate 1, fig.10). Triangularity is a common adaptation and allows the accommodation of a larger pedicle muscle giving stronger attachment.

Isolated specimens of Austrirhynchia cornigera occur both with F. fissicostata in the Lofer Graben and near the reef. This species and the reason for its wide dispersal is separately discussed in detail below (Ecology II).

No brachiopods have been found in the main body of the Steinplatte reef and the only record of their occurrence in such a position is by SIEBER (1934) who discovered them in the Rötclwand coral reef near Salzburg.

It is very noticeable that zeilleriids are rare in the Steinplatte area and in fact they are only commonly found in the classic region near Vienna, which formed the basis of ZUGMAYER's work (1880).

Reef development was not widespread in this area or in the Slovakian Carpathians. Near Vienna very shallow, possibly intertidal, areas with algal mats and Megalodon (see FISCHER 1964) appear to have been fringed by shallow lagoons occupied by encrusting corals and such brachiopod species as Osmarella starhembergica and 'Zeilleria'austriaca, as at Brand in the

in the Pissting Tal. In deeper, more open water, almost the full range of Rhaetian brachiopod species thrived. This area of deposition is now represented by the limestones of the so-called Starhemberg facies. Rich accumulations of more or less broken, transported material occur in the limestone whilst rare marly lenses contain well preserved individuals.

More massive bedded, less bioclastic limestones such as those of Hybe, were probably deposited in sheltered and possibly deeper water. The fauna is more sporadic and slightly restricted, but still contains all the main species.

Carapezzia geyeri is restricted to the immediate neighbourhood of its type locality in the Southern Alps, where it occurs in dense concentrations. In one outcrop (Pirkner Graben) isolated valves are aligned around angular limestone blocks in a sedimentary breccia. SCHLAGER (1963) remarked on similar beds up to 5m. thick in the Rhaetian of this area. These beds may well have been formed as the result of slumping and brecciation associated with submarine faulting.

At its type locality the field relations are obscure. SCHLAGER (1963) believed the brachiopod rich blocks to be conformably intercalated in Liassic Fleckenmergel, and recorded C. geyeri as Liassic. However, the contrast in sediment type suggests to the writer that this is improbable. It may be that the Rhaetian blocks slumped into the Fleckenmergel from an unstable position. This may also explain the breccias of dolomite blocks found by SCHLAGER in the Liassic. It is interesting that BERNOULLI (1964) reported syngenetic brecciation in the Liassic of the Bergamo Alps.

Although there appears to be considerable evidence of instability during the Rhaetian where C. geyeri occurs, the writer hesitates, on the evidence of one locality alone, to make the tacit comparison with Peregrinella made by AGER (1965a). This latter genus is known from half a dozen countries in loose calcareous blocks in a deeper water sediment, and the localities are isolated. AGER concluded that it may have lived in 'the current swept rocky shallows of a tectonically unstable coast-line (p.159). It is quite possible that there is a geographical explanation for the restriction of C. geyeri to the Southern Alps.

ECOLOGY II

Adaptation shown by *Austrirhynchia cornigera*.

The most striking of the brachiopods occurring in the Rhaetian is *Austrirhynchia cornigera*. It has remarkable wings which form oblique faces to the triangular body of the shell and then recurve posteriorly for as much as 1cm. on either side of a $1\frac{1}{2}$ cm. broad main mantle cavity (see text-plate 8, fig.8).

AGER (1965a) regarded *A. cornigera* as an extreme development of the axiniform shape found in such species as '*R. longicollis*, *Crurātula* sp., *Zeilleria hierlatzica* etc. and associated this shape with increased oxygen absorbtion by an expanded mantle on a poorly oxygenated sea floor. However, there is no evidence of such an environment in its field occurrence and the form of *A. cornigera* is here considered to be purely mechanical in function.

It is immediately apparent on examination of a specimen of *A. cornigera* that in a stream of water the wings will cause it to pivot on its pedicle and become oriented at right angles to the current. This was tested and proved in a flume experiment. In addition, it was at first thought that it might ride above the sediment surface, supported by the water pressure under the wings. However, the model used could only be made to lean on one tip, oscillating violently, and it is clear that the catchment area of the wings is insufficient to provide stability. Thus the only, but immediate, effect of the wings is to produce orientation.

The importance of orientation probably lies in the direction of the water flow over the anterior gape of the valves. If the current here is erratic the circulation system within the shell may be disastrously upset by water sweeping into the mantle cavity and disturbing the delicate balance between the inhalant and exhalant streams. In species which are unable to orient themselves bodily then the water flow may be influenced by anterior folding of the valves. It has several times been observed (e.g. AGER, 1965a. MAKRIDIN 1962, 1964) that the more plicate members of a species occur in the

shallower, more current disturbed part of their ecological range. It is just in this area that currents over the anterior margin must be controlled. The major, median plication of rhynchonellids may also perform this function of redirection of errant currents and the sharper ribbing in the shallower environments (e.g. F.fissicostata herein) may aid this process.

A further important advantage of orientation is that harmful detritus is swept over instead of being carried into the gape. This is of particular importance to species in which the gape lies close to the sediment surface. Light food particles will probably be captured by vortices of low pressure adjacent to the gape.

In connection with orientation the work of MAKRIDIN (1964) and RUDWICK (1965) on Tetractinella trigonella and its homeomorphs, which have remarkable flange-like ribs (see text-plate 8), has been considered.

MAKRIDIN (1964), following a lengthy treatment of anchoring and supporting methods of attachment, postulated that the upstanding ribs of Cheirothyris fleuriauxa, Tetractinella trigonella, Trigonellina pectunculus and Cheirothyropsis pseudotrigonella served to aid the pedicle by stabilising the shell. He envisaged (fig.4) the flanges of the brachial valve being embedded in the sediment of the substratum.

However, field evidence associates all these species with shallow water deposits - oolites, coral beds and reefs - where current action will certainly cause scour, thus negating the holding action of the ribs (which may very well accentuate scour). Moreover, any stability produced by embedding of the brachial valve will be counteracted by the projection of the opposing ribs and their obvious vulnerability to the vagaries of the surrounding water flow. MAKRIDIN's hypothesis is therefore rejected.

RUDWICK (1965) discussed the homeomorphy and possible adaptation of I.trigonella and C.fleuriauxa. He concluded that the function of the ribs lies not in their final external form but in the concomitant projections of the anterior margin. These RUDWICK thought to have acted as a housing for sensitive antennae of mantle tissue which gave warning of injurious particles

threatening to invade the mantle cavity. From the paradigm, or optimal specification, for this function the tips of the marginal projections should be equidistant. RUDWICK was therefore forced to exclude from his hypothesis such species as Pentactinella quinquecostata, Trigonellina pectunculus and Anathyris ezquerrai in which the flanges are not equidistant from one another but which otherwise appear very similar to T. trigonellina.

Contrary to RUDWICK's observation Dr. D. SCHUMANN informs the writer that in very many specimens C. fleurbae the projections are also non - equidistant and this species barely satisfies the paradigm for protection. Also, as RUDWICK noted (p.140), in some large specimens of T. trigonella deflections of the anterior commissure almost disappear. However, it is in just such large individuals, with expansive gapes, that greatest protection and therefore prominence of the anterior deflections, would be expected. For these reasons protection is here thought to be only secondary to a more probable mechanical adaptation similar to that of A. cornigera.

Specimens of Tetractinella trigonella are shown on text-plate 8 in comparison with A. cornigera. The pedicle foramen is large and it is evident that it too was attached during life and pivoted on a strong pedicle. The catchment areas formed along the posterior margins in both species are similar, although those of T. trigonella are not recurved. It is quite certain that in a stream of water T. trigonella will inevitably become oriented in exactly the same manner as A. cornigera and this is here thought to be the function of the flanges.

In this case it is unnecessary for them to be equidistant so long as they are symmetrical on either side of the median plane. Neither is it disadvantageous if they cease to be formed late in ontogeny for by then they are fully active and can hardly be impaired in their efficiency. Moreover P. quinquecostata, T. pectunculus and A. ezquerrai instead of being difficult exceptions, as they are to the protection hypothesis, are but easily acceptable variants.

Text-plate 8

Figs. 1-6. Tetractinella trigonella (SCHLOTHEIM). x 2

'Muschelkalk, Recoaro'. Pal.Inst.Univ. Vienna.

Coll. Neumayr, 298. Fig.1 is the original of

RUDWICK (1965), fig.3, 'm'

Figs. 6-7. Austrirhynchia cornigera (SCHAFHAUTL). x 2

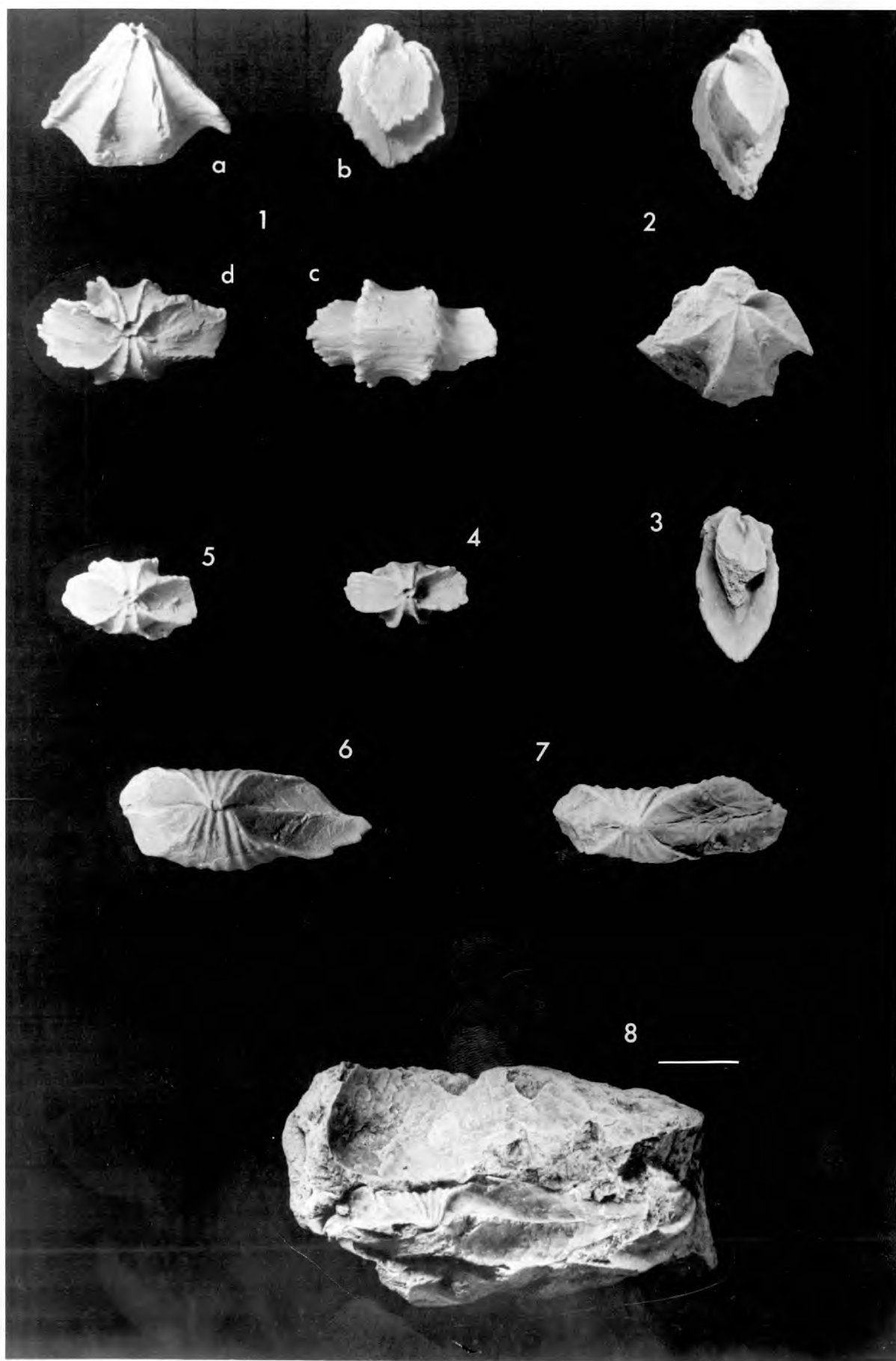
Rhaetian, Axelstein by Jachenau, Walchensee, Bav.

(see descpn. of A.cornigera).

Fig. 8 A.cornigera. 'Dirnbach'. Pal.Inst.Univ. Vienna.

19/7/1

The possible similarity of adaptation in these species is
discussed in the text.



Austrirhynchia cornigera itself is found in two extreme forms: one very small and occurring with dendritic thecosmiliid corals (e.g. Juchtenkopf, the west end of the Steinplatte reef, and possibly the Koth-Alp) and another much larger and most common with thamnastreoid corals (e.g. the Axelstein reef, and possibly Lahnenwies Graben). The latter large form is also found with shell debris in bioclastic limestones (e.g. the Piesting Tal region).

It seems possible that the very small type lived attached to the corallites, but the very large form obviously needed more space and would have become hopelessly twisted and disturbed in such a situation. It therefore anchored itself to shell debris and colonial corals. If these suppositions are correct two ecological subspecies will be useful for the two forms.

The widespread and apparently sporadic distribution of A. cornigera, which led AGER (1965a) to regard it as the antithesis of a colonial species, is due to the ease with which dead individuals must have been distributed by currents. At all the localities mentioned above, with the exception of the Lahnenwies Graben, the species is relatively abundant and probably did live in colonies.

GEOGRAPHICAL DISTRIBUTION

Of the thirty four species now recognised in the European Rhaetian, twelve can be regarded as common and constituting the base of the fauna. These species are:

<u>Vindobonella katzeri</u>	<u>Sinuocosta emmerichi</u>
<u>Fissirhynchia fissicostata</u>	<u>Rhaetina gregaria</u>
<u>Austrirhynchia cornigera</u>	<u>Rhaetina pyriformis</u>
<u>Zugmayerella uncinata</u>	<u>Austrilleria norica</u>
<u>Zugmayerella koessenensis</u>	<u>'Zeilleria' elliptica</u>
<u>Laballa suessi</u>	<u>Oxycolpella oxycolpos</u>

The remainder are rare and many of them are known only through a few individuals from the region of the type locality.

It is notable that the species listed above are found throughout the whole length of the Rhaetian outcrop. This can be seen on a comparison of ZUGMAYER (1880), GOETEL (1917), and PALFY (1925) dealing with the Vienna region, Hybe in Slovakia, and the Persani Mts. of Rumania respectively. Even such a rarity as 'Z' waldegiana occurs in all three areas. Moreover, the small fauna described by DOUGLAS (1929) from Iran is typical of many North Alpine localities. There is not the major contrast in facies which is found in the Liassic and no hint of the distribution areas and ecological groups then encountered (see AGER 1960). The Rhaetian lamellibranchs show a similar uniformity of character to the brachiopods. Evidently the European Rhaetian sea harboured closely comparable environments over a wide area and an essentially uniform fauna was free to migrate over its entire length. PATRULIUS (1964) indicated the probable routes followed in the Carpathians. Locally, particularly favourable conditions encouraged a very rich fauna and allowed rarer species to thrive. Such an area is the Piesting Tal near Vienna, which yielded the bulk of ZUGMAYER's (1880) material.

STRATIGRAPHICAL RELATIONSHIP

Of the twelve species listed above as widespread in the Rhaetian, only two - V.katzeri and A.cornigera - are not found in the Norian, in particular the recently revised Norian of Slovakia, the Bulgarian Balkan Mts., and the Southern Soviet Union. Although A.cornigera is apparently restricted to the Rhaetian and may be regarded as an index fossil, the brachiopod fauna as a whole has the appearance of an impoverished Norian fauna. This has been a major factor in the controversy over the stratigraphical equivalence or otherwise of the present Rhaetian and Norian (see Stratigraphy). However, as a whole the Rhaetian fauna is most distinctive and lacks a considerable number of genera found in the Norian. These genera are as follows:

<u>Trigonirhynchella</u>	<u>Pseudocyrtina</u>
<u>Moisseievia</u>	<u>Majkopella</u>
<u>Halorella</u>	<u>Cubanothyris</u>
<u>Halorelloiden</u>	<u>Adygella</u>
<u>Crurirhynchia</u>	<u>Adygelloides</u> (close to <u>Zugmeyeria</u> ?)
<u>Rimirhynchopsis</u>	<u>Wittenburgella</u>
<u>Triadispira</u>	<u>Worobievella</u>
<u>Pexidella</u>	<u>Pseudorugitella</u>

A much wider variety of genera are also known in the Liassic. Although the Hettangian fauna is not rich, by the Pliensbachian many new genera had become differentiated. This is most clearly seen amongst the rhynchonellids following the recent revision by AGER (1956, 1958, 1962) of the British Middle Liassic rhynchonellids. The Rhaetian fauna thus emerges as a link between the richness and diversity of the Norian and the upper Lower Liassic.

Amongst the Rhaetian rhynchonellids several bases for Liassic diversification are recognisable. Calcirhynchia provides the root stock for Cirpa and its allies, Fissirhynchia for many of the cyclothyrids, and Vindobonella for Pseudogibbirhynchia, whilst Carapezzia is clearly part of the Rhynchonellina lineage well known in the alpine Liassic. However, the main stock of the Tetrarhynchiinae cannot yet be recognised. Although there is no

modern revision of the Liassic spiriferinids many of them are certainly related to Laballa and Zugmayerella. The zeilleriids are conservative and show few significant changes from the Rhaetian to the Liassic. Only Austrilleria, which has a cardinal process, has no recognisable Liassic descendants.

Nevertheless, it is clear that a number of genera remain to be found in the Rhaetian, for instance Lobothyris is known in the Upper Triassic of Siberia and also in the European Liassic and must therefore be present in the Rhaetian somewhere. BITTNER's work (1890, 1892) has shown that the alpine Norian fauna is rich and probably almost all missing Rhaetian links will be discovered in the Alps, particularly in the more brachiopod rich facies of such regions as the Piesting Tal near Vienna.

SYSTEMATIC PALAEONTOLOGYNotes

The following abbreviations are used throughout:

Bayer.St.Slg.	- Bayerische Staatssammlung für Paläontologie u. historische Geologie.
Pal.Inst.Univ. Vienna	- Paläontologisches Institut der Universität Wien.
Geol.Bundes. Vienna	- Geologische Bundesanstalt, Wien.
Nat.hist.Mus. Vienna	- Naturhistorisches Museum, Wien.

mm. - millimetres

m. - metres

All specimen measurements are in millimetres, and the following special abbreviations are used:

- (d) - damaged specimen, measurement approximate.
- (r) - reconstructed measurement, e.g. twice half-width.

The PC.Nr. of a sectioned specimen refers to the acetate peel and plaster cast number in the writer's collection.

All specimens referred to are in the writer's collection unless otherwise stated. Figured specimens are catalogued as they appear on the plate, thus the specimen on plate 15, fig.2 is numbered 15/2. General material is catalogued as T.1, T., etc.

Types and appropriate figured and general material will be deposited with a suitable museum prior to publication.

Map references of ground specimens are given to 5'. ZUGMAYER's type localities are to be found on the Geologische Karte des Hohe Wandgebietes (Niederösterreich) geol.Bundesanst., Wien, 1964, and when this is the case it is pointed out in the figure caption. Other map numbers refer to the Austrian

and Bavarian topographic maps mentioned in connection with the Programme of Study.

Figured specimens show the dorsal valve uppermost in anterior view and the pedicle valve uppermost in posterior view.

All specimens are Rhaetian unless otherwise stated.

LABORATORY TECHNIQUES

The internal structure of all species of which sufficient material was available was investigated using serial transverse grinding. Plaster casts of the specimens to be so treated were prepared first employing a rubber-like compound, Vinamold which can be heated to fluidity at a relatively low temperature. Following this the specimen was dipped in molten paraffin wax in order to restrict later etching to the ground surface, and then mounted in semi-solid modelling plaster with the posterior part of the lateral commissure vertical as described by AGER (1956). On drying the block was fixed to a steel plate with paraffin wax and the specimen ground using the apparatus described by HENDRY et. al (1961).

At suitable intervals (commonly 0.1mm., but less when passing through the dorsal umbo of rhynchonellids and more when the loops of zeilleriids were being ground) acetate peels were taken for which the dry technique was employed. The light oil (Honilo 50 - Fletcher Miller Ltd., London) used to lubricate the diamond grinding wheel was cleared with acetone from the abraded surface which was then washed, dried with acetone and etched for about ten seconds with 5% HCl. In this way a topography relative to the shell and its matrix is produced. Finally the surface was flooded with acetone and the dull side of a strip of acetate film pressed to it. The underside of the film in contact with the acetone becomes gelatinous and takes on the form of the etched surface. After allowing about a minute for drying the acetate peel was removed with forceps and examined under a microscope. In the case of imperfections a further peel was taken.

The acetate film employed was purple Acetobutyratfolie-Triafol BN, .04mm. thick, and kindly supplied free of charge by the Bayer Chemical Company of Frankfurt a. M., Germany. It was found suitable in all respects.

On completion of the grinding (disappearance of the crura, loop, spires etc.) all the peels taken were re-examined and about 14 selected for drawing. Each of these was placed in turn in a 35mm. slide holder and projected at a suitable magnification - usually x12 or x15. An accurate outline was obtained in this way and details of growth lines added using a microscope with

a magnification of x50. Subsequently these drawings were traced, then photographically reduced and printed on document paper. Care was taken throughout the drawing of sections to indicate as precisely as possible the varying pattern shown by the calcite crystals within the shell. This alters according to the orientation of the length of the crystal to the angle of grinding and reveals the shell layers, homology, and mode of growth of internal structures which cannot be seen in blacked in sections. The work of SCHUMANN (1965) and COPPER (1965, 1965a, 1965b, 1966) sets a high standard in the use of this technique and it must be regarded as indispensable to future systematic morphological studies. Text-plates 9 and 10 show the application of ornament in this thesis.

Photomicrographs of selected peels supplement the sections and were taken using an Asahi Pentax camera attached to a Leitz Orthlux microscope. Magnifications of x40 - x60 were found convenient for general use but x300 is practicable for more detailed work (see plate 9).

Specimens to be photographed were cleaned using an air abrasive machine and then coated with MgO by holding them over a small piece of burning magnesium ribbon. All photographs were taken on Adox KB 14 film with an Asahi Pentax camera fitted with a variety of extension rings. A black velvet covered board was used to obtain the background. Each plate was then made up using prints of a magnification of x2 mounted on exposed photographic paper, rephotographed on quarter plate negatives and finally reproduced on Ilfordprint Projection paper (R3.1P Grade 3).

TERMINOLOGY

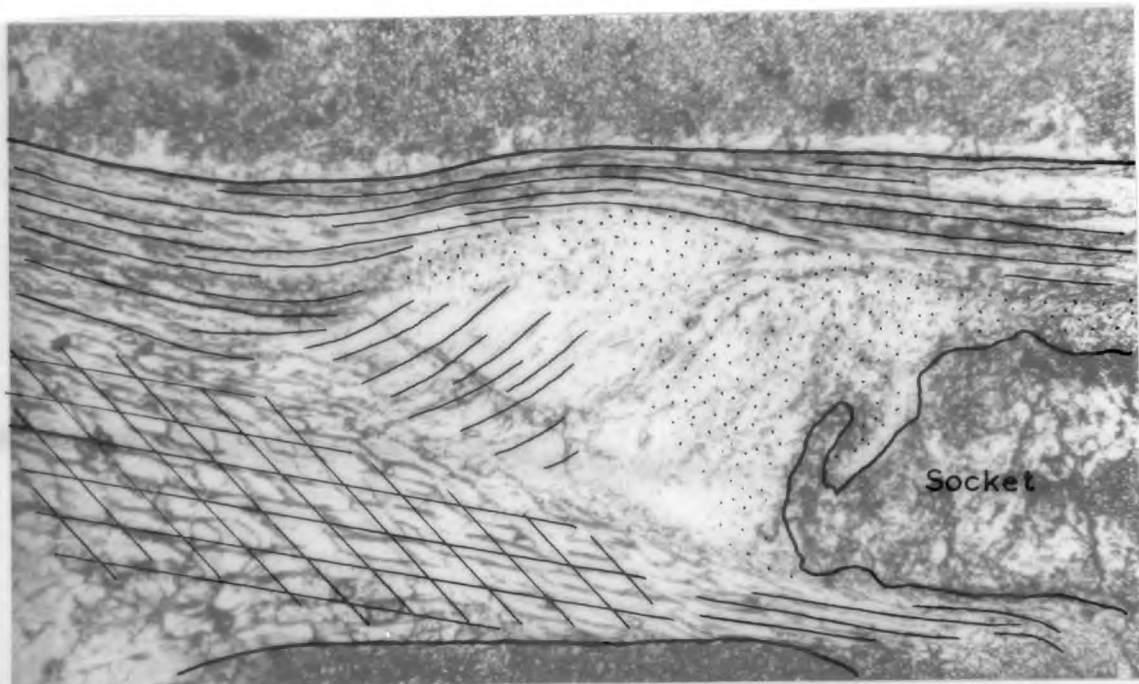
The terminology employed here is in all groups the same as that given in the Geol. Soc. Amer. treatise (1965) with the exceptions and additions discussed below.

1. Septalium

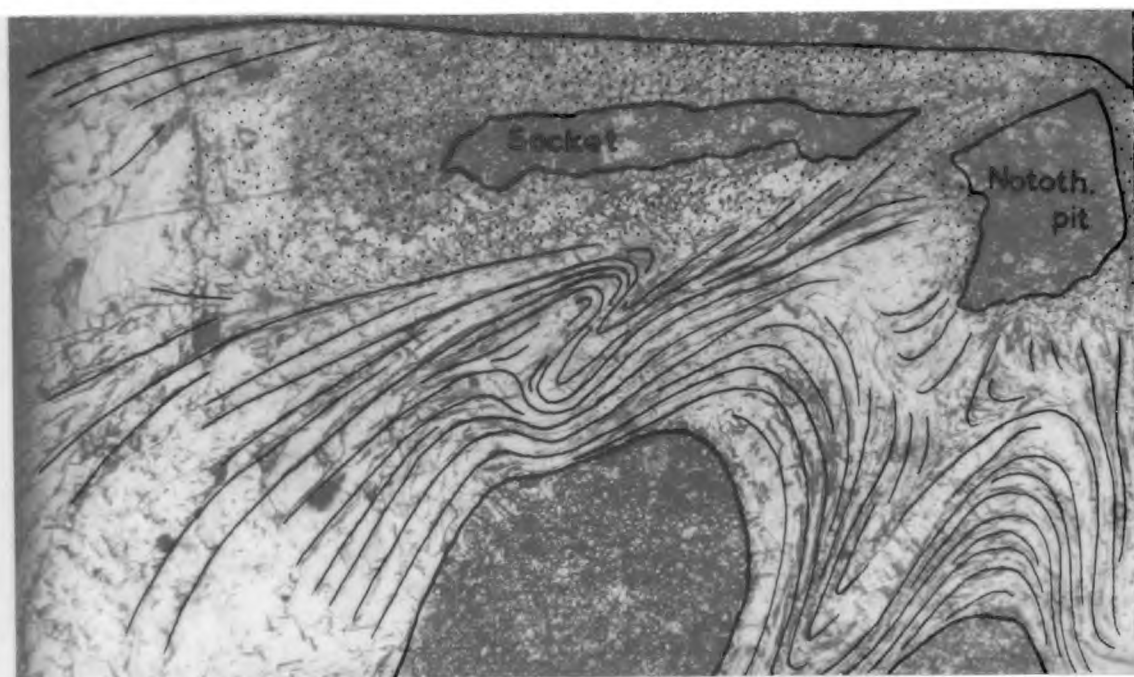
The term septalium is not used in this thesis. Since it was introduced by LEIDHOLD (1920) it has been so often misinterpreted, misused and credited with unwarranted importance that it is now quite useless as a descriptive term.

Text-plates 9 and 10

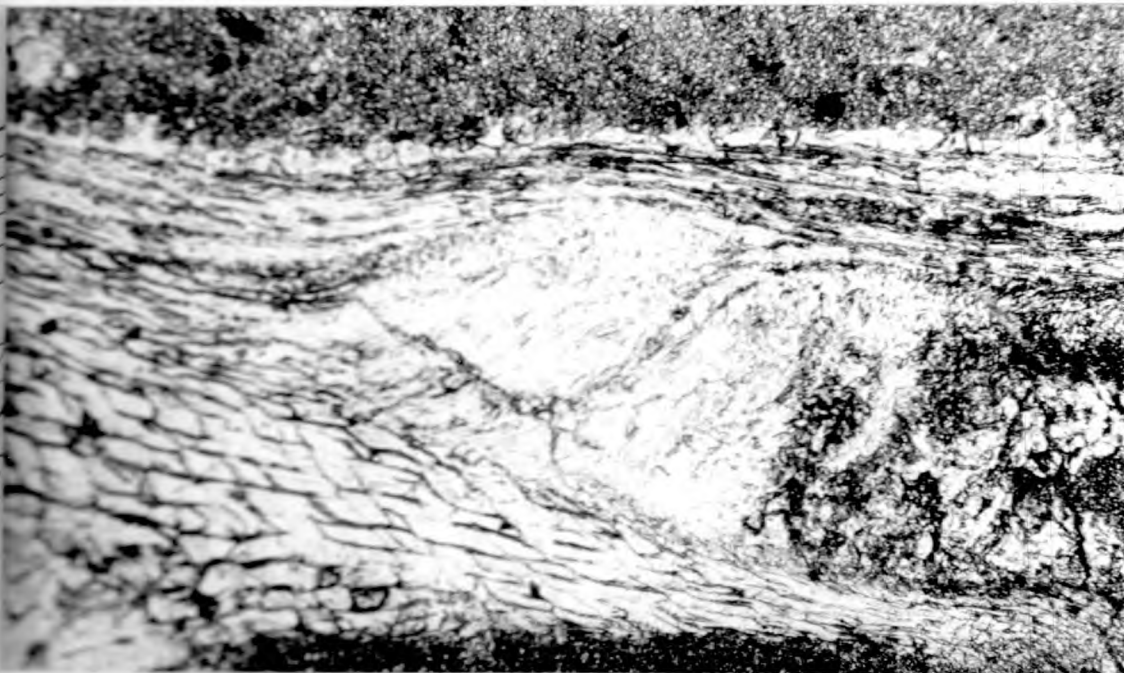
Transverse sections through the border of the tooth socket (plate 9), and the apex of the socket and notothyrial pit (plate 10), showing the use of ornament to indicate the growth lines and disposition of the fibres. Plate 9 - x 300; plate 10 - x 175.



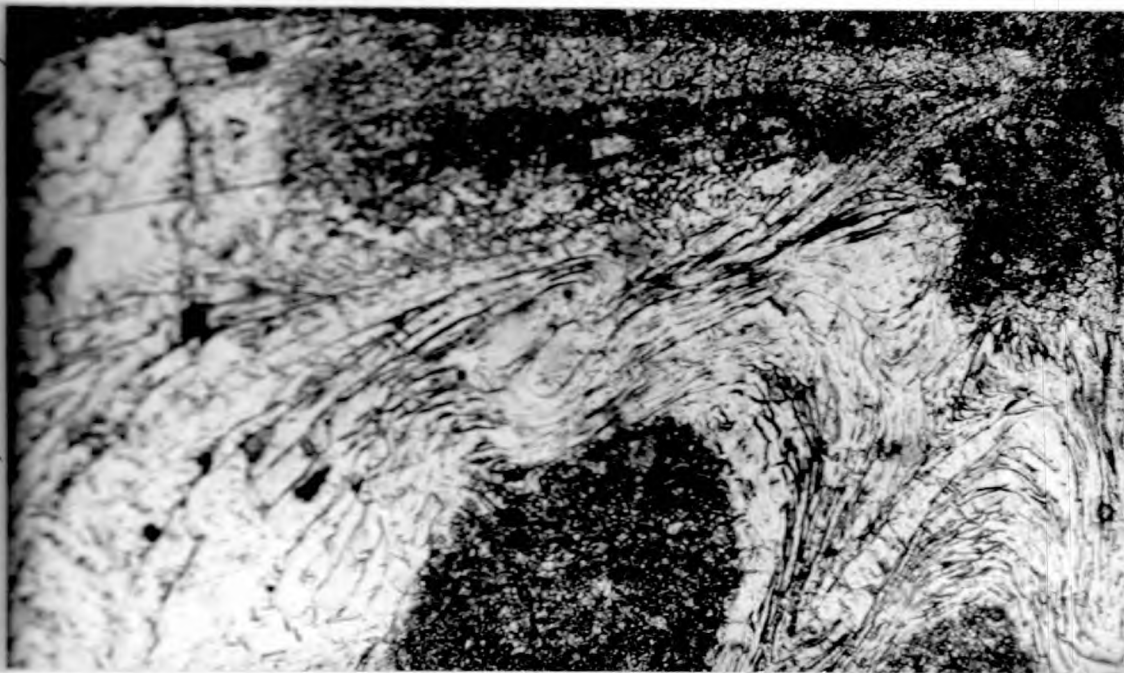
Text-plate 9



Text-plate 10



Text-plate 9



Text-plate 10

LEIDHOLD figured the apical structure of the brachial valve of Septaliphoria arduennensis in his description of that species and called the V-shaped trough, formed by the inner hinge plates, a 'septalium'. LEIDHOLD only gave a drawing of a silicified valve and because of the impossibility of deciphering the structural detail of the septalium, numerous multicostate species in which transverse sections show the inner hinge plates united and forming a trough above a median septum, have been placed in Septaliphoria. As a result the genus now apparently ranges from the Upper Triassic to the Upper Jurassic but certainly includes species quite different in structural detail. CHILDS (1966) gave a photomicrograph of a transverse section of the inner hinge plates of Septaliphoria and it is quite clear that, at least, the Rhaetian species formerly placed in the genus is quite distinctive and it is here removed as the type of a new genus Fissirhynchia. Study of the micro-structure of the hinge plates of other species with a 'septalium' will certainly reveal further diversity.

As well as the actual range of form encompassed by the term the form of the 'septalium' and often indeed, its apparent occurrence depends on the angle to the plane containing the hinge line at which the hinge plate and the median septum are ground. A low septum ground at a shallow angle may appear very tall and narrow inner hinge plates similarly ground appear wide and may simulate a median septum (e.g. text-fig. S.viii herein). The globosity of the brachial valve clearly affects the angle at which the umbo is cut and ROUSELLE (1965) drew attention to this problem.

In addition to being applied to rhynchonellids a 'septalium' has also been recognised in terebratulids. THOMSON (1926) preferred to describe the hinge plate as excavate but MUIR-WOOD (1934) adopted LEIDHOLD's term. This was unfortunate since the structure in terebratulids is different in function and development to that in rhynchonellids. In the latter group the function of the trough in the hinge plate is to anchor the diductor muscles. The crural bases are only united posterior of the plane of articulation where they can perform this function and in many Palaeozoic species a cardinal process is additionally present. Similarly, a cardinal process may lie in the apex of the brachial valve of terebratulids, e.g. Rhaetina and Austrilleria herein, but

the crural bases are commonly united anterior of the plane of articulation where diductor muscles cannot possibly have been anchored.

Because of this ambiguity in the use of septalium, the trough in the brachial valve of rhynchonellids is here called the muscle trough. This name emphasises the relation between the sessile structure in Pseudogibbirhynchia and its allies and that in septate rhynchonellids in which it is raised from the valve floor. Moreover it avoids any tendency to make an inappropriate comparison with the structure in the hinge plate of terebratulids.

2. Double deltidial plates

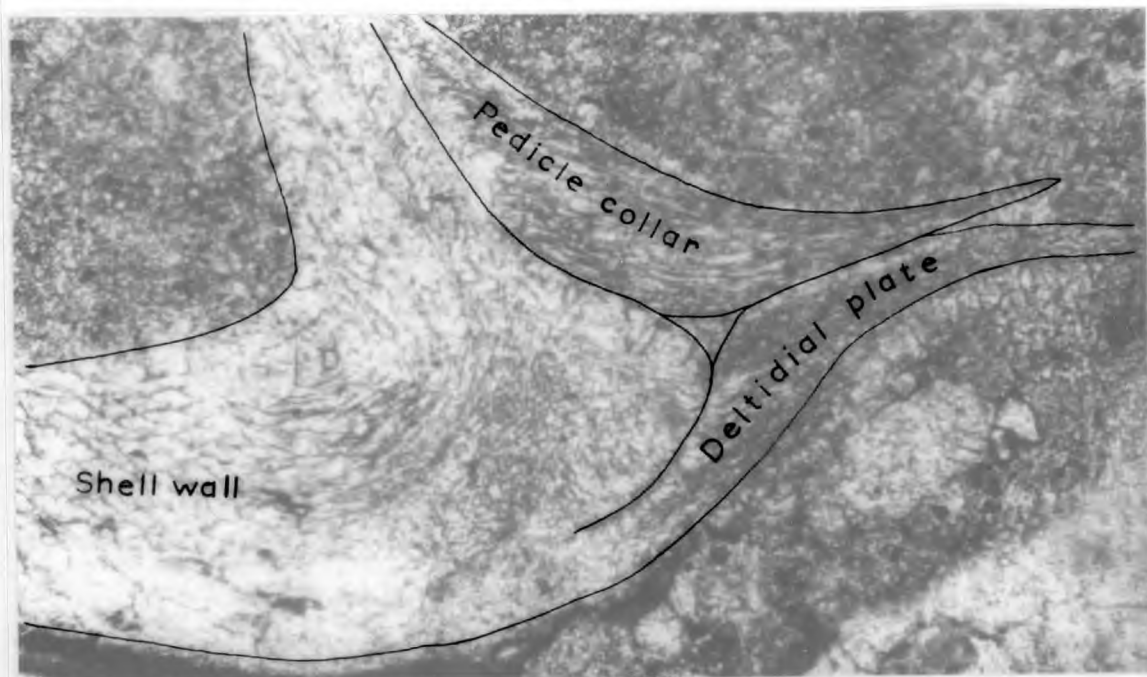
'Double deltidial plates' of the kind found in Calcirhynchia subrimosa were first described by AGER (1958) in the closely related species Cirpa langi. AGER's figures show hollow deltidial plates detached from the dental lamellae but, in fact, the appearance of hollowness is caused by the juxtaposition of quite normal plates with the pedicle collar and the description 'buttressed deltidial plates' is more appropriate and is used here.

In Cirpa, Calcirhynchia, and several other members of the Cirpinae, the ventral part of the pedicle collar adjoining the shell wall is deposited in the normal manner described by WILLIAMS (1956). The pediculate-outer epithelial junction in this region retreats anteriorly and restricts the pedicle with a ridge of secondary calcite. Deposition occurs in the resulting cavity and a block of callus is present between the pedicle and the shell wall (see text-fig. S.xvii). Laterally the pedicle is contained by the dental lamellae but dorsally it^{is} once again restricted by a ridge of calcite continuous with that on its ventral side. Medianly this part of the collar is split and it is the juxtaposition of the two segments with the deltidial plates which gives the appearance of hollowness (see text-plates 11, 12, 13). As in the case of the ventral arc of the collar, deposition occurs on the outer side of these two segments and the cavity becomes infilled.

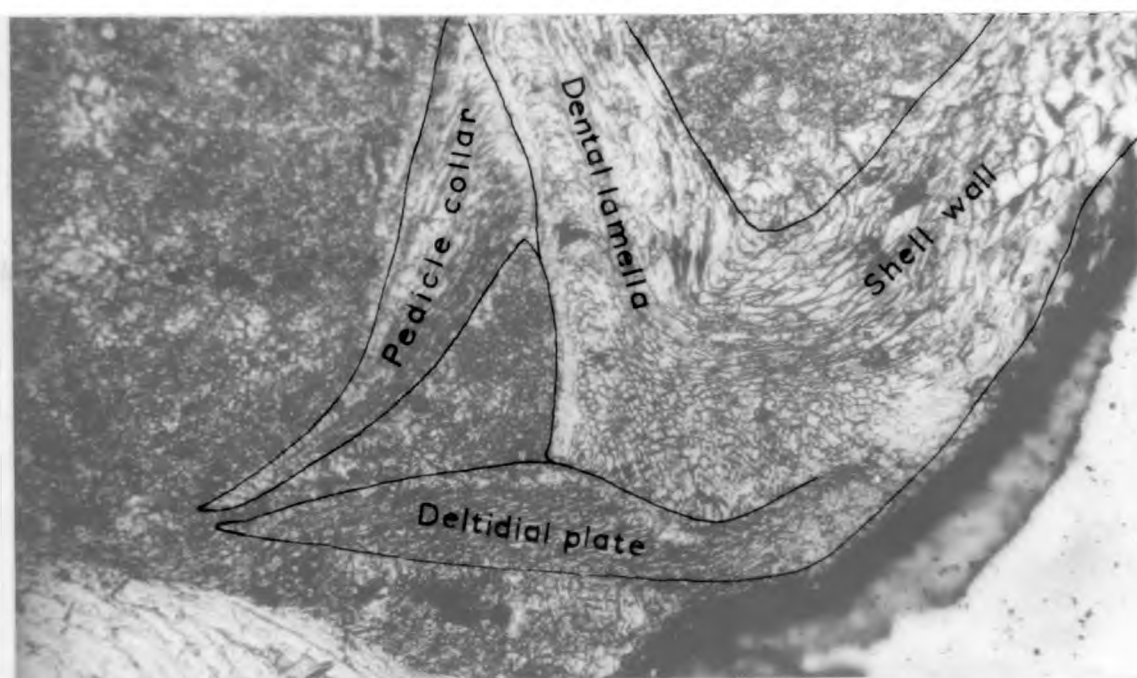
Throughout the formation of the pedicle collar the deltidial plates remain discrete and are never depositionally continuous with it as stated by WILLIAMS (1956). In fact the deltidial plates are deposited only in continuity with the main body of the shell. However, hollow plates continuous with

Text-plates 11 and 12.

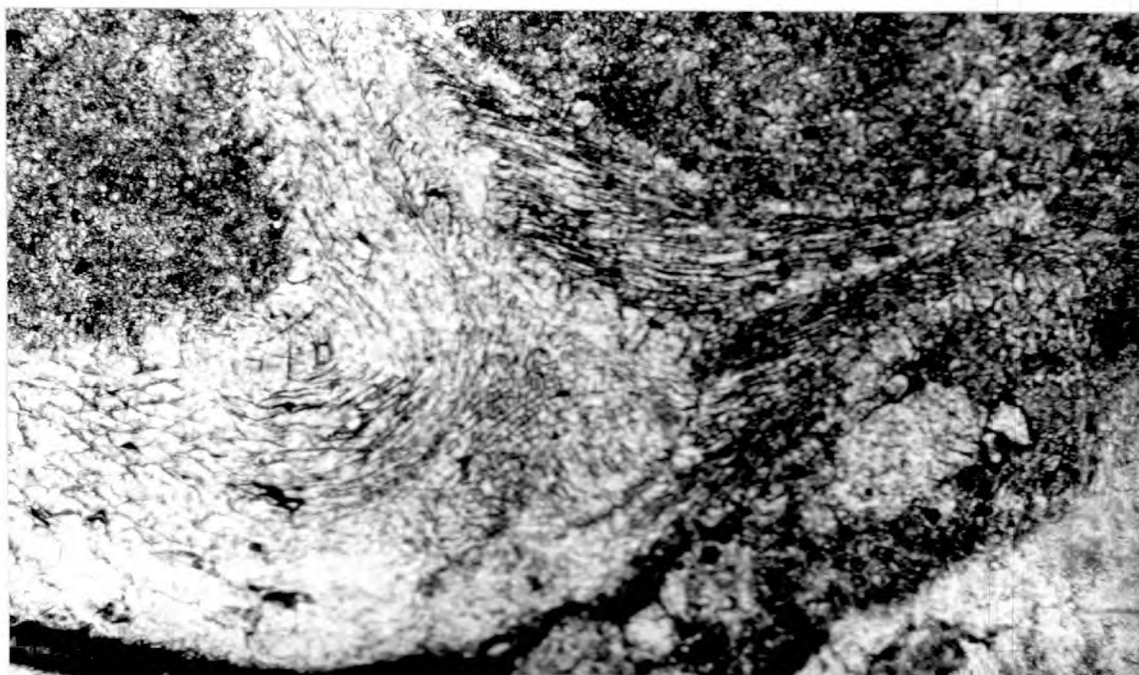
Transverse sections of the 'double deltidial plates' of Calcirhynchia subrimosa, showing the juxtaposition of the deltidial plate with the dorsal segment of the pedicle collar. Both x 300.



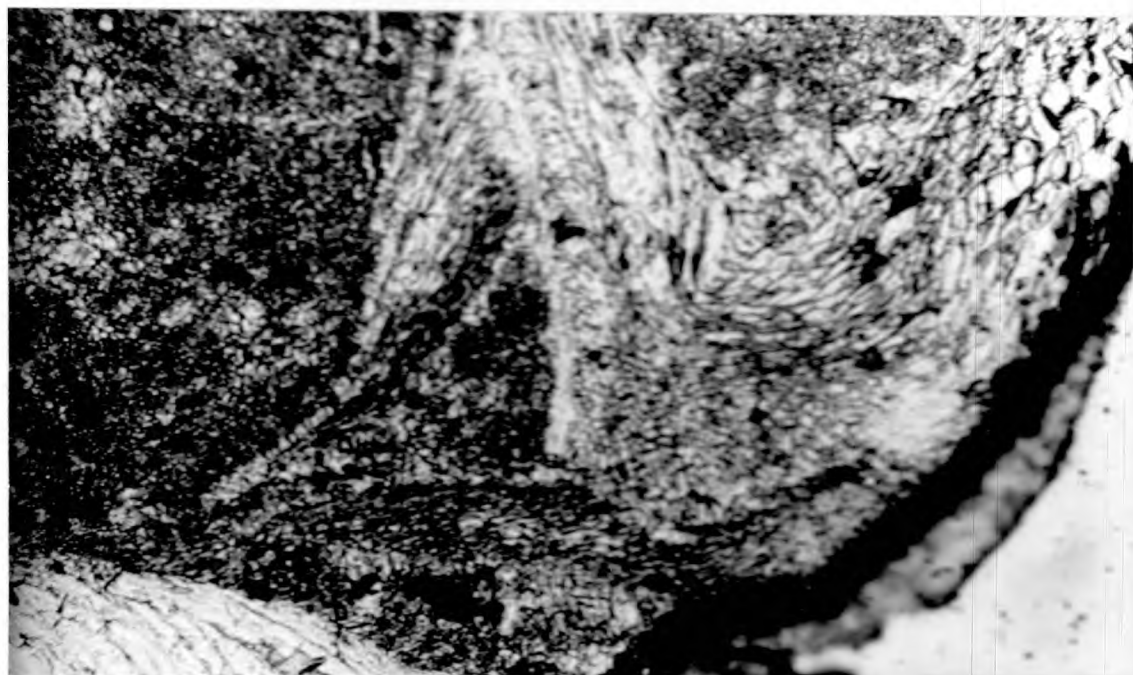
Text-plate 11



Text-plate 12



Text-plate 11



Text-plate 12



Text-plate 13

Transverse section of C.subrimosa showing the last remnant of the pedicle collar attached to the dental lamella. x 120.

the pedicle collar have been clearly figured in Mimatrypa by COPPER(1965), whilst in another atrypid genus, Desquamatia, similar plates are quite separate from the pedicle collar - COPPER (1966).

The deposition of deltidial plates is evidently of some complexity and requires further investigation.

3. Crura

Crural terminology in the rhynchonellids is still based on form and analogy and a broad revision using modern techniques to produce a classification based on microstructural homology is required. Although ROTHPLETZ's original (1886) terminology of raduliform, falciform and septiform emphasising as it does, that form is the sole basis of the grouping, is to be preferred to the modern translation of these to radulifer, falcifer etc. no change has been made here.

4. Descendent and Ascendent crural processes.

In the terebratulids the crural processes are described here as 'ascendent' or 'descendent' in reference to the direction of the processes when viewed from above. If ventrally directed as in Terebratula and Zeilleria they are ascendent, and if dorsally directed, as in Triadithyris, descendent.

SYSTEMATIC PALAEOLOGY

1

RHYNCHONELLIDA

Special Note

A paper covering the evolution of the Mesozoic rhynchonellids is at present being prepared by Dr.D.V.AGER, Dr.A.CHILDS and the writer. This necessarily involves agreement regarding the grouping of genera into families and subfamilies and possible modification of the classification given in AGER (1965). Prior to this agreement the several divisions outlined below are only suggested and not formally proposed.

ADDENDUM

Note re Family Wellerellidae LIKHAREV. (See Calcirhynchia herein).

There is confusion over the date of this family and its subfamily. Both AGER (1965) and SCHMIDT (1965) give the authorship and date of the family as 'LIKHAREV in RZHONSNITSKAYA, 1956'. However, RZHONSNITSKAYA in 1956 only lists (p.24) 'Wellerellidae LIKHAREV, 1955' without a diagnosis, and this is insufficient to give the name validity (ICZN Art.13). In citing LIKHAREV, 1955, RZHONSNITSKAYA referred to the manuscript of Osnovy Paleontologii not to be published until 1960 (see footnote in RZHONSNITSKAYA (1959)).

The first valid use of the name Wellerellidae the writer has been able to find is in RZHONSNITSKAYA (1959 p.29) in which a diagnosis of the family is given (again credited to LIKHAREV 'in litt'). However, SCHMIDT (1965 p.590) refers to the source of the subfamily, Wellerellinae, as 'nom.transl. LIKHAREV in RZHONSNITSKAYA, 1958, p.114'. This 1958 paper has not been traced: it is not to be found in the Zoological Record and is not cited by RZHONSNITSKAYA herself in 1959. Moreover DAGIS (1963) in using both the family and subfamily does not recognise this paper. If it does exist then it appears that both the Wellerellidae and Wellerellinae owe their date to it. If not then they should be as follows:

Family Wellerellidae LIKHAREV in RZHONSNITSKAYA, 1959

Subfamily Wellerellinae LIKHAREV in RZHONSNITSKAYA, 1959 (nom. transl. LIKHAREV in RZHONSNITSKAYA, LIKHAREV and MAKRIDIN, 1960, p.247).

Order Rhynchonellida KUHN, 1949

Superfamily Rhynchonellacea GRAY, 1848

Family Rhynchonellidae GRAY, 1848

Subfamily Cyclothyridinae MAKRIDIN, 1955

Remarks:

This subfamily was founded by MAKRIDIN (1955) on a genus recognised by BUCKMAN (1918 p.14) as more than generically separable from the normal Jurassic rhynchonellids. RZHONSNITSKAYA (1959) placed a large number of genera in it, many of which were to be removed, principally by AGER (1965) when he established the Tetrarhynchiinae for the 'ordinary - looking rhynchonellids constituting 'the bulk ... of the Mesozoic forms'.

DAGIS (1963) raised the Cyclothyridinae to a full family - the Cyclothyrididae (nom.correct herein pro Cyclothyridae MAKRIDIN, by DAGIS 1963, p.53). However the group is retained here as a subfamily, mainly because it and the Tetrarhynchiinae (not yet used by a Soviet author) are difficult to distinguish in practice and can only be regarded as equal divisions. The best course may well be the restriction of the Cyclothyridinae and the creation of several small subfamilies within the Rhynchonellidae, rather than the elevation of present groupings and the precipitation of overweighted familial distinctions.

At the same time as revising the contents of the subfamily AGER (1965 p.600) noted that canalifer crura are one of the best criteria for recognising the group. Of the Rhaetian genera only Fissirhynchia has this form of crura and is here placed in the Cyclothyridinae. It is the earliest known member of the subfamily, possibly extending back to the Middle Triassic, and may represent its central stock.

Type species:Rhynchonella fissicostata SUESS, 1854 p.30, pl.4, figs.1-4Range and Distribution: (records of type species only)Norian of Slovakia (Drnava, Stratenska hornatina), N. Rumania (Bukowina), E.Bulgaria (Luda-Kamcia), the Crimea, and Caucasus.Rhaetian of the Northern Alps, central Italy (Siena), Slovakia (Hybe), N.W.Rumania (Apuseni Mts.)Liassic of the Northern Alps (Hierlatz), and Sicily.Possibly present in the Lower Tagling Lst. of Spiti (Himalayas), = ?Rhaeto-Liassic, but STOLICKA^Z's record (1866 p.67) has not been confirmed by later workers.Included species:At present only the type species is recognised as belonging to Fissirhynchia but there are several North Alpine Liassic species which may be members of the genus, e.g.?F.latifrons GEYER, 1889 p.54, pl.6, figs.25-31?F.polyptycha OPPEL, 1861, p.544, pl.12, fig.4

A probable early member widely distributed in the Anisian is

?F.mentzelii BUCH, 1843, p.253, pl.2a, figs.1-3

(see also BITTNER 1890, p.12, pl.32, figs.14-16)

Derivation of Name:

From Latin, findere, fissum-to cleave; referring to the prominent branching of the ribbing, and a partial tautonym of the type species.

Diagnosis:

Medium sized rhynchonellids. Fully ribbed; ribs sharp, branching prominently near umbones. Pedicle foramen submesothyrid in position. Outer hinge plates arched; inner hinge plate raised by long median septum. Crural bases calcate; crura canalifer.

Remarks:-Timorhynchia AGER (in press) known only through its type species from the Late Triassic of Timor, appears to be a close relative of Fissirhynchia. Sections of T.nimassica (text-fig.Siv), kindly made available by Dr.D.V.AGER, show that Timorhynchia has a similar hinge plate, a long and deep median septum, typical cyclothyrid canalifer crura and laterally expanded teeth. Externally however, the types of

the two genera are extremely different: F.fissicostata is medium sized and characterised by sharp, deep ribs which persist to the umbones, whereas T.nimassica is very much smaller with blunt ribs hardly discernible near the apices of the valves. The two genera are thus readily distinguishable.

MOISSEIEV (1947) and DAGIS (1963) placed F.fissicostata in the Late Jurassic genus Septaliphoria, presumably because they regarded a 'septalium' as diagnostic. However, very many species have the point of attachment of the dorsal diductors raised from the valve floor and only after a close examination of the details of the form of the resultant 'septalium' (= muscle trough herein), can it be used as a generic character. DAGIS later (1965 p.176) listed 'Septaliphoria(s.l.)' in the Rhaetian and obviously felt that fissicostata needed reconsideration.

Fissirhynchia fissicostata (SUESS), 1854

Plate 1, figs.1-10; plate 2, figs.1,2;
text-figs. S.i,ii; text-plates S.1,2.

- 1854 Rhynchonella fissicostata SUESS, p.30, pl.4, figs.1-4
- 1861 Rhynchonella fissicostata SUSS; GÜMBEL, p.401
var.longirostris GÜMBEL, p.401
var.applanata GÜMBEL, p.401
- 1864 Rhynchonella fissicostata SUSS; DITTMAR, p.152
- 1868 Rhynchonella fissicostata SUESS; QUENSTEDT, (partim) p.147, pl.40,
figs. 91,92
- 1880 Rhynchonella fissicostata SUESS; ZUGMAYER, p.36, pl.4, figs.13-18
var.longirostris GÜMBEL, p.36
var.applanata GÜMBEL, p.36
var.inflata ZUGMAYER, p.37
- ?1887 Rhynchonella cfr.fissicostata SUESS; di STEFANO, p.63, pl.2, figs.
36-38
- 1890 Rhynchonella fissicostata SUESS; BITTNER, p.280
- 1891 Rhynchonella fissicostata SUESS; SIMONELLI, p.636, pl.1, fig.15
- 1905 Rhynchonella fissicostata SUESS; von ARTHABER, pl.50, fig.5
- 1917 Rhynchonella fissicostata SUESS; GOETTEL, p.104, pl.7, fig.1
- 1947 Septaliphoria fissicostata SUESS; MOISSELEV, p.72, pl.8, fig.5
- 1958 Rhynchonella fissicostata SUESS; MAHEL, p.127, pl.3, figs.1-3
- 1958 Rhynchonella sp.ind., aff.fissicostata SUESS; MAHEL, p.129, pl.3,
figs.4-9
- 1962 Rhynchonella fissicostata SUESS; PRÉDA, p.62, pl.1, fig.4
- 1963 Septaliphoria fissicostata (SUESS); DAGIS, p.50, pl.3, figs.7-11
- non 1927 Rhynchonella fissicostata SUESS; MOISSELEV, p.751, pl.23, figs.21-24

Lectotype:

The original of SUESS 1854, pl.4, fig.1, was selected by DAGIS 1963, p.50. This specimen has not been traced in the Geol. Bundes. Vienna, and must be presumed lost.

Dimensions of Lectotype:

Measurements taken from SUESS's figure - length 21.3mm., breadth 24.7mm., thickness 14.6mm.

Type Locality:

Given by SUESS as 'Mandling Wand bei Wallegg'. This probably refers to the lower part of the Vorder Mandling just behind the village of Waldegg, in the Piesting Tal, where material would have been collected from loose blocks piled between vineyards. Although the area is now forested specimens can still be found.

Range and Distribution:

As for the genus.

Diagnosis:

Rounded pentagonal in outline; 10-26 ribs present. Otherwise as genus.

Description.-

Fissirhynchia fissicostata is a medium sized, biconvex rhynchonellid, varying in outline from transversely oval to rounded triangular. Early authors recognised and named several form varieties and these are dealt with under Remarks. Normally it is ornamented with between 15 and 20 sharp ribs, but exceptionally may have as few as 10 or as many as 26. Characteristically 5-9 of them reach the extreme apex of the valves whilst the remainder arise by primary, or occasionally secondary bifurcation within 3 or 4 mm. of the umbones. SUESS remarked on this feature in his original description and from it chose the specific name. The writer has also found it to be a constant character despite GOETEL's remark (1917 p.105) that it occurred in only half his material (from Hybe, Slovakia). The anterior commissure is broadly plicate, involving 5-9 brachial ribs (rarely as few as 3), and most specimens show a marked depression of the resultant broad, slightly rounded ligule continuous with the flat median field, but the fold is absorbed in the lateral convexity of the dorsal valve. The pedicle opening is rimmed and submesothyrid in position beneath a suberect to erect beak of varying prominence, - it may be low and pressed close to the brachial valve with an inconspicuous pedicle opening in transversely oval individuals (e.g.pl.1, figs.1,2), or it may be protrusive with a

large foramen and give a triangular outline to the specimen (e.g. pl.1, figs.9,10). The beak ridges are not sharp but the area is impressed, clearly defined and matched by smooth, somewhat sunken fields on the cardinal flanks of the pinched brachial valve. Individuals vary considerably in profile from the rather inflated equi-biconvex specimens of pl.1, figs.1 and 2 to those with very flat pedicle valves as in pl.1, fig.5; there may be both stratigraphical and environmental significance in this variation and it is discussed under Remarks below. In anterior or posterior view the pedicle valve is the flatter and commonly the brachial valve is medianly accentuated.

The delthyrial cavity is rounded and may have a considerable padding of callus as in text-fig. S.ii where the lateral cavities are also thickened.

The muscle trough is commonly U-shaped and raised by a long, slender median septum. Its form and development are clearly seen in text-fig. S.i and text-plate S.1. The septum may be tall (e.g. DAGIS 1963, text-fig.15) or it may be low and only keel the muscle trough, (e.g. sections herein). The outer hinge plates are characteristically arched and the inner socket ridges therefore lack emphasis. The crural bases are calcate and small, and the crura themselves are of the canalifer type.

Remarks:

In addition to being well-known in the Norian, F. fissicostata is the most widely distributed and abundant of the Rhaetian rhynchonellids. Its distribution through several environments is reflected in the variation of adult shape and ribbing, and this has been discussed in detail in the Ecology section. Several early authors used varietal names for the forms they described but none of them are retained here. GÜMBEL (1861 p.401) distinguished 'zwei verwandte kleinere Abarten, welche wahrscheinlich nur junge Individuen sind' - var. longirostris and var. applanata. To these ZUGMAYER (1880 p.36-7) added 'dem Beinamen inflata for the typical 'vollen Formen mit kurzem, oft fast angepressten Schnabel und tief eingesenkten Schlosskanten'. In addition to his own variety he figured what he considered to be examples of GÜMBEL's varieties and these are refigured on pl.1, figs. 7 and 8. GÜMBEL himself gave only descriptions but from them it is clear that his varieties are indeed young individuals as he thought. He noted both to be small and almost

TEXT-PLATES S.1 and S.2

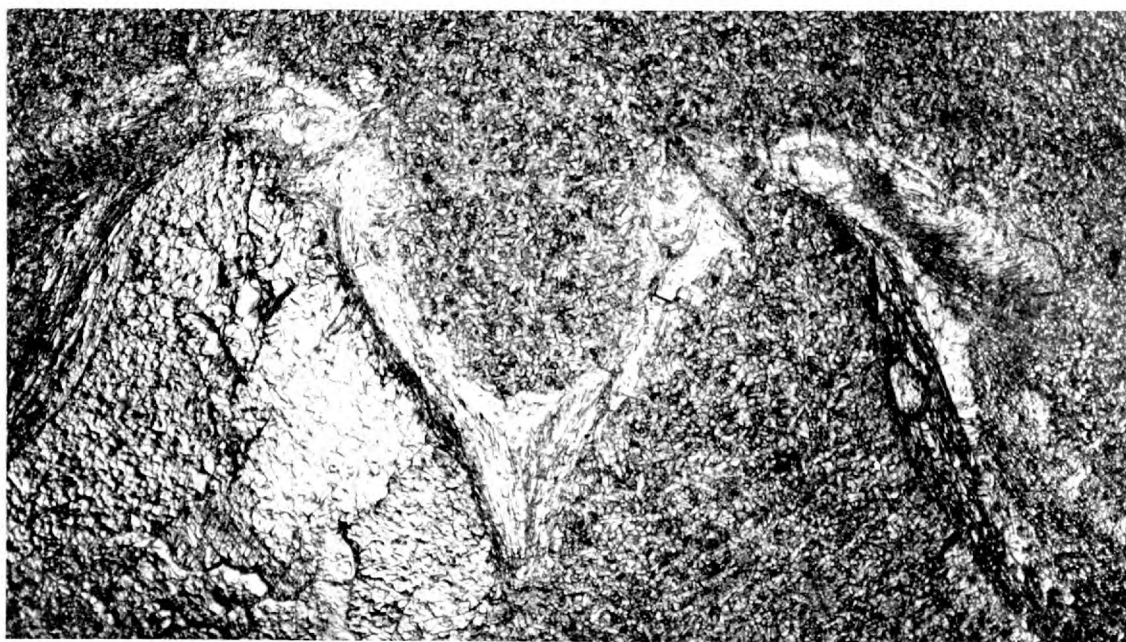
Fissirhynchia fissicostata (Suess)

Text-plate. S.1

Transverse section through the central part
of the hinge plate of Fissirhynchia fissicostata,
showing the socket plates bounded by the inner
socket ridges, the arched inner hinge plates, the
crural bases, and the U-shaped, keeled muscle trough.
Detail of section 3.05, text-fig.S.i x60.

Text-plate. S.2

Transverse section through the central part of the
hinge plate of a second specimen of F.fissicostata showing
the markedly different form of the hinge trough.
Detail of section at 3.1mms. of specimen in text-fig.
S.ii x60.



Text-plate S.1



Text-plate S.2

rectimarginate and the depressed, anteriorly rounded var.applanata is certainly composed of typical immature members of the species. Var. longirostris includes the young of elongate forms with prominent beaks and large pedicle openings (e.g. pl.1, fig.10). Elongate individuals occur commonly in the more coarse detrital limestones and contrast with the transversely oval forms found in dark calcilutites.

In using 'Abarten' and 'var.' GÜMBEL cannot be considered to have clearly established applanata and longirostris as subspecies (see ICZN Art.45). Since applanata is simply a typical young specimen and longirostris is only representative of an ecological type found in many species, neither are here recognised as subspecies. Similarly ZUGMAYER's var. inflata is regarded as infrasubspecific.

Specimens from the late Norian crinoidal limestone of Drnava are notable for the transverse flatness of their pedicle valve, and MAHEL (1958 p.129) described similar specimens from the late Norian of the Slovakian Stratenka hornatina Mts. as 'Rh'.sp.ind., aff.fissicostata. At Drnava, and at three of MAHEL's localities, the flat forms occur together with more typical, inflated F.fissicostata and all MAHEL's specimens are here referred to that species, although no specimens comparable with the exceptional Slovakian individuals have been seen by the writer from a North Alpine Rhaetian locality. Even individuals with a similar rib depth and density (e.g.pl.1, fig.3), from possible facies equivalents, do not show this marked flatness. It therefore seems likely that stratigraphy and perhaps geography are partly responsible for the richness of these forms in Slovakia.

F.fissicostata has also been reported from the Liassic on several occasions. RENEVIER's unillustrated record (1864 p.46) from the Liassic of S.Switzerland was not substantiated by either HAAS(1885) or PETERHANS (1926) who both considered RENEVIER's localities and material. NEUMAYR (1879 p.8) listed the species from the early Liassic of Zlambach Graben, Pfonsjoch and Breitenberg but also gave no figures.

GEYER (1889) only figured one of the two specimens he collected from Hierlatz, but both are figured here (pl.2, 1 and 2). The sharpness and branching of the ribbing, the pointed beak, pinching of the brachial umbo and the indentation of the area are all characteristic of fissicostata. The only point of difference is that the fold is a little more prominent

than in the Rhaetian specimens, but despite this they are referable to F.fissicostata without hesitation. The only doubt is over the stratigraphy of Hierlatz. The Liassic sediments there are found in small pockets on an eroded surface of late Triassic Dachsteinkalk from which F.fissicostata and Rhaetina gregaria, also well known in the Rhaetian, could have been derived. This possibility is discussed in more detail in Remarks under R.gregaria.

The occurrence in the Liassic of Sicily documented with figures by di STEFANO (1887) may be correct, but his two specimens are markedly more depressed than is common in adults of F.fissicostata and, as GEYER (1889 p.57) noted, they approach the form of GÜMBEL's var. applanata and perhaps they are indeed slightly immature F.fissicostata. Di STEFANO included 'Rh.'tauromenitana SEGUENZA in his synonymy and some controversy existed between him and SEGUENZA over the stratigraphy and faunal identifications of the ?Rhaetian and Liassic in the Taormina area (see also ROTHPLETZ 1886 p.171).

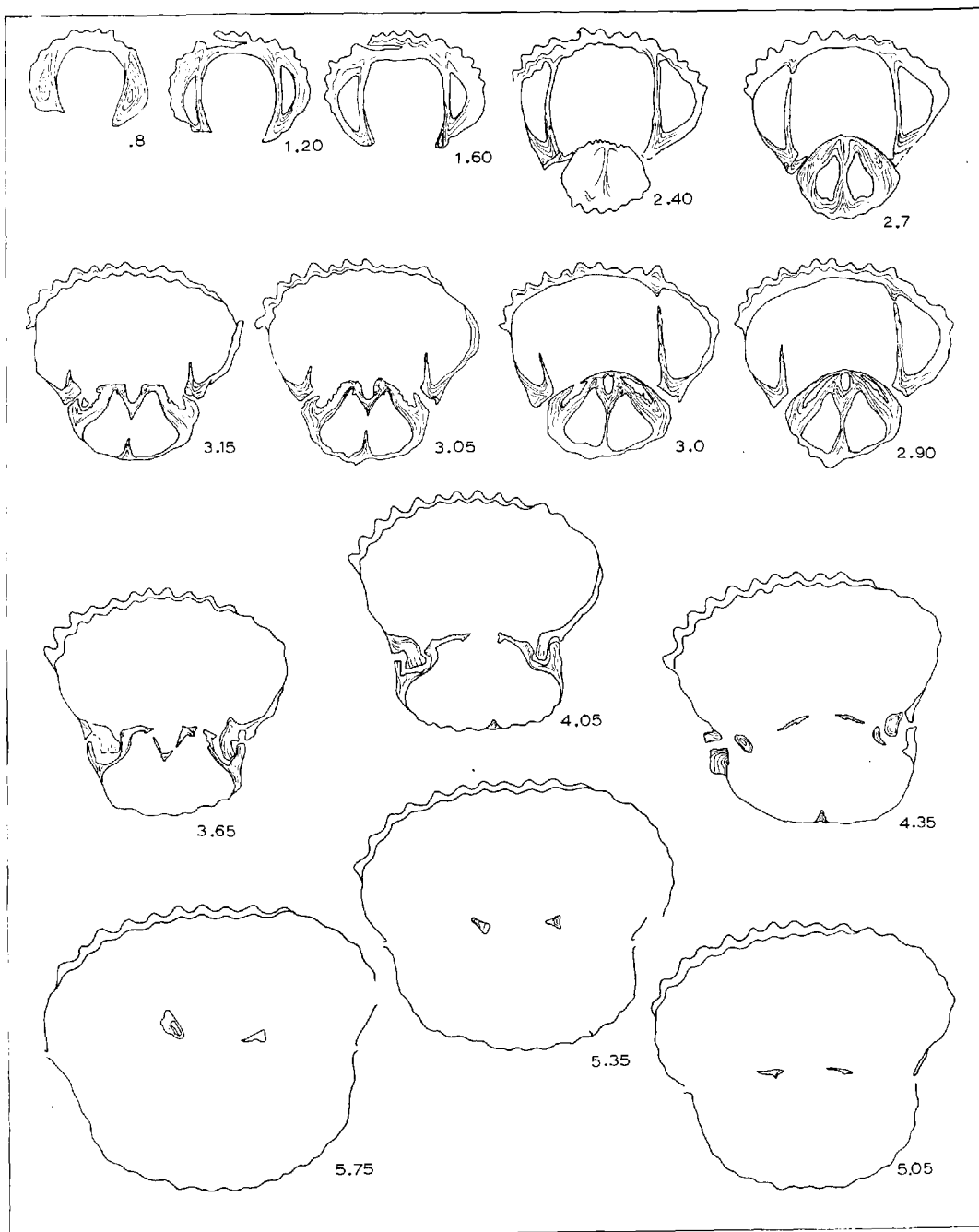
One of the specimens figured by SCHAFHÄUTL as Terebratula subrimosa (1851, pl.7, fig.4) may belong to this species but since his fig.3, which is certainly distinct, has been chosen as lectotype, (herein). F.fissicostata remains unaffected.

Dimensions of Figured Specimens:

	length	breadth	thickness
1/1	17.6	20.0	13.7
1/2	17.1	19.2	14.0
1/3	17.7	19.3	11.8
1/4	17.5	18.5	12.6
1/5	16.9	22.0	10.9
1/6	14.1	15.7	7.6
1/7	11.7	17.9	9.6
1/8	18.6	14.1	9.6
1/9	16.0	15.7	11.8
1/10	19.1	17.4	13.1
2/1	21.1	24.3	15.8
2/2	22.0	24.0(d)	15.5

Material:

Vorder Mandling, by Waldegg, Piesting Tal, (type locality, see above)
 - 5, T.6; Brand, Piesting Tal - 1, T.7; Ober Kaisersteffel, Piesting Tal
 - 10, T.8; Hirtenberg, Triesting Tal, nr.Wr.Neustadt - 5, T.9;
 Kitzberg by Neusiedl, Piesting Tal - 4, T.11; Vorder Mandling, by
 Waldegg, locality in 'Starhenbergkalklagen' on Hohes Wandgebietes, Geol.
 Bundes. Vienna - 15, T.13; Hohe Mandling, Piesting Tal, forest path
 630 - 670m. - 4, T.14; Steinplatte above Waidring, 4, T.10; Lofer Graben,
 by Reit im Winkl - 5, T.12; Hybe, Slovakia, 6, T.15; Val Frunsi, Ferice,
 Arieseni, N.W.Rumania - 8, T.16; Tarkăița, Moneasa, W.Rumania - 8, T.17;
 'Mandlinger Wald', Piesting Tal (as T.6 or T.13) - 11, B.M.N.H., B 39204.

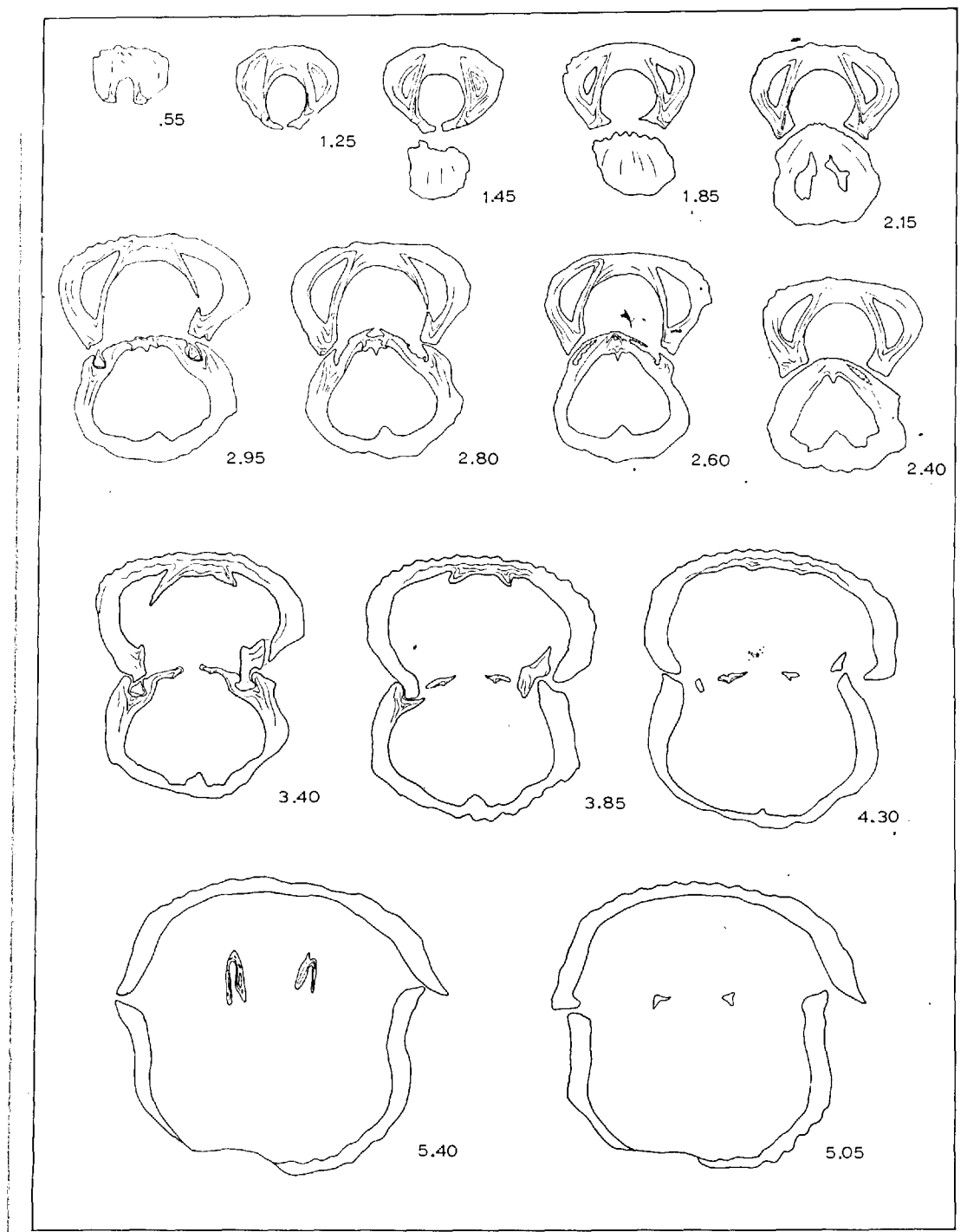


Text-fig. S.i

Serial transverse sections of *Fissirhynchia fissicostata* (SUESS). Rhaetian; specimen from the Pal. Inst. Univ. Vienna, labelled 'Kitzberg', - by Neusiedl, Piesting Tal, Lower Austria;

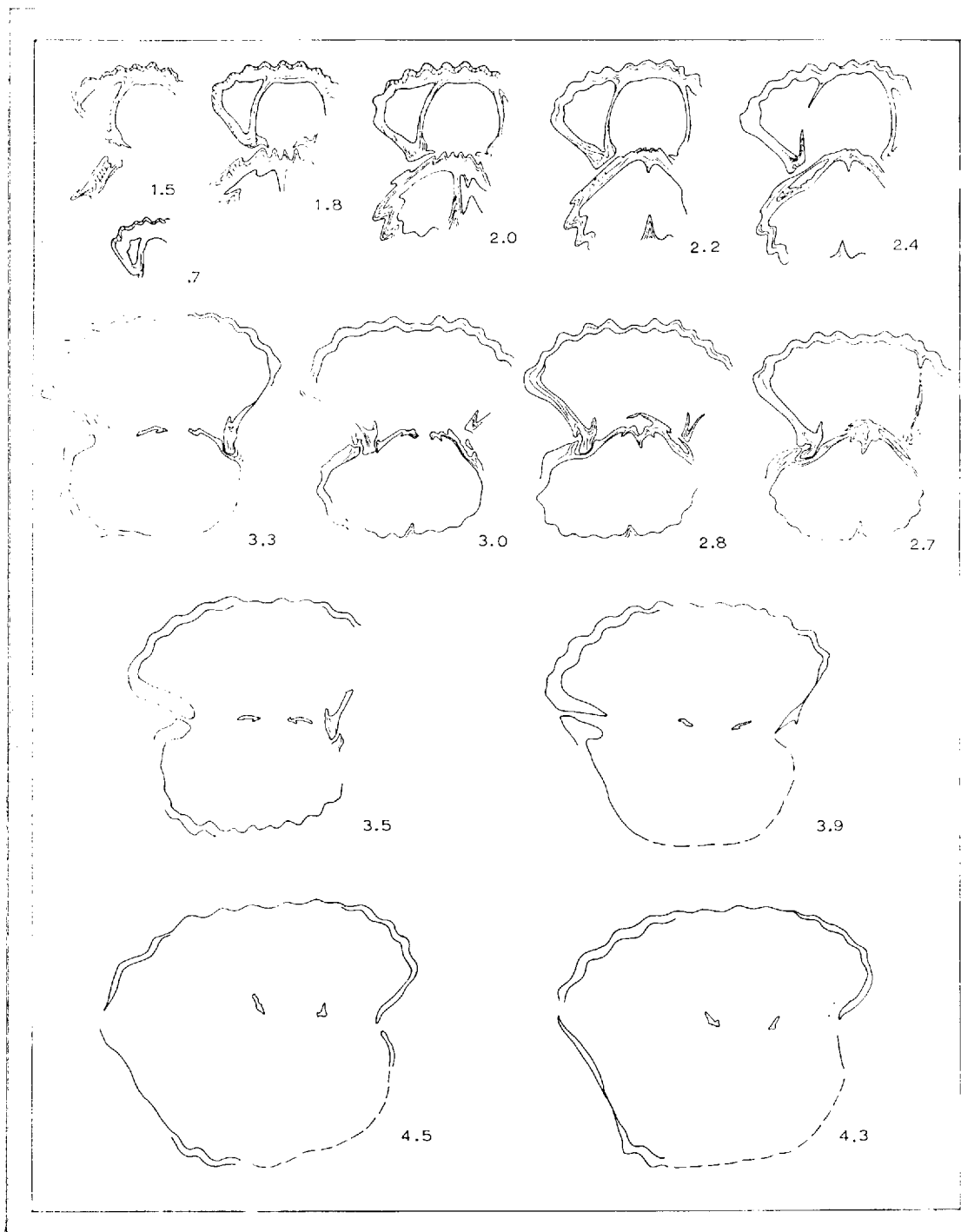
x4 Crura end 5.85mm. Total length of specimen 17.3mm.

PC.Nr.2.



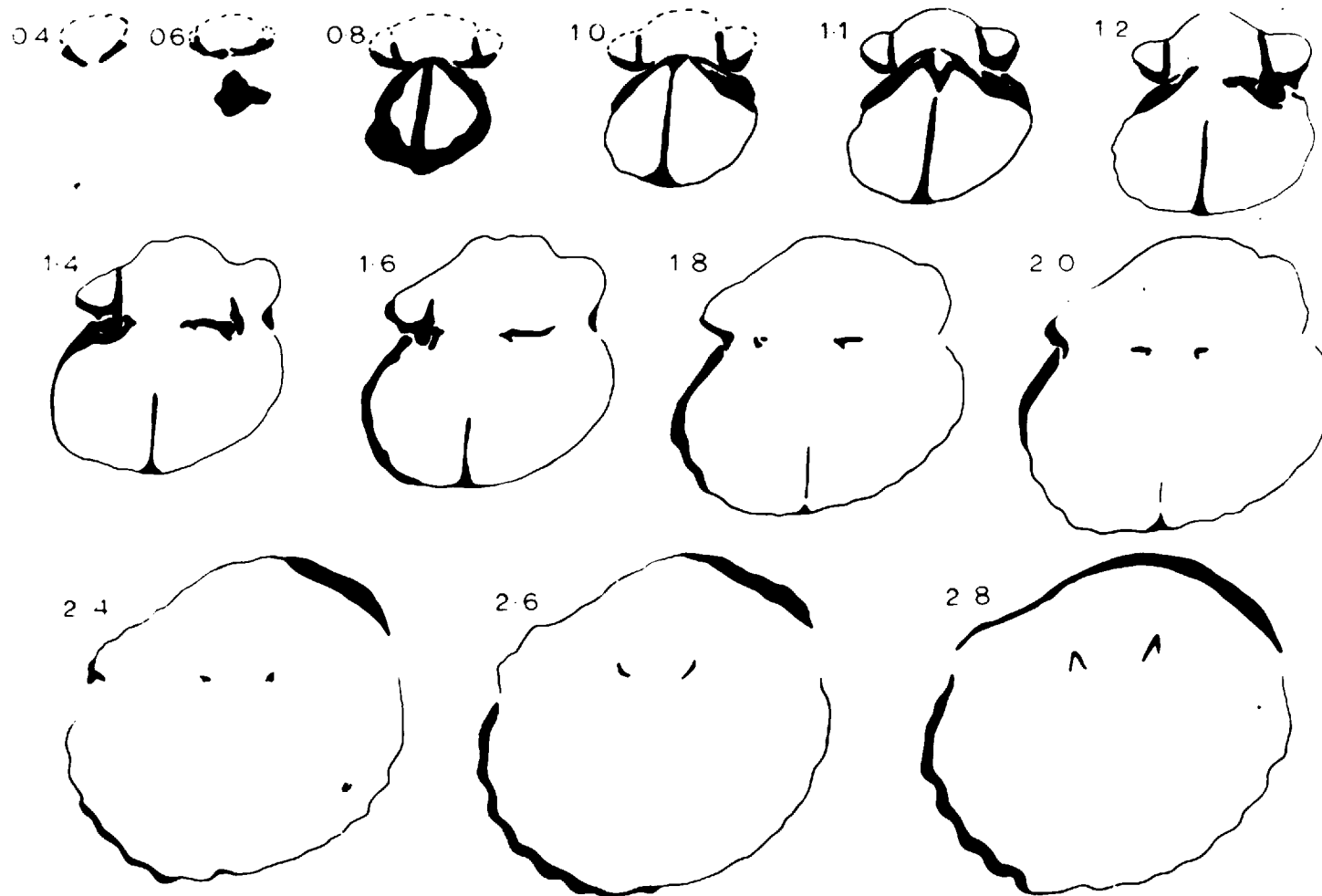
Text-fig. S.ii

Serial transverse sections of Fissirhynchia fissicostata (SULESS). Rhaetian; Auf der Mandling by Waldegg, Piesting Tal, Lower Austria; 47°52'40''N. 33°43'45''E. Locality indicated on Hohe Wandgebietes, Geol.Bundes.Vienna. x4 Crura end 5.5mm. Total length of specimen 19.0mm. PC.Nr.12.



Text-fig. S.iii

Serial transverse sections of Fissirhynchia fissicostata (SULESS). Late Norian; Bleskovy pramen, by Drnava, north west of Plesivec, S.Slovakia. x4 Crura end 4.7/mms. Total length of specimen 11.0mms. PC.Nr.9.



Text-fig. S.iv

Timorhynchia nimassica (KRUMBECK). Upper Triassic, Aitutu Formation, near Allanbutu, Portuguese Timor. ex. AGER - '... Halorella and its relations.' in press.

Sections provided by Dr.D.V.AGER. x7

Subfamily Tetrarhynchiinae AGER, 1965

Remarks:

The Tetrarhynchiinae contains twenty three of the fifty nine genera in the Rhynchonellidae (in AGER 1965), and the inevitable diversity of such a large assemblage makes it difficult to recognise the character of the lineages it groups. Small numbers of genera, apparently forming continuous morphological stocks, may therefore be isolated as subfamilies with just the same gain in clarity as the Rhynchonellinae gives to the cynocephalous Homeorhynchia - Costirhynchia - Rhynchonella stock of the Jurassic. One of the genera which appears to have sufficient allies to make a useful subfamily is Piarorhynchia, and this is discussed in detail below.

Piarorhynchia was first recognised in Europe (BUCKMAN 1918) where it is widespread in the Liassic (AGER 1959). Since then two species - and probably a third which was placed in Sakawairhynchia - have been recorded in Alaska (AGER and WESTERMANN 1963), eleven in the Late Triassic of N.E. Siberia (DAGIS 1965), and several of the generically undetermined species described by TOKUYAMA (1957) from the Carnian of Japan also belong here. In addition sections kindly provided by Dr. D.V. AGER show that 'R'. trinodosi BITTNER from the Anisian can be placed in Piarorhynchia thus confirming the external appearance. Finally the genus is here recognised for the first time in the Rhaetian of the Northern Alps. It is therefore known from the Anisian to the Liassic. Externally the most characteristic features of Piarorhynchia are the long posterior smooth stage, the flattened pedicle valve and the very small beak; internally the hinge plates are horizontal, the crura radulifer and the whole of the cardinalia and the dorsal septum are massive with encasing callus which obscures the lateral cavities (see sections of AGER 1959). A similar thickening and the deposition of a pad in the muscle trough is found in the species investigated by DAGIS (1965).

Probably the closest associate of Piarorhynchia is Sinuplicorhynchia from the Carnian of Siberia (DAGIS 1965), which only differs in having more extensive, very shallow ribs.

Sakawairhynchia TOKUYAMA, 1957, is also an obvious ally of Piarorhynchia. Described from the Carnian of the Sakawa basin in Japan, it is more densely ribbed but still has a short posterior smooth stage. The original sections show a callus pad in the muscle trough but this is not seen in those of DAGIS (1965), and he only provisionally referred his material to Sakawairhynchia. However, there can be little doubt that DAGIS was in fact dealing with this genus: externally his species are very close to TOKUYAMA's, and the crura he shows are somewhat blade like and correspond with the prefalcifer looking crura drawn by TOKUYAMA from obviously poorly preserved material. The species figured by AGER and WESTERMANN (1963) as S.cf.S.tokomboensis is much less densely ribbed than known members of the genus and is clearly more comparable with the species of Piarorhynchia figured by DAGIS (1965).

Cuneirhynchia from the Sinemurian and Pliensbachian has a similar overall internal (see AGER 1959) and external character to the previous genera, but is distinctively wedge shaped and in detail is most similar to MOISSEIEV's (1936) genus, Omolonella, from the Norian of N.E.Siberia. DAGIS (1965) reviewed this genus and its three species, and his sections clearly show the massive apical callosity, the reduced inner hinge plates, very strong sockets, and curious incurved deltidial plates which are paralleled in Cuneirhynchia (see AGER 1959). Externally the two genera are extremely similar and they may be regarded as directly linked. Internally Omolonella is immediately reminiscent of the species sectioned and described by DAGIS (1965) as Holcorhynchia (following TOKUYAMA 1957). The type of this genus is an early Toarcian species from Gloucestershire which has not yet been revised and its internal structure is unknown. Externally DAGIS's Ladinian and Carnian species appear to have more in common with the type than the Liassic species described by AGER (1959a) as Holcorhynchia? yakacikensis (= Rhynchonella n.f. NEUMAYR, 1879 pl.1, fig.3, and probably ancestral to Monticlarella). The Triassic material is similarly depressed, almost wholly smooth with a slight flattening or sulcation of the dorsal valve, and a low, insignificant beak. Internally the muscle trough is padded, the crura are radulifer and long, the cardinalia as a whole is massively thickened and the pattern of its construction is essentially the

same as Omolonella. Thus Holcorhynchia, sensu DAGIS (1965), may be placed with the previous genera. However its closest, on internal character, associate appears to be another poorly known BUCKMAN genus, Maxillirhynchia, also as interpreted by DAGIS (1965). The significance of the striations on DAGIS's Carnian specimens and whether they are identical with those on the British Toarcian type is uncertain. Maxillirhynchia is at present being investigated by Dr.D.V.AGER.

Therefore it is suggested that Piarorhynchia, Sinuplicorhynchia, Sakawairhynchia, Cuneirhynchia, Omolonella, Holcorhynchia, and Maxillirhynchia may be isolated from the present Tetrarhynchiinae as a separate subfamily. However, the choice of parent family for this group is difficult.

It is possible that the Sakawairhynchia branch of the plexus discussed above is the root of the strongly ribbed rhynchonellids with radulifer crura so common in the Jurassic but apparently rare in the Triassic. This group forms the Rhynchonellidae. On the other hand there are indications of a relationship to the Dimerellidae, in particular the Norellinae.

The Norellinae was founded by AGER (1959) for small, smooth, sulcate forms with minute delthyria, all of which are poorly known. Norella itself is clearly sulcate and sections of one species N.tibetica were published by DAGIS (1965). They show thick shelled umbones, long radulifer crura, and, allowing for the flatness of the brachial valve, all the elements of the cardinalia appear similar to those of e.g. Omolonella and Holcorhynchia (sensu DAGIS).

Apart from Norella, at least three other genera are acceptable in the Norellinae: Pisirhynchia, Rectirhynchia and Austriellula. All of these are wholly smooth and dorsally sulcate, but whereas Pisirhynchia is very strongly so, Austriellula also contains rectimarginate and uniplicate species (AGER 1965). Thus dorsal sulcation is a flexible character and reasonably acceptable in a stock ancestral to plicate rhynchonellids.

Indeed the slight dorsal sulcation of Holcorhynchia is suggestive of such descent and both this genus and Omolonella were placed in the Dimerellidae (subfamily Rhynchonellinae) by AGER (1965).

BUCKMAN (1918) proposed that the normal uniplicate rhynchonellids were derived from a sulcate or 'norelliform' ancestor by the progressive restriction of the norelliform phase to the earlier growth stages followed by its final elimination. This proposal has now fallen into disrepute (e.g. AGER 1959). He applied it too widely, attempted to recognise a relict norelliform stage in species where it is not present, and constructed his generic groupings on the assumption that all Mesozoic genera shared the same morphological stages in their shell development. Inevitably his hypothesis has suffered from the modern reaction against the simplicities of early theories concerning ontogeny and phylogeny. However, the derivation of a uniplicate form from a Norella-like ancestor needs no more than the progressive emphasis of a median plication which is already present in the sulcus of the type species in the Anisian (see BITTNER 1890, pl.31, figs.6-10).

Nevertheless considerable further research is needed to establish this link between Piarorhynchia and Norella. The microstructural development of the genera concerned must be examined: it is for instance uncertain if the umbonal thickening of Norella and Piarorhynchia is comparable, for that of Norella may be more similar to Carapezzia (see herein). At present any grouping around Piarorhynchia must be retained in the Rhynchonellidae and any connection with Norella and the Dimerellidae regarded as speculative.

Genus Piarorhynchia BUCKMAN, 1918

Piarorhynchia cf. P.juvenis (QUENSTEDT), 1852

Plate 3, figs. 6, 7.

Description:

The four specimens described here belong to a small, subtrigonal species with a flat brachial valve. They have a short posterior smooth stage and are bluntly ribbed for about three quarters of the length of the valves. Three individuals have 7 ribs and the other 6, of which 2 or 3 are involved in the trapezoidal plication of the anterior commissure. A low, flat fold and shallow sinus are developed. The beak is minute, pointed and suberect and although moderately sharp beak ridges can be seen, the area is barely discernible.

The internal structure was not examined.

Remarks:

All four specimens found by the writer were loose but accompanied by typical Rhaetian fossils and there is no reason to doubt their age. In outline, profile and extent of ribbing, they closely resemble P.juvenis, well known in the Liassic alpha of S.W.Germany. They are also very similar to 'Rhynchonella' trinodosi BITTNER, from the Anisian, sections of which, kindly provided by Dr.D.V.AGER, show it to belong to Piarorhynchia. However provisional reference to the more stratigraphically close Liassic species is preferred here.

Localities and Material:

Rhaetian of Ober Kaisersteffel (3 spec.), and Hohe Mandling (1 spec.), near Waldegg, Piesting Tal, Lower Austria.

Dimensions of Figured Specimens:

	length	breadth	thickness
3/6	6.9	7.0	3.8
3/7	8.9	11.0	5.8

? Subfamily Tetrarhynchiinae AGIER, 1965

Gen.nov.A

Remarks:

Three previously undescribed species are included in this genus, of which two are fully ribbed and only provisionally separated, whilst the third is posteriorly smooth. Internally sp.nov.A has a very low median septum raising the muscle trough, and arched outer hinge plates which twist towards themselves and give rise to radulifer crura. It is posteriorly smooth. Similar hinge plates and crura are seen in the fully ribbed sp. nov.B, which, however lacks a median septum. ? sp.nov.C, fully ribbed and also with a sessile muscle trough, differs from sp.nov.B in having pre - falcifer, distally ridged crura. This seems likely to be a specific difference.

Although there is no recognised genus in which these species can be placed, a new one has not been created since no satisfactory type species is available: sp.nov.A has not been found in the field, sp.nov.B is rare and difficult to collect and moreover its relation to ?sp.nov.C is uncertain.

Because of the very small, unrimmed pedicle opening and the radulifer crura in two of the species, gen.nov.A is placed provisionally in the Tetrarhynchiinae, although an even less decisive assignation to the Rhynchonellidae may be better.

The relations of the genus are not clear and may be in generically undetermined species.

Gen.nov.A sp.nov.A

Plate 3, figs.1-5; text-fig. S.v.

Range and Distribution:

Known only from a single Rhaetian locality near Mittenwald in the Northern Alps (see Locality and Material below).

Diagnosis:

Medium sized rhynchonellid, posteriorly smooth, 12 - 17 ribs present anteriorly. Anterior commissure plicate; ligule high, narrow; low fold and sinus. Dorsal median septum very low, short; muscle trough barely raised. Crural bases rounded calcate, crura radulifer like.

Description:

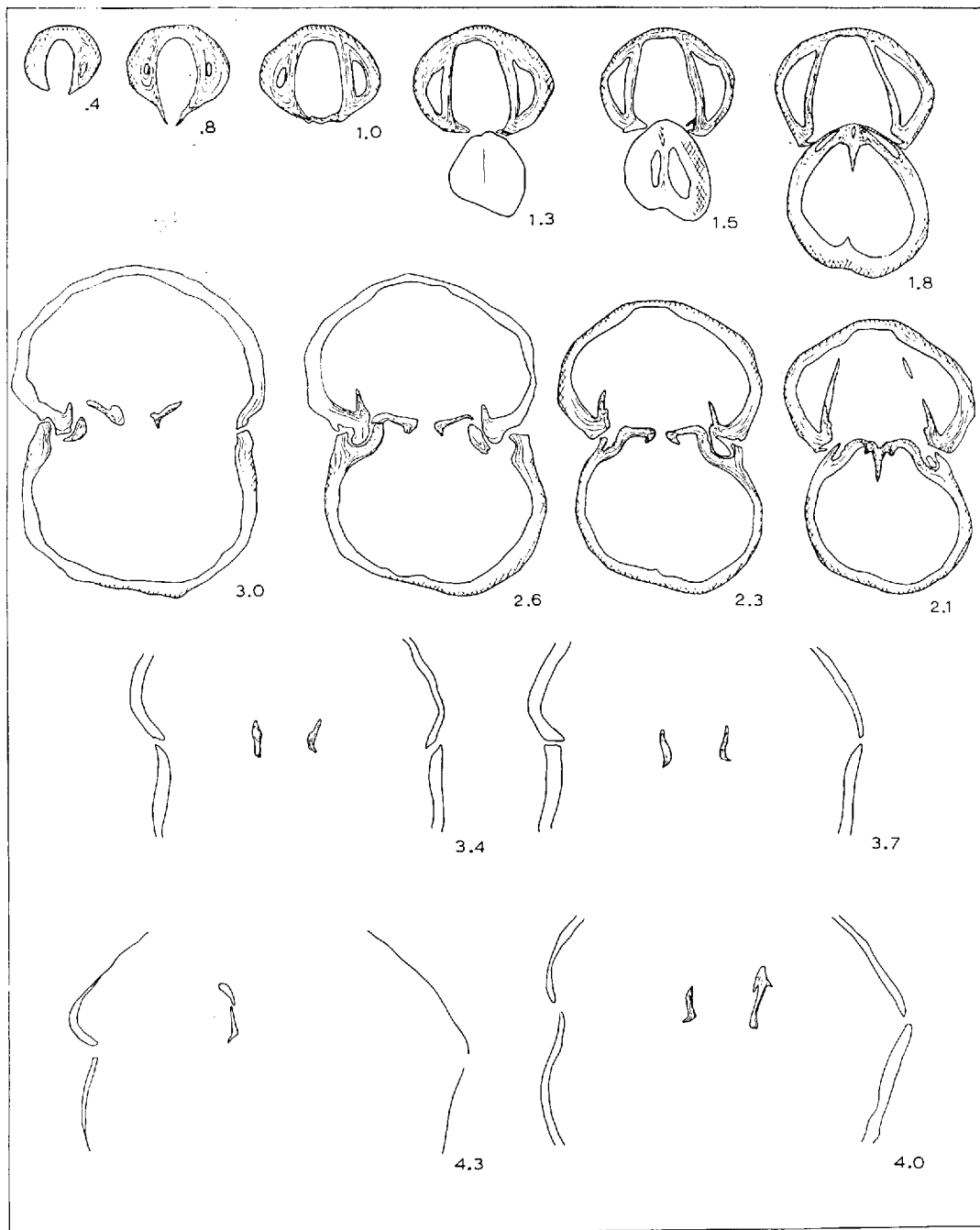
This species includes medium sized transversely oval rhynchonellids, anteriorly ornamented with between 12 and 17 somewhat blunt ribs, but posteriorly smooth for a distance of 3 - 4 mm. The anterior commissure involves 3, or more rarely 4 brachial ribs in a narrow, subtrapezoidal plication. The ligule reaches verticality, sharply increasing the convexity of the relatively flatter pedicle valve and giving the specimen a globose aspect. A low, narrow fold and sinus are also produced. In specimens with four brachial ribs on the fold the two central ones are lower than their neighbours giving the fold a distinctive appearance, and a corresponding depressed median field is traceable even to the smooth part of the dorsal valve. In those with three ribs this feature is not defined. The beak is very low, broad, pointed and strongly recurved, and although the beak ridges are apically sharp the area is poorly defined and the pedicle foramen is totally indistinguishable.

The dental lamellae are only slightly divergent on the floor of the valve and because of the recurvature of the beak the delthyrial cavity appears elongate and trapezoidal in transverse section. The deltidial plates are conjunct. The teeth are smooth and laterally expanded. A small denticulum may be apparent.

There is a very low and short median septum in the apex of the dorsal valve which raises the muscle trough. The outer socket ridges are strong but the inner ridges are weak and the socket plates themselves curve to contain the teeth. The crural bases are knob like and the outer hinge plates twist medially to give rise to radulifer like crura.

Remarks:

The narrow well expressed fold and low beak distinguish this species from Vindobonella katzeri (= 'R'. subrimosa auctt.), the only other posteriorly smooth species in the Rhaetian, but since it has not been possible to find specimens in the field and so nominate a type locality, a new species is not formally established.



Text-fig. S.v

Serial transverse sections of Gen.nov.A sp.nov.A.

Specimen from the Brit. Mus. Nat. Hist - labelled B.24614

'Kössener Sch.; Marmorgraben, bei Mittenwald.' x5

Crura end 4.5mms. Total length of specimen 13.5mms. PC.Nr.17.

The very low median septum slightly raising the muscle trough cannot be regarded as grounds for excluding this species from Gen.nov.A. for the roundness of the anterior ribbing, the low beak, and the formation of the crura are all closely similar to the Pfonsjoch specimens - sp.nov.B.

Dimensions of Figured Specimens:

	Length	Breadth	Thickness	
3/1	15.7	15.8	13.1	
3/2	13.3	15.5(d)	12.4	
3/3	14.2	16.1	12.3	
3/4	16.5	21.0	12.2	(BB43201)
3/5	17.7	21.5	16.3	(BB43200)

Material:

'Marmorgraben bei Mittenwald' - 10, B.M.N.H., B 24614 (this area was visited by the writer but the locality could not be found);
'Lahnenwiesgraben' by Farchant - 2, B.M.N.H., BB 43200, - 1, ex. B 24617.

Gen.nov.A sp.nov.B

Plate 4, figs.1,2; text-figs. S.vi, S.vii; text-plate S.3

Diagnosis:

Medium sized rhynchonellid, equi-biconvex; 12 - 16 rounded ribs originating at valve apices, bifurcation early. Beak pointed, erect; beak ridges moderately sharp. Anterior commissure plicate, ligule trapezoidal, no fold or sinus. Pedicle opening small, submesothyrid in position. No median septum, muscle trough sessile. Crural bases calcate, crura radulifer like.

Description:

This species includes medium sized, equi-biconvex rhynchonellids, subcircular in outline and commonly ornamented with between 12 and 16 ribs. The ribs are rounded and originate at the valve apices; bifurcation occurs very early in growth and may be discerned within 1mm. of the

umbones. The beak is low and pointed, and the beak ridges maintain their strength laterally. The pedicle foramen is very small and submesothyrid in position. A subtrapezoidal plication of the anterior commissure involving 2 - 4 brachial ribs, produces a high ligule and globosity of the shell, no sinus or fold is developed.

No median septum is present and it must be emphasised that the structure in text-fig.S.viii, sectns. 2.05 - 2.15, is not homologous with the septum found in other rhynchonellids. Its appearance is produced by a combination of the angle of grinding and the infilling of the narrow muscle trough (see text-plate S.3).

The delthyrial cavity is subquadrate with moderately thick deltidial plates. The teeth are transversely quadrate, strong and crenulated. Denticula are present on the outer socket ridges. The hinge plates are slightly medially sloped and twist distally to give rise to radulifer like crura.

Remarks:

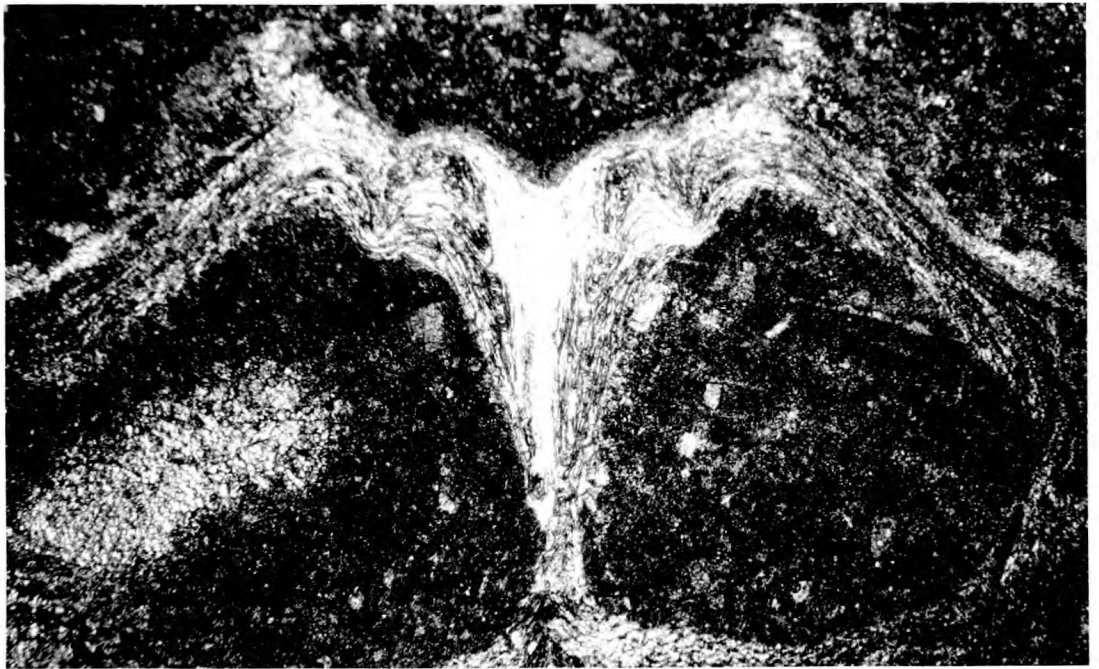
This species is certainly that recorded by VORTISCH (1926 p.19, profile j.) as Rhynchonella fissicostata, from which it differs obviously in many respects. Its relationship to Gen.nov.A ?sp.nov.C is discussed under that heading below.

Dimensions of Figured Specimens:

	length	breadth	thickness
4/1	16.5(d)	17.6	13.2
4/2	16.2	17.5(d)	14.5

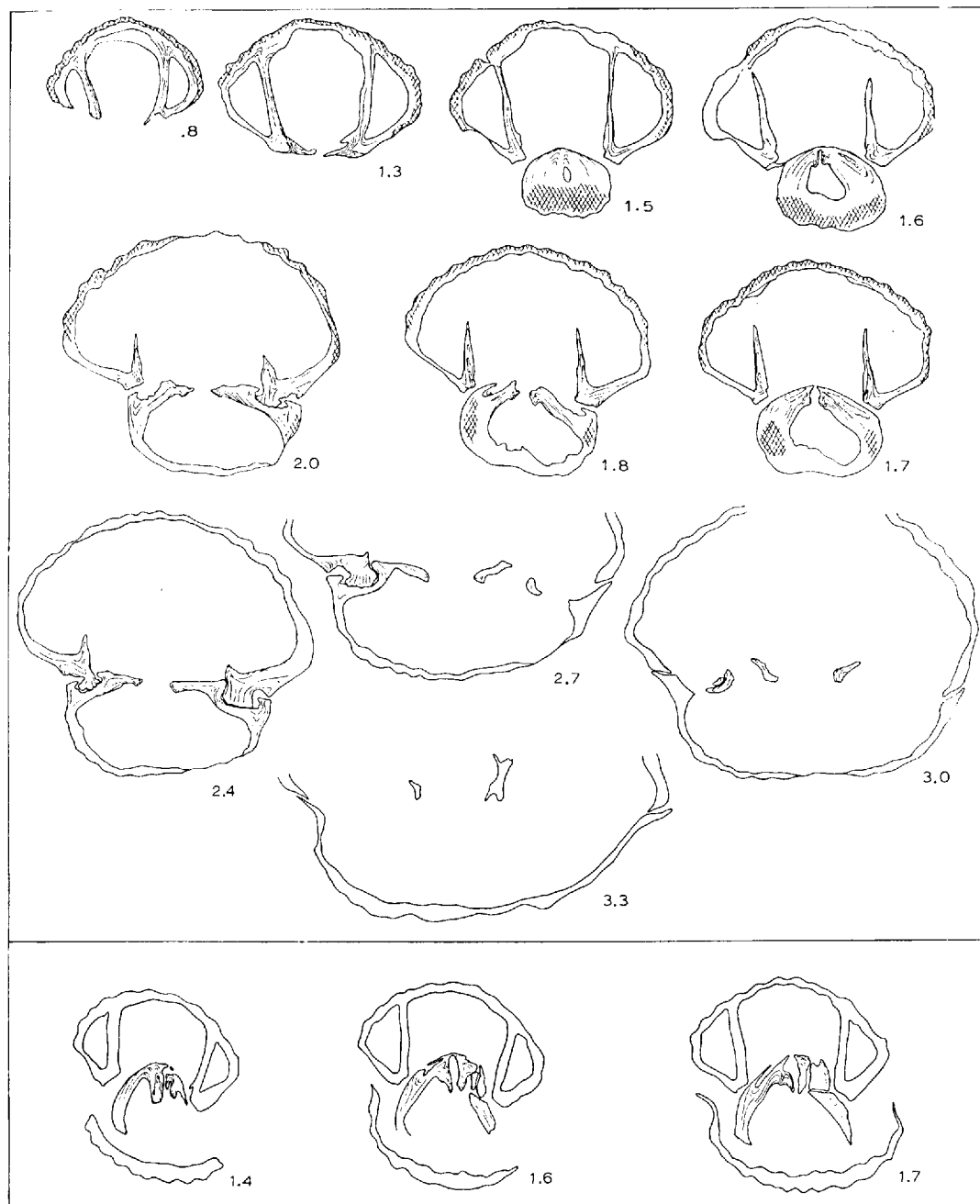
Material:

Juchtenkopf (Pfonsjoch), by Pertisau - 12, T.18.



Text-plate S.5

Transverse section through the brachial umbo of Gen.nov.A
sp.nov.B, showing the sockets, socket ridges, crural bases and
inner hinge plates. The specimen was slightly crushed and the
muscle trough, ground along its length, simulates a median septum.
Detail of section 2.15, text-fig. S.viii x60

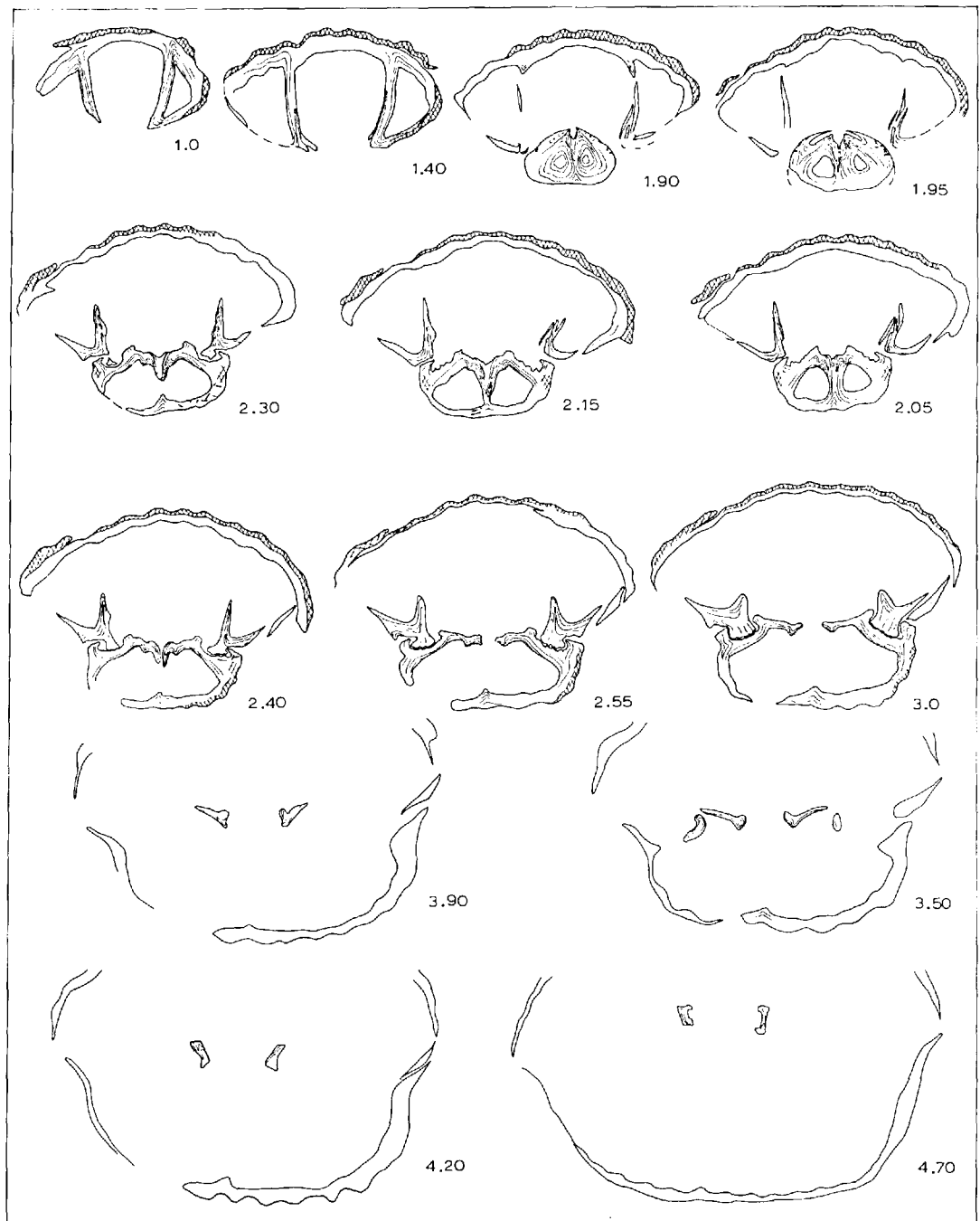


Text-fig. S.vi

Serial transverse sections of Gen.nov.A sp.nov.B.
 Rhaetian; Juchtenkopf, by Pertisau, Achensee, Austria;
 (Pfonsjoch in VORTISCH 1926). x5 Crura end 3.4mm.
 Total length of specimen 14.3mm. PC.Nr.36.

Text-fig. S.vii

Locality as above. PC.Nr.22.



Text-fig. S.viii

Serial transverse sections of Gen.nov.A sp.nov.B.

Rhaetian; locality as text-fig. S.vii x5 Crura end 4.85mm.

Total length of specimen 14.2mm. PC.Nr.16.

Gen.nov.A ?sp.nov.C

Plate 4, figs.3 - 5; text-fig.Six

Remarks:

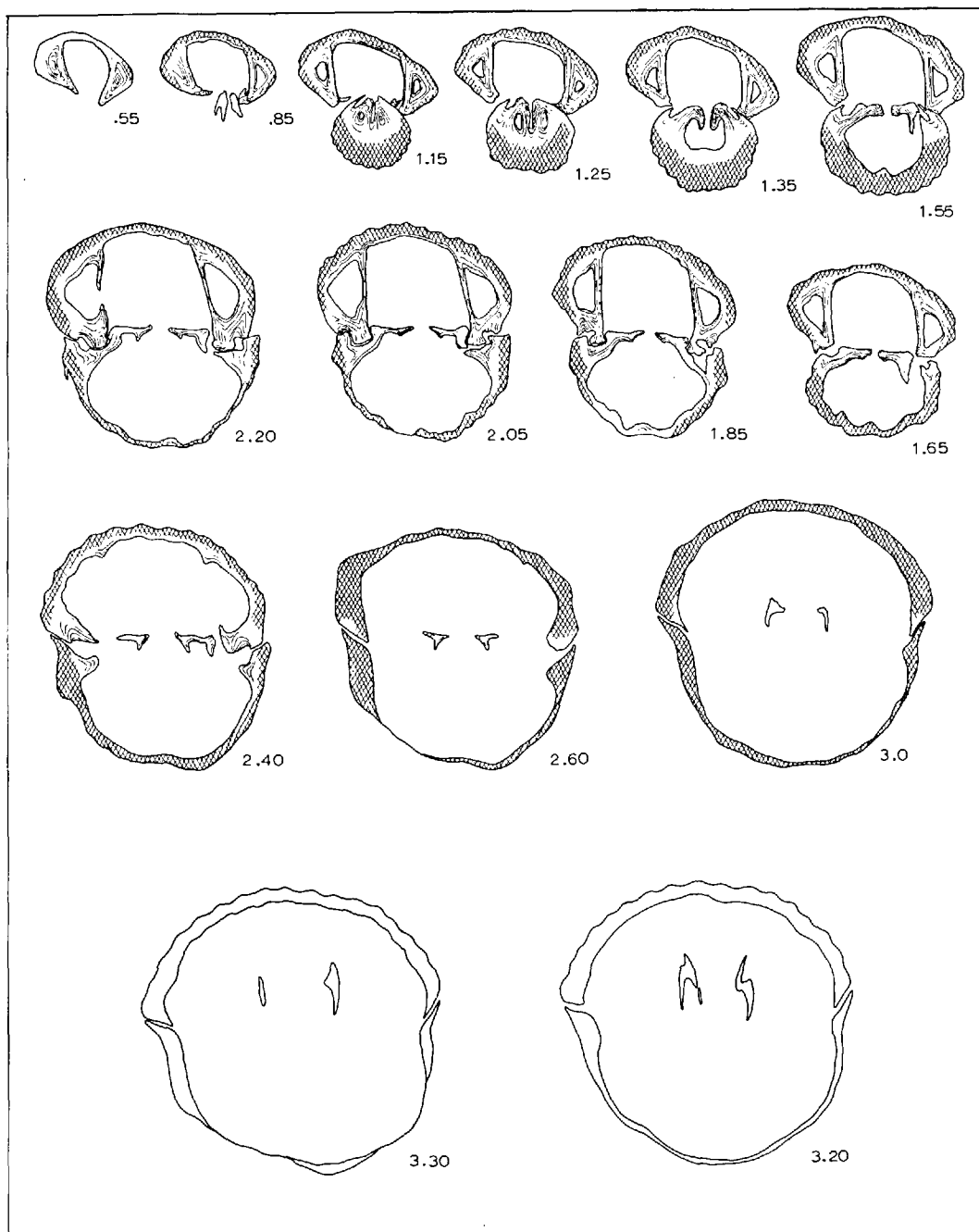
23 specimens collected from the Rhaetian of Lahnenwies Graben near Farchant, Bavaria, differ from sp.nov.B, described above, only in the density and concomitant sharpness of their ribbing: all of them have between 16 and 19 slightly blunted ribs whereas those from Pfonsjoch have 12 to 16 rounded ribs and only large, gerontic individuals may have more. Internally they also appear to differ, for the ground specimen from Farchant has prefalcifer like crura. Two distinct species are probably represented but material from other localities is necessary before they can be distinguished with confidence.

Dimensions of Figured Specimens:

	length	breadth	thickness
4/3	14.1	14.2	13.2
4/4	17.0	17.5	15.2
4/5	12.3	12.3	9.0

Material:

Lahnenwiesgraben, by Farchant - 19, T.19; locality as T.19, 3spec., Bay.St.Slg. 1956 V 15.



Text-fig. S.ix

Serial transverse sections of Gen.nov.A ?sp.nov.C.
 Rhaetian; Lahnenwies Graben, near Farchant, - right bank,
 first bridge above Pflieger See - R/44301:H/52660 (8432
 Oberammergau). x5 Crura end 3.5mms. Total length of
 specimen 12.1mms. PC.Nr.27.

Family Rhynchonellidae GRAY, 1848

Subfamily Austrirhynchiinae AGER, 1959

(nom. transl. herein ex Austrirhynchiidae AGER,
1959. p.325)

Remarks:

Austrirhynchia was diagnosed by AGER (1959) as the type of a new family, the Austrirhynchiidae. Possibly because of the preservation of the ground specimen, a bilobed cardinal process was thought to be present and was included in the generic diagnosis. This remarkable structure does not, however exist (see sections herein) and therefore Austrirhynchia does not appear to be sufficiently distinctive to form the basis of a family. In fact in the Geol. Soc. Amer. Treatise AGER (1965 p.620) thought it may be better regarded as a subfamily of the Dimerellidae. There do not however, appear to be any compelling reasons for assigning it to this distinctive family and here the Austrirhynchiidae is reduced to a subfamily and placed in the Rhynchonellidae. The peculiarity of the subfamily lies in the external appearance of its genera and not in any dramatic internal feature as first thought, and there is no need for radical separation from 'normal' rhynchonellids.

GAETANI (1966 p.344) placed his very closely related Middle Triassic genus Decurtella in the Tetrarhynchiinae, but following the reinvestigation of Austrirhynchia the two genera must be associated in the Austrirhynchiinae.

Genus Austrirhynchia AGER, 1959Type species:Terebratula cornigera SCHAFHÄUTL, 1851, p.408, pl.7, fig.1; OD.Range and Distribution:Norian of the Northern Alps and W.Greece.Rhaetian of the Northern Alps, Slovakia (Hybe, Bystry potok),

Polish sub-Tatra, N.W.Rumania (Apuseni Mts.).

Included species:

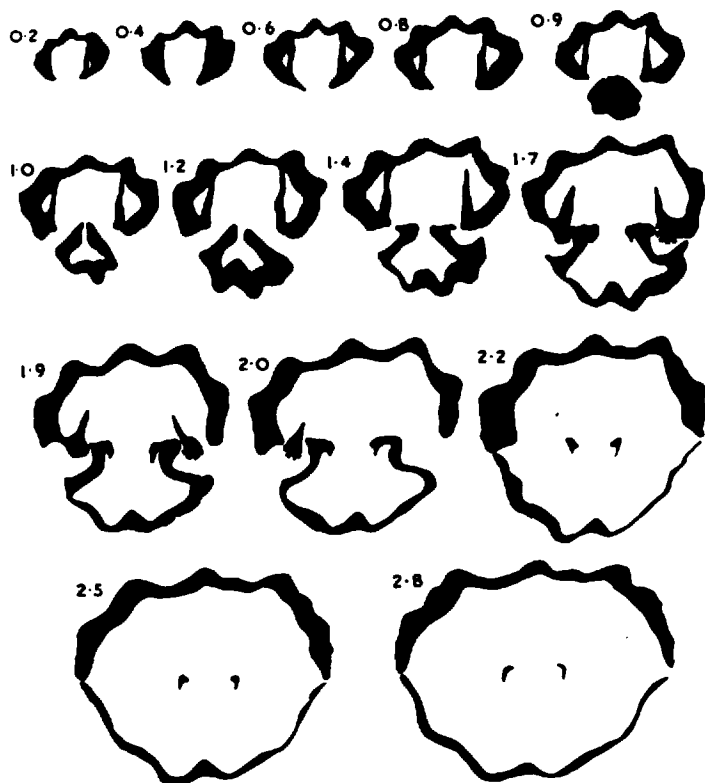
A.cornigera and A.concordiae BITTNER, 1890 are at present included in the genus and further study will undoubtedly reveal several others amongst already distinguished species, particularly in the Carnian, but they cannot be separated on external features from potential members of Decurtella (see Remarks).

Diagnosis:

Small, triangular rhynchonellids, may have laterally extended 'wings'. Ribbed to apex of valves. Pedicle collar may be present. No inner hinge plate, dorsal myophragm may be joined with socket plates in older specimens. Outer hinge plates reduced or absent; crura rooted on massive inner socket ridges. Crura radulifer.

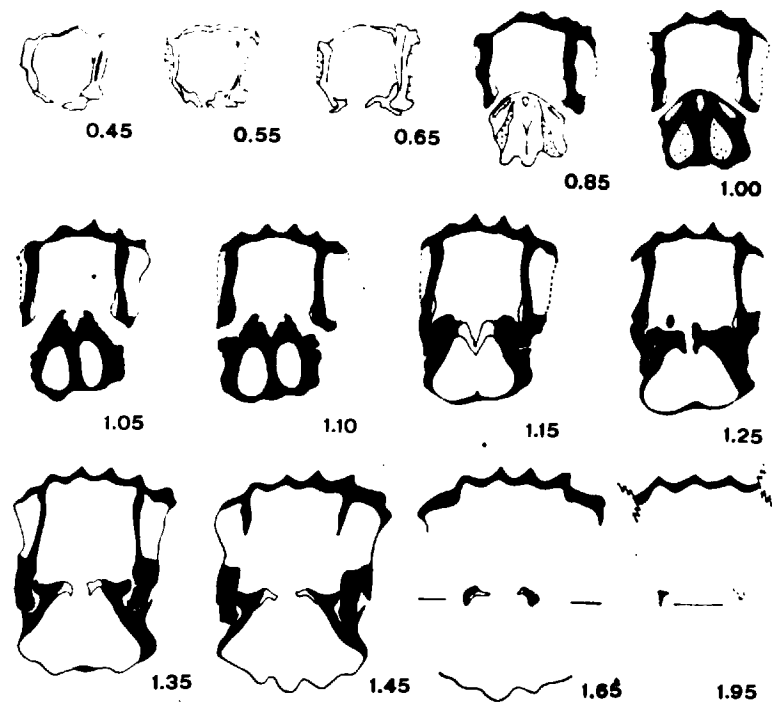
Remarks:

Several species are known from the Triassic, particularly the Middle Triassic, which are notable for their triangularity although they lack the extraordinary wings of A.cornigera, and AGER 1959 (p.327) mentioned 'R'.cornaliana' from the Carnian and 'R'.decurtata' from the Anisian as possible members of Austrirhynchia. Recently the latter species has been investigated by GAETANI (1966) who used it as the type species of a new genus Decurtella, which he distinguished from Austrirhynchia because of its possession of a 'septalium' and lack of a cardinal process (p.346). The last, and major of these differences has now been eliminated (see description of A.cornigera below), and the 'septalium' appears to be exactly the same in its method of formation, although certainly different in size to the rudimentary notothyrial chamber seen in text-fig.S.xiii, sectn. 1.8 of A.cornigera herein. Without the cardinal process to distinguish Austrirhynchia the difference between the genera is slight and may be covered by intra-generic variation. The only other potential member of either of these genera of which the internal structure is known is



Text-fig. S.x

Austrirhynchia concordiae (BITTNER). ?Norian; Levkas, Greece. Specimen presented by Mme.GUILLAUME. Sections provided by Dr.D.V.AGER. D.V.A. colln. J.119. x5



Text-fig. S.xi

Decurtella decurtata (GIRARD). Anisisan; Val Trompia, N. Italy. ex. GAETANI 1966, text-fig. 1. x9.

'R'.concordiae BITTNER, from the Norian. Externally it is a small, triangular rhynchonellid very similar to the species listed below which GAETANI provisionally included in Decurtella, but sections, kindly made available by Dr.D.V.AGLER (text-fig.S.x) show that it is best placed in Austrirhynchia.

GAETANI listed the following Anisian species as possible members of Decurtella -

' <u>R'.vivida</u> BITT.	' <u>R'.vicaria</u> BITT
' <u>R'.pironiana</u> BITT.	' <u>R'.illyrica</u> BITT
' <u>R'.toemmasii</u> BITT.	

to which may be added from the Anisian of Rumania (ex JEKELIUS 1936) -

' <u>R'.coronae</u> JEK.	' <u>R'.dacica</u> JEK.
' <u>R'.brasovaei</u> JEK.	' <u>R'.alutae</u> JEK.

and 'R'.cornaliana from the Carnian.

The study of the above species will provide the evidence necessary to resolve the relationship of Austrirhynchia and Decurtella.

Range and Distribution:

Rhaetian of the Northern Alps, Slovakia (Hybe), Polish sub-Tatra and N.W. Rumania (Apuseni Mts.).

Diagnosis:

Small; antero-lateral angles very considerably extended; 8-15 ribs present; anterior commissure broadly plicate. Pedicle collar may be present. Otherwise as genus.

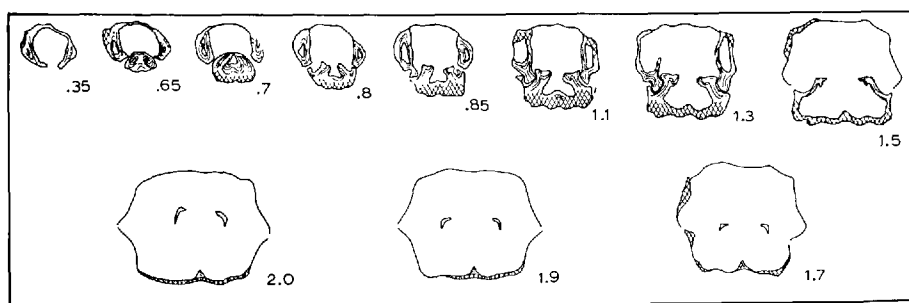
Description:

Austrirhynchia cornigera is a small, subtrigonal rhynchonellid with remarkable anterolateral wings. Superficially these wings appear similar to the planareas of Cirpa. In the latter case however, the beak ridges are continuous with the borders of the ventral area and the flat, paired planareas are simply an unusual development of the situation seen in very many ribbed rhynchonellids. In Austrirhynchia the beak ridges delimit a small area within the smooth surface of the wings (see plate 5, figs. 5b and 6b), and their formation is therefore different from that in Cirpa. The possible function of these structures is discussed under Ecology. The wings are divided by the lateral commissure and form gently curved, oblique faces to the main triangular body of the shell from which they are delimited by sharp, slightly recurved ridges. Antero-laterally the wings are pointed and may extend, recurving posteriorly, for 1cm. on either side of a $\frac{1}{2}$ cm. broad main mantle cavity, (see text-plate fig.8). The recurved lateral and posterior surfaces of the wings only show growth lines and are not ribbed, but the anterior surface bears very low, poorly developed ribs. In all between 9 and 15 ribs are present and on the bulk of the shell are strong and only slightly rounded. Only 4 or 5 ribs reach the apices of the valves and the remainder arise from the edges of the wings or through bifurcation. The anterior commissure has a broad, flat plication involving the 6 to 9 ribs on the body of the brachial valve and giving it the appearance of a broad flat fold, which may be accompanied by a slight sulcation of the pedicle valve. In anterior view many specimens have a markedly rectangular aspect. The beak is small, pointed and suberect with a large, elliptical, rimmed pedicle opening.

The delthyrial cavity is quadrate but in larger individuals may be

rounded by a delthyrial lining which may be partially detached as a pedicle collar. The deltidial plates in such specimens are thick. The teeth are massive and accompanied by strong denticula.

No cardinal process is present, (contra AGLER, 1959 p.326, text-fig.1). A dorsal myophragm is present and in older specimens may be united with the median edges of the oblique socket plates forming a notothyrial pit, but there is no muscle trough. Broad sockets are developed and bounded by massive socket ridges. Outer socket plates are not present and the crura are rooted on the edges of the inner socket ridges. The crura themselves are radulifer - like.



Text-fig. S.xiii

Serial transverse sections of Austrirhynchia cornigera (SCHAFHÄUTL). Rhaetian; Koth-Alpe, north of Bayerischzell, Bavaria; R44/98925:H52/86128 - 8237 Miesbach. x5 Crura end 2.0mm. (?broken). Total length of specimen 6.2mm. PC.Nr.33 Topotype.

Remarks:

A.cornigera is a ubiquitous species and present in all the important Rhaetian brachiopod localities covering a range of facies in the Northern Alps, Slovakia and Rumania. This breadth of distribution is probably due to the hydrodynamic effect of its unusual morphology which facilitates dispersal by currents (see Ecology). It is therefore most significant that it has never been recorded from the Alpine or Slovakian Norian nor in

the very rich so-called 'Norian-Rhaetian' beds (DAGIS 1963) of the Caucasus, Crimea etc., here regarded as wholly Norian (see Stratigraphy). A. cornigera may therefore be confidently recognised as an index species of the Rhaetian.

ZUGMAYER (1880 p.39-40) noted the extreme variability of this species and the obvious differences between SCHAFHÄUTL's originals and those specimens figured by SUESS (1854). His recognition of the two varieties karpatica and koessenensis is probably one of the first instances of a brachiopod species being split because of habitat as well as form. Var. koessenensis was applied to the large form from the 'Kössener Facies' and 'Starhenberger Facies', and var. karpatica to small specimens from the 'Karpatische Facies' (equated by GOETTEL 1917, p.109, with the type specimen). These names were not clearly established as subspecific and through the ICZN Art.45 are not here recognised as such, although sub-species may indeed be found useful after more investigation. This question is discussed further under Ecology.

It must be emphasised that A. cornigera has no cardinal process and its relation Decurtella decurtata, the type species of Decurtella GAETANI, 1966, which was separated from it mainly because of the presence of this structure, is discussed under the generic description of Austrirhynchia.

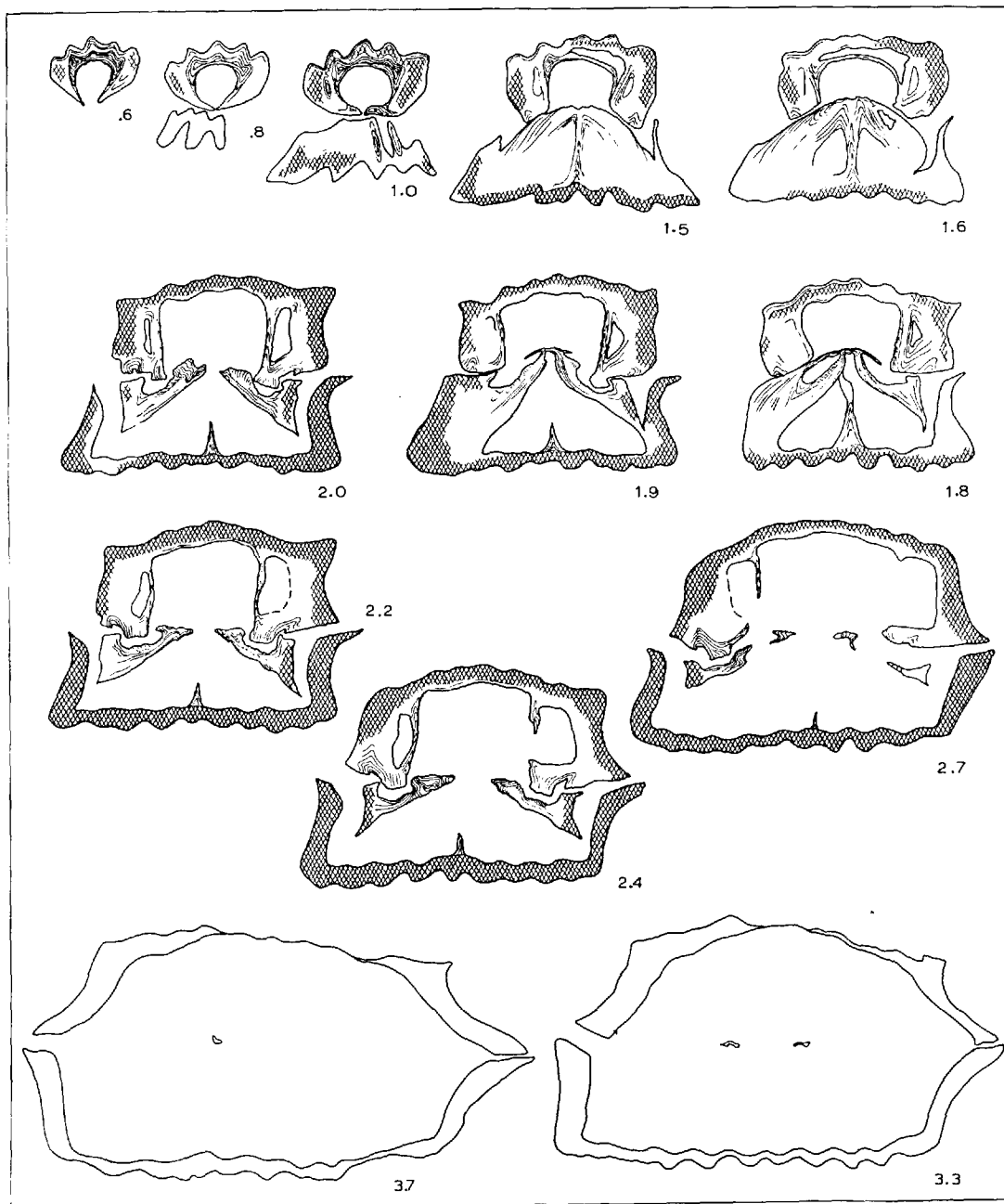
Dimensions of Figured Specimens:

	length	breadth	thickness
5/1	6.5	10.6	3.6
5/2	6.0	12.3	3.1
5/3	6.1	9.0	4.5
5/5	9.5	24.5(r)	8.3
		20.2(a)	
5/6	9.0	19.4(r)	7.5
		17.9(a)	
5/7	8.3	23.0(r)	6.0
		18.6(a)	

a - actual breadth; r - reconstructed maximum breadth i.e. twice the maximum actual half breadth.

Material:

Koth Alpe, by Bayerischzell (type locality, see above) - 21, T.20;
Juchtenkopf (Pfonsjoch), by Pertisau, in loose block - 10, - T.21;
Steinplatte above Waidring - 4, T.22; Axelstein, by Jachenau - 50, T.23;
Hirtenberg, Triesting Tal, by Wr.Neustadt - 2, T.24; 'Mittenwald'
(?Marmor Graben), - 8, B.M.N.H., B 24615; 'Rote Wand beim Schliersee' - 4,
B.M.N.H., B24616; Bystřý potok by Gombas, Slovakia - 2, T.24; Hybe by
Ruzomberok, Slovakia - 2,,T.41; Val Frunsi by Ferice, N.W.Rumania 2, T.40.



Text-fig. S.xiv

Serial transverse sections of Austrirhynchia cornigera (SCHAFHÄUTL). Rhaetian; Axelstein by Jachenau, Walchensee, Bavaria; 47°37'25''N. 11°26'40''E. Locality indicated on map of LUTYJ-LUTENKO 1951. x5 Crura end 3.85mm. Total length of specimen 10.0mm. PC.Nr.23

Family Wellerellidae LIKHAREV in RZHONSNITSKAYA, 1956

Remarks:

DAGIS (1963) placed Euxinella (=Calcirhynchia herein) in the Wellerellinae, a subfamily then including genera from the Middle Devonian to the Early Jurassic. Subsequently AGER (1965) proposed the Cirpinae to separate the Mesozoic members of the Wellerellinae, and the usefulness of this smaller grouping is accepted here.

The writer agrees with CHILDS (1966) that the lacunosellids should be excluded from the Wellerellidae. The fact that both groups have ventrally descendent crura cannot be regarded as more than a superficial resemblance. The lacunosellids completely lack a muscle trough, even a sessile one, and the writer cannot accept the implication that the falcifer crura of the lacunosellids have arisen from the prefalcifer crura of the wellerellids. In the writer's opinion prefalcifer crura, as recognised at present, are polyphyletic having arisen in a variety of stocks with and without a raised muscle trough. Their origin from radulifer like crura is postulated herein in the case of Vindobonella and Pseudogibbi-rhynchia. The ancestry of the lacunosellids - Lacunosellidae SMIRNOVA, by CHILDS 1966 - remains to be investigated in the Alpine Liassic and the Triassic.

Subfamily Cirpinae AGER, 1965

Remarks:

Several of the genera included in the Cirpinae on its establishment require further investigation: the exclusion of Pseudogibbirhynchia has been dealt with in connection with Vindobonella; Rimirhynchopsis seems more naturally associated with Rimirhynchia, perhaps in a new subfamily of the Rhynchonellidae; Hagabirhynchia and Squamirhynchia (of which Robinsonella is regarded by the writer as a junior synonym) are more difficult to place.

The principal stock of the subfamily in the late Triassic and the early Jurassic is certainly the abundant and widespread Cirpa - Calcirhynchia plexus.

Genus Calcirhynchia BUCKMAN, 1918

- 1914 Calcirhynchia BUCKMAN, p.1 (nomen nudum).
 1918 Calcirhynchia S.BUCKMAN; BUCKMAN, p.30
 1936 Euxinella MOISSEIEV, p.41
 1947 Euxinella MOISSEIEV; MOISSEIEV, p.69
 1962 Calcirhynchia S.S.BUCKMAN; AGER, p.85
 ? 1963 Euxinella MOISSEIEV; AGER, p.609
 1963 Euxinella MOISSEIEV; DAGIS, p.25
 1965 Calcirhynchia BUCKMAN; AGER, p.606
 1965 Euxinella MOISSEIEV; AGER, p.607

Type species:

Calcirhynchia calcaria S.S.BUCKMAN, 1918 p.30, pl.19, fig.11; OD.

Range and Distribution:

Rhaetian of the Northern Alps (Reit im Winkl area).

Norian of the N.W.Caucasus, Crimea, Pamirs and E.Turkey. Possibly the Carnian of British Columbia.

Included species:

All the species described by DAGIS (1963) as belonging to Euxinella are included here in Calcirhynchia -

C.iatingvartaensis(MOISSEIEV), 1936 p.42 pl.1, figs.1-4

C.robinsoni(MOISSEIEV), 1936 p.43 pl.1, figs.5-8 (?not separable from C.iatingvartaensis)

C.anatolica(BITTNER), DAGIS. (?non BITTNER 1891, p.106, pl.1, fig.5)

C.levantina(BITTNER), 1891 p.107, pl.1, figs.1-4

C.pamirensis(DAGIS), 1963 p.35, pl.1, figs.12,13

C.cubana(DAGIS), 1963 p.36, pl.1, figs.14; pl.2, figs.1-3

also

C.subrimosa(SCHAFHAÜTL), 1851 p.412, pl.7, figs.3,4

? C.plicatissima(QUENSTEDT), 1852 p.451, pl.36, fig.3

? C.salisburgensis(NEUMAYR), 1879 p.8, fig.1

? C.cf.decussata(ROEMER), UHLIG 1879 p.295, figs.5-8

? C.cf.obtusifrons(SUESS); ZUGMAYER, 1880 p.39, pl.4, fig.29

? C.fringilla(BITTNER), 1892 p.18, pl.4, fig.23

in addition to the type species.

Diagnosis:

Small to medium sized; subtrigonal to subcircular outline, globose to depressed in lateral view. Many sharp ribs. Anterior plication trapezoidal. Beak small, suberect; beak ridges short, sharp. Median septum low, short, keels inner hinge plate. Outer hinge plates flat. Crural bases calcate, crura prefalcoifer. Deltidial plates buttressed by delthyrial lining.

Remarks:

Calcirhynchia was proposed by BUCKMAN (1918 p.30) and revised by AGER (1962 p.85) who gave details of the internal structure of the type species, C.calcaria. Previous to this Calcirhynchia was one of the many BUCKMAN genera which were too poorly known to be usable and was listed as such by RZHONSNITSKAYA et al. (1960 p.256). MOISSEIEV therefore established Euxinella without any knowledge of the internal structure of Calcirhynchia and DAGIS (1963), who revised Euxinella was in a similar position.

Both Calcirhynchia and Euxinella contain species with many moderately fine ribs, no posterior smooth stage (contra BUCKMAN's misleading remarks on Calcirhynchia - 1918), a flat trapezoidal uniplication, a small in - curved beak, short, sharp beak ridges, and a poorly developed fold and sulcus. Internally they both have buttressed deltidial plates, a low septum keeling the shallow muscle trough, prominent calcate crural bases, and prefalcoifer crura. The types of the two genera are certainly externally dissimilar: C.calcaria is depressed whereas E.iatirgvartaensis is globose. However the additional species figured by DAGIS (1963) give Euxinella an aspect identical with Calcirhynchia if the Liassic species listed above are admitted as members of that genus. Moreover species of both genera occur most commonly in similar lithologies - argillaceous limestones - and Calcirhynchia is most frequent in the lower part of the lower Liassic (AGER 1962). Therefore both palaeontological and geological factors support the synonymy of the two genera.

Cirpa and Calcirhynchia are also most certainly closely related (compare particularly the internals of Cirpa kiragliae AGER, 1959 and C.calcaria), but eight species of Cirpa have now been recognised, all of them characterised by strong ribs, well marked planareas and obvious anterior flattening. Two distinct genera are therefore recognisable.

Calcirhynchia subrimosa (SCHAFHÄUTL), 1851

Plate 6, figs.1-4; text-figs. S.xvi - S.xviii; text-plates S.4, S.5

1851 Terebratula subrimosa SCHAFHÄUTL, p.411, pl.7, figs.3,?4

1859 Rhynchonella subrimosa SCHAFH.; WINKLER, p.25

non Rhynchonella subrimosa auctt.

Lectotype:

Neither of the originals of SCHAFHÄUTL's two figures were found during a personal examination of the collection in the Bayer.St.Slg. in Munich, made through the kindness of Professor DEHM, and they must be presumed lost. The original of pl.7, fig.3 is here designated lectotype, (see also Remarks below).

Dimensions of Lectotype

Although SCHAFHÄUTL gave three sets of dimensions for his species he omitted to say to which of his figures, if any, these referred. Measurements taken from his fig.3 (to .5mm.) are length 13.5, breadth 13.0, thickness 13.0.

Type Locality:

SCHAFHÄUTL wrote of the locality of his fig.3 (1851 p.409) as follows -'mit der T.tumida B. (T.Boissyi-sic) bei Reit im Winkel in jenen schwarzen Kalk-Flötzen vorkommt, die ebenfalls die Gervillia inflata (mihi, G.tortuosa) enthalten'. This certainly refers to the Rhaetian exposed in the Lofer Graben near Reit im Winkel, Bavaria, - 47° 40'35''N. 12°26'55''E. where Gervillia occurs and T.tumida was later identified as Oxycolpella oxycolpos(see description of that species herein). Specimens are still obtainable there.

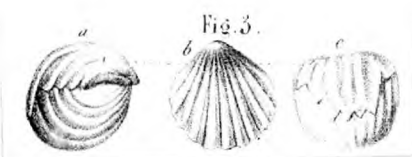
Range and Distribution:

Known only from the Rhaetian in the immediate neighbourhood of the type locality; possibly present in the Late Norian of Slovakia (Drnava).

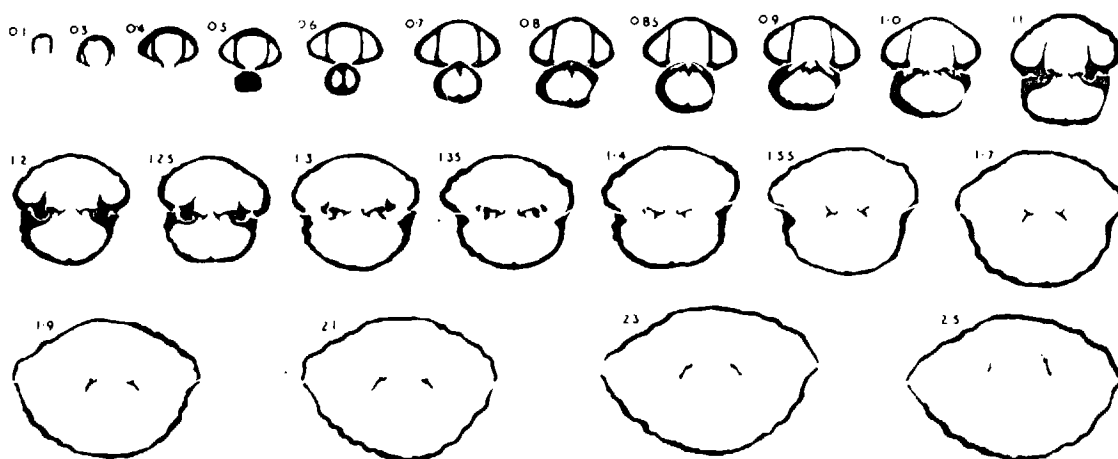
Diagnosis:

Globose; 11-18 ribs present. Otherwise as genus.

Text-fig. S.xvi



From SCHAFHÄUTL, 1851, pl.7, fig.3,
here chosen as lectotype of Calcirhynchia
subrimosa (SCHAFHÄUTL). xl



Text-fig. S.x v

Calcirhynchia calcaria BUCKMAN. Upper Hettangian or Lower Sinemurian; New Bitton, Rugby. ex. AGER 1962, text-fig. 50. x9

Description:

Calcirhynchia subrimosa is a small to medium sized rhynchonellid, subcircular to transversely oval in outline and equibiconvex in lateral profile. All the specimens collected by the writer are somewhat globose, but depressed individuals may also be included in the species (see Remarks below). Between 11 and 18 slightly blunted ribs are present, the majority of which originate at the apices of the umbones and 4 or 5 through bifurcation within 2-3mms., but this feature is rarely obvious because the bluntness of the ribs makes them faint posteriorly. Later bifurcation is uncommon. The anterior commissure is plicate involving 3-6 brachial ribs and the subtrapezoidal ligule may reach verticality in globose specimens. In flatter individuals a low broad fold is developed. There is no tendency to produce the anterior vertical zone of depressed ornament and quadrate lateral profile seen in the related genus Cirpa. The beak ridges delimiting a broad area. The pedicle foramen is submesothyrid in position.

The insertion of the dental lamellae on the floor of the valve is almost parallel and the delthyrial cavity is transversely quadrate apically but becomes subtrapezoidal in the plane of articulation. The cavity is lined and the deltidial plates are buttressed in older specimens (see text-plates 11-13, and accompanying discussion). The teeth are transversely quadrate.

The median septum is low and keels the narrow U-shaped muscle trough (see text-plates S.4 and S.5). The outer hinge plates are flat and the inner socket ridges strongly emphasised; the outer socket ridges are also well developed. The crural bases are calcate and prominent, and the crura themselves prefalcifer-like.

Remarks:

In the original description of C. subrimosa SCHAFHÄUTL wrote of the continuity of the ribs to the apex of the beak and this feature is clearly to be seen on his figs. 3 and 4. SUESS, however described under this name individuals which were obviously posteriorly smooth (1854 p.26-27) and stated that this was contrary to sense of SCHAFHÄUTL's description. With the exception of WINKLER (1859) all later revisors followed SUESS's misinterpretation. ZUGMAYER (1880 p.36) felt that SCHAFHÄUTL's material probably belonged to SUESS's 'R. fissicostata', and this may indeed be true

of fig.4. The original of this figure was said (p.416) to be from the 'Gastetter Graben, von Chiemsee', but the writer has not checked this locality. The outline and sinus of the specimen suggest that it is of a different species to that of fig.3, chosen above as the lectotype of C.subrimosa. This latter figure shows no trace of the division or sharpness of the ribs characteristic of fissicostata, whereas its globose outline and profile can easily be matched in specimens of Calcirhynchia still obtainable at the type locality. Moreover it may be compared with the larger members of the colonial assemblages which occur there and need not be confused with the flatter forms which may in future be recognised as ecological subspecies, (see Ecology). There is therefore no doubt over the identification and distinctiveness of C.subrimosa.

All the in situ specimens collected by the writer at the type locality are small, more or less globose individuals (plate 6, figs.1-3) and occurred in a closely packed group thought to represent a colony possibly attached to anchored algae (see Ecology). Although the largest of them is relatively wider than SCHAFHÄUTL's type there is no difficulty in accepting this material as conspecific with his species. In addition to these specimens, 25 from the Nat.hist.Mus. Vienna were examined through the kindness of Prof.H.ZAPFE. One box - D 3769 - labelled 'Küss. Schichten, Weissloferbach^{graben}, bei Reit im Winkl' contains 3 specimens and they are almost certainly topotypes. One extremely similar to the lectotype is refigured here (plate 6, fig.4). The remainder - 1963 Nr.563/5 - are simply labelled 'Rhät, Ober Weidring', and may therefore be from the flanks of the Steinplatte reef, some 10kms. from the type locality where C.subrimosa has been found associated with Zugmayerella uncinata (see Ecology). The remarkable feature is the wide range of form shown by the museum material, in particular the presence of very flat and very large individuals. Their relation to the colonial material is shown graphically in text-fig. S.xix. Pending further collecting it is only practicable to recognise one species some members of which were small, globose and lived colonially, whilst others were in a less crowded habitat and became both larger and more variable in form. If the latter are to be distinguished as an ecological subspecies then their environment must be accurately deduced from precisely located material, and not from museum collections.

In view of this diversity of form within so small an area in the N.Alps, the writer cannot escape the feeling that some of the five species recorded by DAGIS (1963) from the region between the rivers Belaya and Laba in the north west Caucasus may be regarded as conspecific. C. robinsoni certainly seems inseparable from C. iatirgavartaensis, in fact C. robinsoni occurs at both localities where the latter has been identified and the difference noted by DAGIS (1963 p.29) that robinsoni has smoother ribs near the umbones seems slight.

'R'. anatolica BITTNER, 1891, is almost certainly not the species described by DAGIS (1963 p.29), following MOISSEIEV (1927) as Euxinella anatolica. The outline and beak character of BITTNER's figure is not suggestive of this genus.

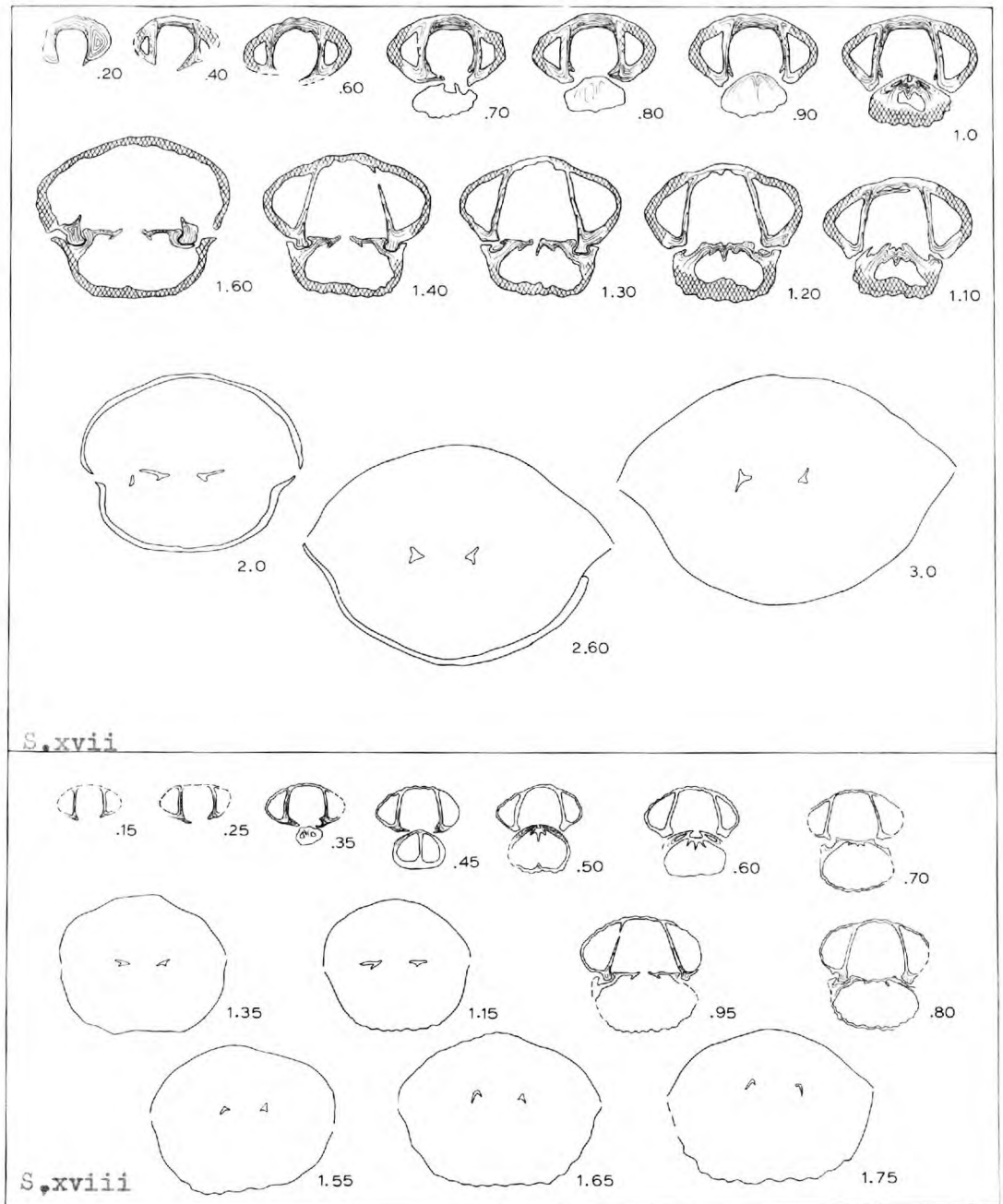
The writer has several specimens from the late Norian of Drnava which may be referable to subrimosa but they have not yet been fully examined.

Dimensions of Figured Specimens:

	length	breadth	thickness
6/1	12.2	15.0	11.9
6/2	10.0	11.2	9.7
6/3	9.7	10.4	7.0
6/4	13.5	14.2	11.5

Material:

Lofer Graben, by Reit im Winkl (type locality, see above) - 30, T.25;
 'Ober Weidring', Nat.hist.Mus. Vienna, 1963, Nr.563/5 - 22; 'Weissloferbach Graben, bei Reit im Winkl', Nat.hist.Mus. Vienna, D 3769 - 3;
 'Weissloferbach Graben, bei Reit im Winkl', Nat.hist.Mus. Vienna, C 1597 - 7;
 beneath the Scheibelberg, N.end Steinplatte reef - 4, T.26.



Text-figs. S.xvii and S.xviii

Serial transverse sections of Calcirhynchia subrimosa (SCHAFHÄUTL). Rhaetian; Lofer Graben between Kössen (Austria) and Reit im Winkl, (Bavaria); 47°40'35''N. 12°26'55''E. - 91, St Johann in Tirol. Both x4 S.xvii Crura end 3.2mm. Total length of specimen 12.9mm. PC.Nr.1; S.xviii Crura end 1.85mm. Total length of specimen 8.7mm. PC.Nr.10. Topotypes.

TEXT-PLATES S.4 and S.5

Calceirhynchia subrimosa (SCHLFFHAUTL)

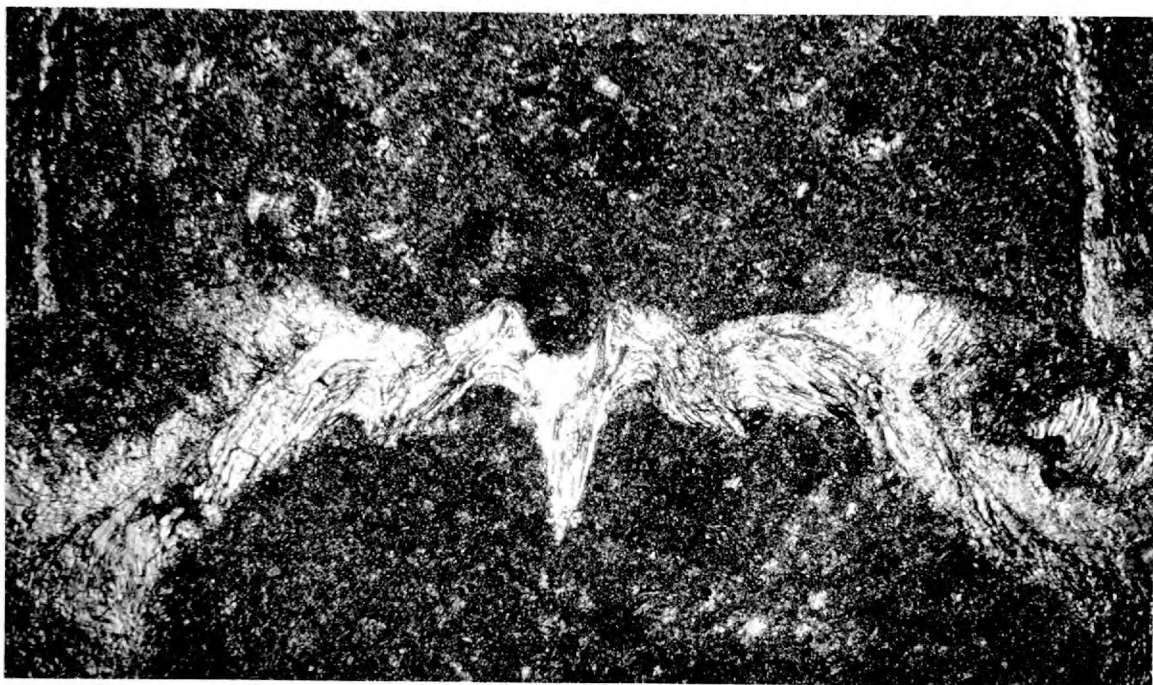
811

Text-plate. S.4

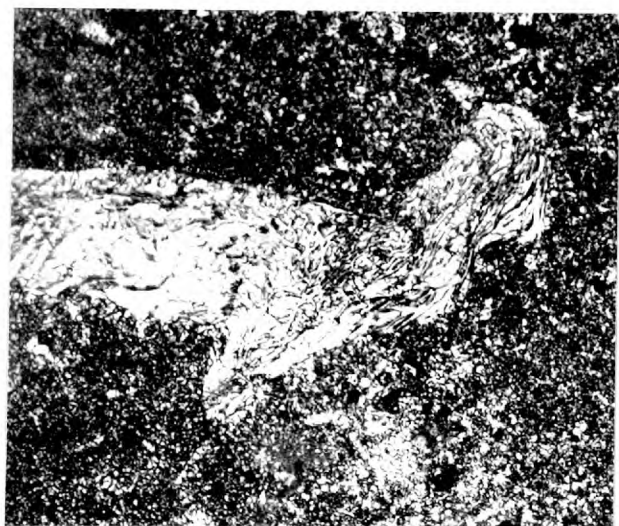
Transverse section of the hinge plate and sockets of Calcirhynchia subrimosa, showing the two layers of the socket plates, the calcate crural bases, and the keeled, U-shaped muscle trough. Detail of section 1.2 of text-fig. S.xvii x50.

Text-plate, S.5

Transverse sections of the outer hinge plate and part of the socket and tooth, (A) and the median edge of the outer hinge plate, (B) of C.subrimosa. Detail of section 1.4 of text-fig. S.xvii A x120 B x60.



Text-plate S.4

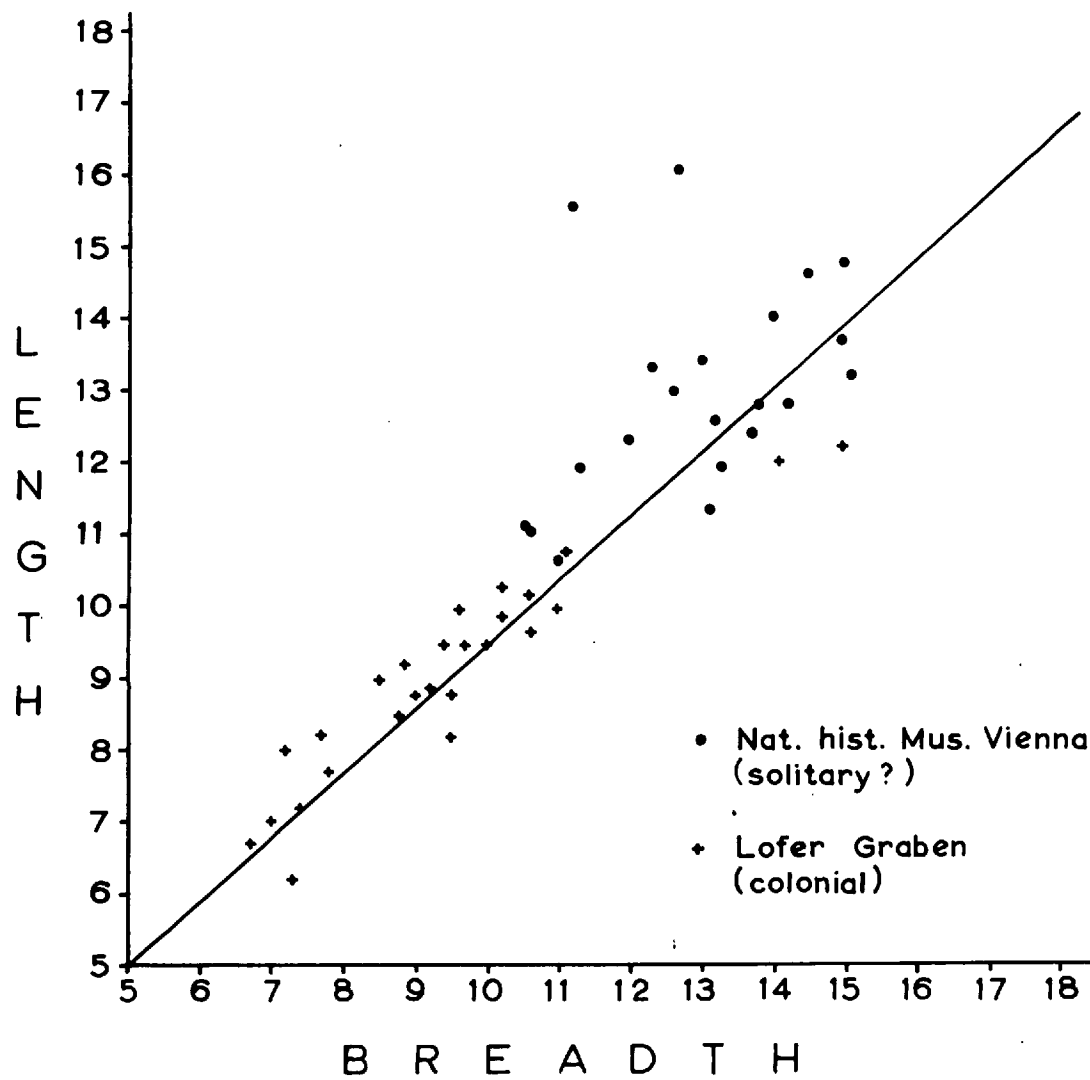


Text-plate S.5

A



B



Text. fig. S. xix.

?Calceirhynchia cf. obtusifrons (SUESS), 1854

Plate 7, figs. 6, 7

?1854 Rhynchonella obtusifrons SUESS, p. 27, pl. 4, fig. 121880 Rhynchonella cf. obtusifrons SUESS; ZUGMAYER, p. 39, pl. 4, fig. 29Range and Distribution:

ZUGMAYER's original is from the Rhaetian of the Vienna area of the Northern Alps, and the writer has 2 specimens from the late Norian of Drnava (Slovakia). SUESS's type was from the early Sinemurian near Vienna, but is not certainly conspecific with the Rhaetian specimens.

Diagnosis:

Small rhynchonellid, outline subcircular. 11 - 14 ribs. Beak low, pointed. Anterior commissure uniplicate, ligule trapezoidal. Hinge plate entire; low median septum.

Description:

The three specimens described here are small, subcircular rhynchonellids. Two have 11 ribs and the third, damaged specimen probably 13 or 14. They are only slightly blunted, present to the apices of the valves, and on the only fully preserved specimen (ZUGMAYER's original) they branch simply within 2mm. The anterior commissure is plicate in - volving in each case 3 brachial ribs, and producing a moderately high trapezoidal ligule. No fold or sinus is developed and the brachial valve tends to flatten rather than become globose. The beak is low and pointed, above a small area.

The damaged posterior of one specimen was ground and revealed an entire hinge plate keeled by a low median septum. Dental lamellae are also present but no other internal details are known.

Remarks:

The two poorly preserved specimens from Drnava are certainly conspecific with ZUGMAYER's original, and in all probability are the same species as SUESS's type, (by monotypy), from the early Sinemurian of Enzesfeld (Vienna region). In his lengthy description SUESS included a wide range of the catch-all species 'Rhynchonella' variabilis but since no

later author appears to have considered the species and a satisfactory revision is beyond the scope of the present work, the Triassic material is only provisionally referred to 'Rh'.obtusifrons SUESS.

The entire hinge plate and low median septum found in the specimen on plate 7, fig. 7 suggest that this species belongs to Calcirhynchia, and the low beak, full ribbing and lack of fold and sinus, support this, but further internal details are needed for confirmation.

'Rhynchonella'fringilla BITTNER, from the Carnian of the Southern Alps may well be a close relative of the present species, and BITTNER's holotype is refigured on plate 7, fig.8.

Dimensions of Figured Specimens:

	length	breadth	thickness
7/6	13.2	12.6	7.5
7/7	12.0(d)	13.0	9.0

Dimensions of ?C.fringilla:

	length	breadth	thickness
7/8	12.5(d)	13.7	6.7

Calcirhynchia cf. ?C. pectiniformis CANAVARI; TRAUTH, 1909

Plate 7, figs. 1-5; text-figs. S.xx - S.xxii

?1909 Rhynchonella pectiniformis CAN.; TRAUTH, P.64, pl.1, fig.15

Range and Distribution:

Norian of S.Slovakia (Drnava).

Rhaetian of the Northern Alps (Vienna area).

TRAUTH's material of ?C. pectiniformis came from the Middle Liassic of the Gresten region of the Northern Alps and may be conspecific with the Triassic specimens (see under Remarks).

Diagnosis:

Medium sized rhynchonellids, subcircular to transversely oval outline. Beak small, pointed, suberect. 13 - 18 rounded, simple ribs; faint posteriorly. No fold or sinus. Low median septum. Outer hinge plates almost horizontal. Crura prefalcifer.

Description:

This species includes medium sized rhynchonellids ranging from subcircular, globose forms to slightly transversely oval, more depressed individuals. 13 - 18 rounded ribs are present, faint near the apices but covering the whole of the valves. No branching can be distinguished. The beak is pointed, suberect and low, with well marked beak ridges outlining a small area. The pedicle foramen is submesothyrid in position. The plication of the anterior commissure involves 3 - 5 brachial ribs and may be low and sinuate leaving the profile somewhat depressed, or high, in which case globosity results: no fold or sinus is produced.

The delthyrial cavity is transversely quadrate and formed by slender dental lamellae. The teeth are very slightly inwardly inclined and quadrate in section. A low median septum keels the muscle trough and unites the narrow, oblique inner hinge plates. The outer hinge plates are gently arched in the more globose of the two specimens ground, but almost horizontal in the other with a corresponding difference in the emphasis of the inner socket ridge. The outer socket ridges are strong. The crural bases are calcate and the crura themselves are prefalcifer.

Remarks:

There is little doubt that the depressed and globose examples figured here are conspecific, for a series of seven collected from Kaisersteffel show a complete gradation between the two extremes.

The flat, probably young specimen in plate 7, fig.3 is almost identical in every external respect to one from the Middle Liassic near Gresten figured by TRAUTH (1909, pl.1, fig.15) as Rhynchonella pectiniformis CANAVARI, 1883. However CANAVARI's single specimen, from the Middle Liassic of the central Apennines, is more densely ribbed and is probably a separate species. Further investigation of these occurrences is necessary before the Rhnetian species can be identified.

The series of specimens from Kaisersteffel are comparable in their range of form with Calcirhynchia subrimosa from the Lofer Graben (Bavaria) together with the museum material of that species (see under C.subrimosa). The Kaisersteffel series is distinguished by more rounded ribs. Additionally the depressed individuals have a sinuate plication rather than a flat fold. However, a flat fold is found in the Drnava (Slovakia) specimens which are here regarded as probably conspecific with the Kaisersteffel material.

The feature which unites the Slovakian and Austrian specimens in contrast to the Bavarian specimens is the shape of the delthyrial cavity and the lack of a deposit lining it. A delthyrial lining buttressing the deltidial plates characteristic of C.subrimosa topotypes larger than 6 - 7mm. Its absence or poor development in the present case is probably connected with a difference in the size and strength of the pedicle and may therefore indicate an environmentally differentiated species of Calcirhynchia. The Bavarian specimens occur in a fine grained, argillaceous limestone, deposited under quiet conditions, whilst the Austrian and Slovakian material comes from bioclastic limestones of a much more wave washed, disturbed environment demanding a stronger and larger pedicle.

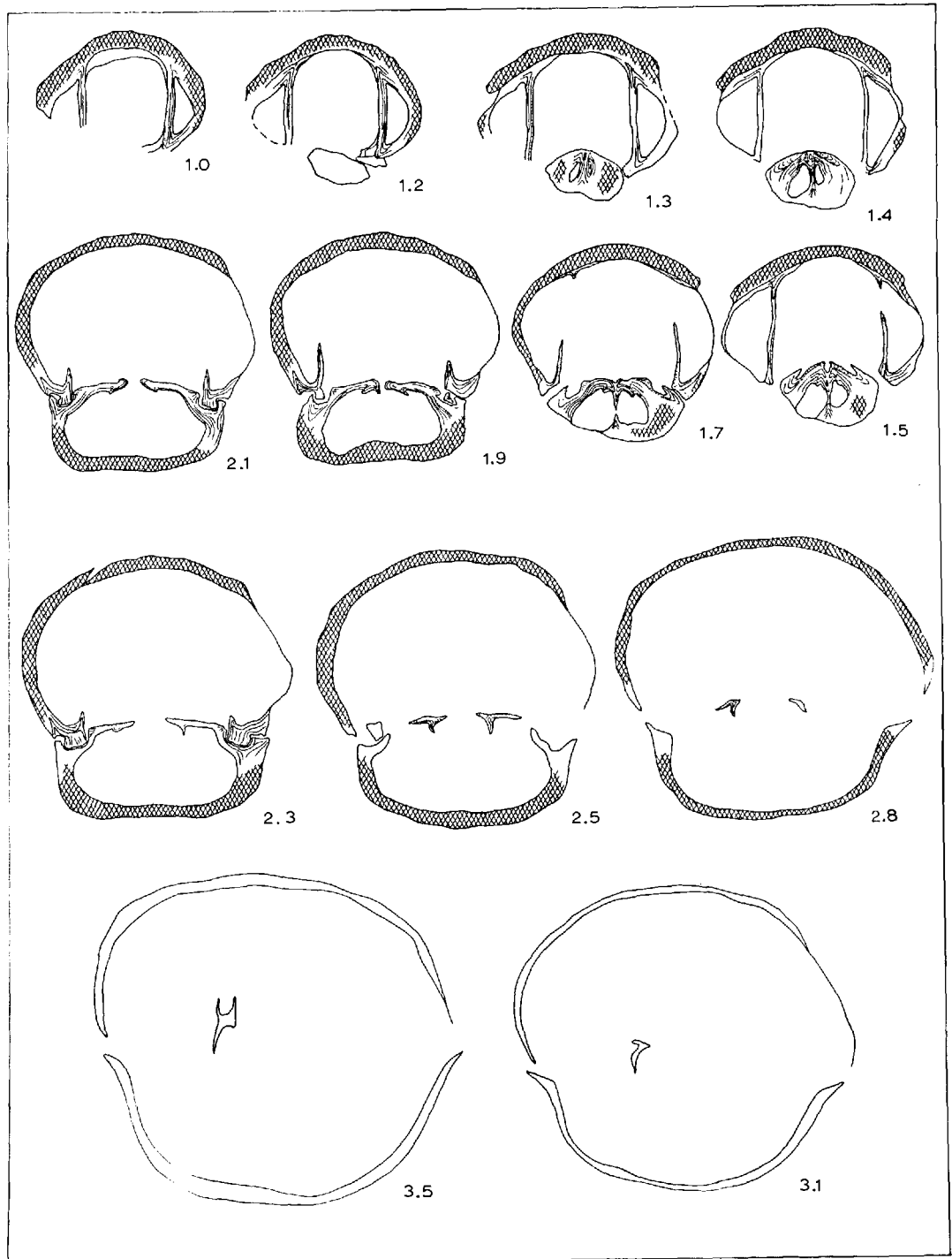
It is perhaps worth noting that the slight arching of the hinge plates in the more globose of the Kaisersteffel specimens is quite opposite to the condition found by AGER (1959a - text-figs. 2 and 3). In this case the globose subspecies has the flatter hinge plates.

Dimensions of Figured Specimens:

	length	breadth	thickness
7/1	16.0	17.9	11.2
7/2	12.0	13.7	10.2
7/3	14.3	14.8	7.5
7/4	14.4	16.4	9.1
7/5	14.8	16.8	13.3
7/6	13.2	12.6	7.5

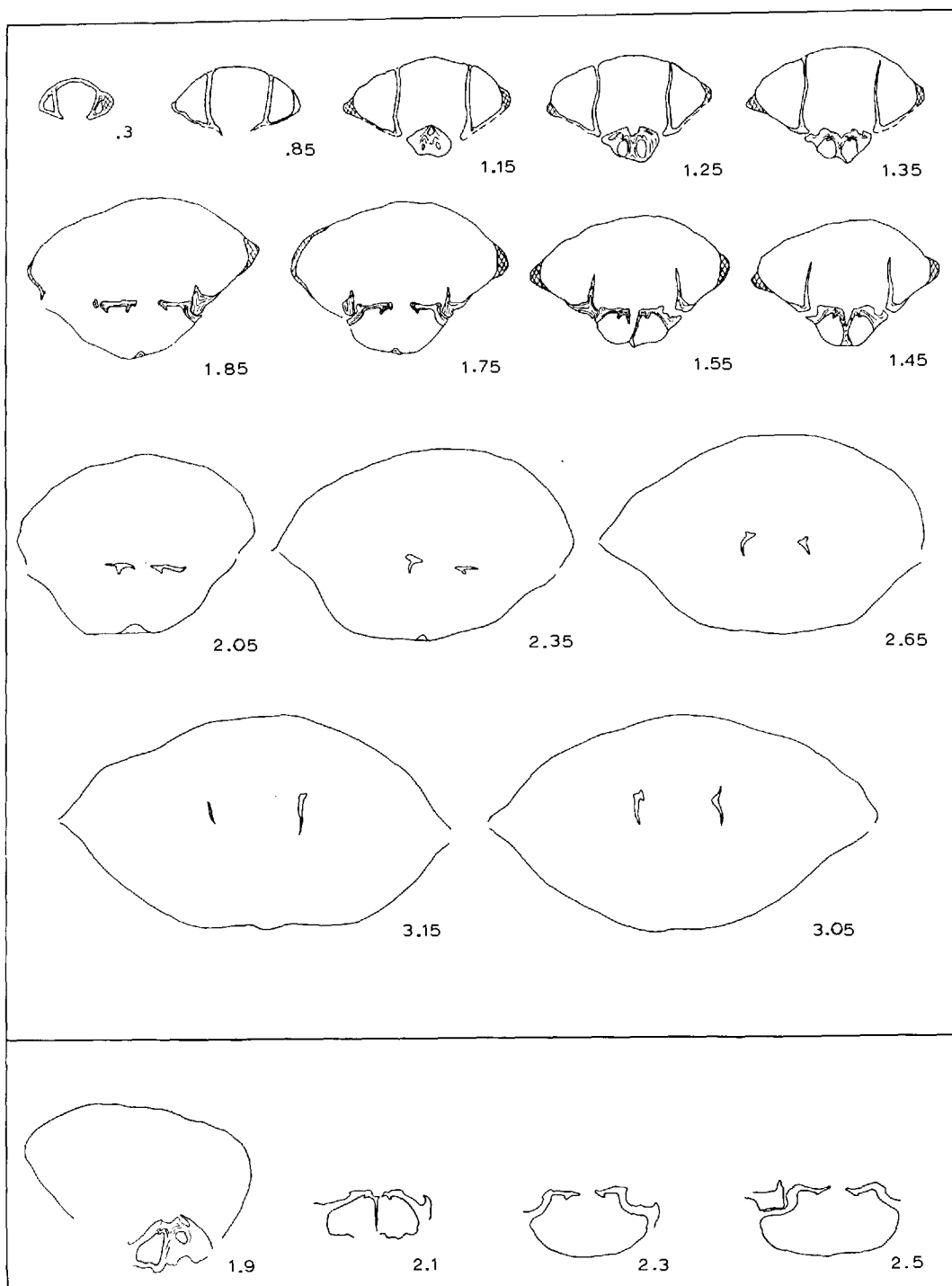
Material:

Hohe Mandling, Piesting Tal, forest path 630 - 670m. - 3, T.27;
 'Mandlinger Wald', B.M.N.H. BB43205 and BB43206 ex. B39205 - 2; Ober
 Kaisersteffel, Piesting Tal - 7, T.28; behind Hirtenberg station - 1, T.29;
 Drnava, by Gombas, S.Slovakia - 9, T.30



Text-fig. S.xx

Serial transverse sections of Calcirhynchia cf. ?U. pectini-formis CANAVARI; TRAUTH. Rhaetian; Forest path, Hohe Mandling, by Waldegg, Piesting Tal, Lower Austria; 630-670m., 47°53'45''N. 33°39'55''E. 75 (Pr)Puchberg am Schneeberg. x5 Crura end ?3.7mm. (unclear). Total length of specimen 14.6mm. PC.Nr.29.



Text-fig. S.xxi

Serial transverse sections of Calcirhynchia cf. ?C. pectini-formis CANAVARI; TRAUTH. Rhaetian; Ober Kaisersteffel, by Waldegg Piesting Tal - 550m., 47°52'15''N. 33°42'10''E. - Hohe Wandgebietes.

x5 Crura end 3.35mm. Total length of specimen 14.0mm. PC.Nr.30

Text-fig. S.xxii

Drnava, S.Slovakia. x5 Provisional C.cf. ?C. pectiniformis
PC.Nr.35

?Caucasorhynchia sp.

Plate 6, figs.5,6

Description:

The two damaged specimens described and figured here are medium sized, moderately inflated, subtrigonal rhynchonellids. On one 12 rounded ribs are present and on the other 15, of which 4 or 5 originate through bifurcation within 3mm. of the brachial umbones, where they are clearly defined. The anterior commissure is plicate involving 3 or 4 brachial ribs, but the ligule is low, no fold or sinus is developed, and the maximum convexity of the valves is left towards the posterior.

The internal structure could not be studied.

Remarks:

These two specimens probably belong to Caucasorhynchia even though this genus has not previously been recognised outside the Norian of the N.W.Caucasus. The rounded, bifurcating ribs and lack of sinus and fold are characteristic of Caucasorhynchia. In outline both specimens are similar to C.worobievi but have fewer ribs (the latter has 16 - 20), and their cardinal commissure is indented, pinching the apex of the brachial valve, in contrast to that of the Caucasian species.

Localities and Materials:

1 specimen from Nat.hist.Mus. Vienna - 1963 Nr.563/5 labelled 'Rhät, Ober Weidring'. This locality probably lies on the slopes of the Steinplatte Reef.

1 specimen from the ZUGMAYER Collection in the Pal.Inst.Univ. Vienna, labelled 'Schwarzlofer Alm', and probably from the same area as the specimen above.

Dimensions of Figured Specimens:

	length	breadth	thickness
6/5	---	15.0	11.0
6/6	---	14.7	11.6

Subfamily uncertain

Genus Vindobonella gen.nov.

Type species:

Vindobonella katzeri sp.nov.

Range and Distribution:

Norian of Slovakia (Stratenska hornatina).

Rhaetian of the Northern Alps, Slovakia (Hybe), and N.W.Rumania (Apuseni Mts).

Included species:

At present only the type species is recognised in Vindobonella.

Derivation of Name:

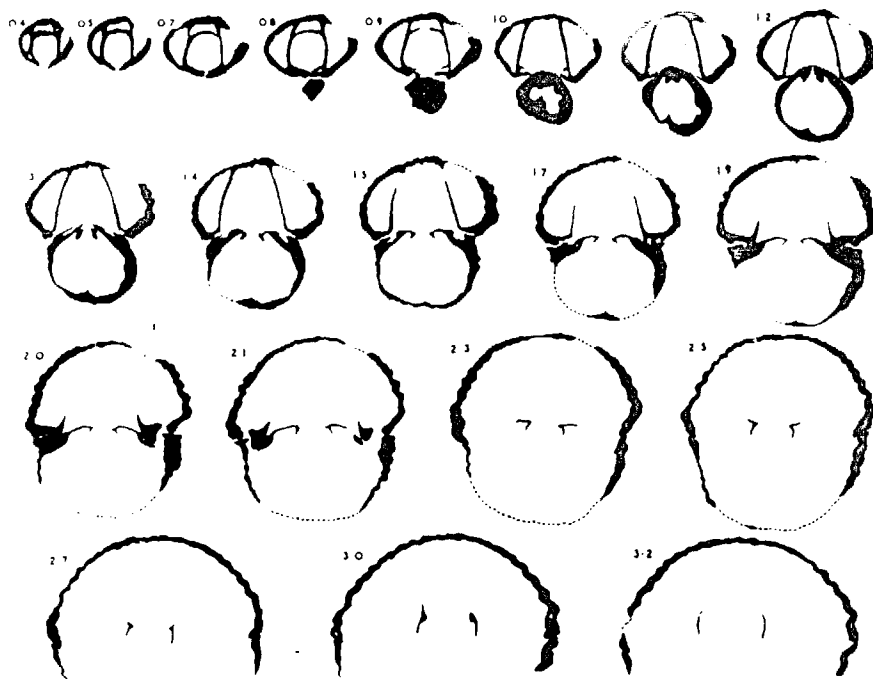
From Vindobonae - Vienna, the species being common in the Vienna area of the Northern Alps; and ellus -a -um, a diminutive often used for rhynchonellids.

Diagnosis:

Medium sized; posteriorly smooth, ribbed anteriorly. Anterior commissure plicate, fold and sulcus very poorly developed. Beak low, pedicle foramen submesothyrid in position. Muscle trough sessile. Crura radulifer.

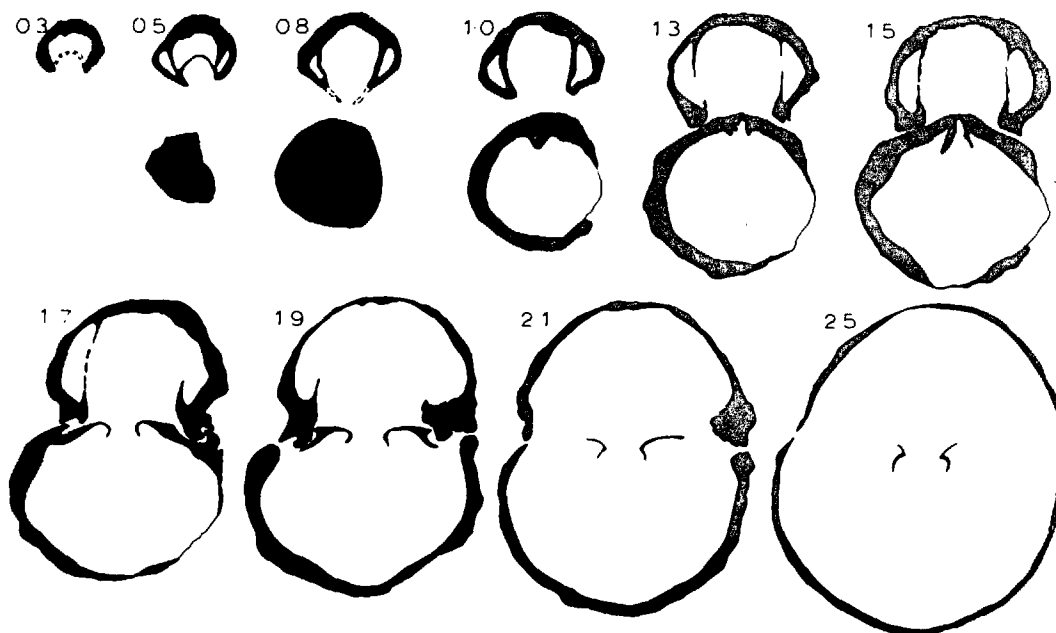
Remarks:

Externally the type species of Vindobonella gen.nov. is very similar to an undescribed species from the Liassic of Turnak, Bulgaria. Both are smooth posteriorly, and of the same size and outline, but the Bulgarian specimens can be easily distinguished by their very few, broad ribs, high ligule and indistinct area. On grinding, moreover, the Turnak species reveals the pedicle collar and well developed prealcaifer crura of Pseudogibbirhynchia, (see text-plate S.xxiii kindly provided by Dr.D.V.AGER who also collected the material), and is certainly a close associate of that genus, if not a member of it. Nevertheless V.katzeri has very thick deltidial plates and calcate crural bases and, although it and the Bulgarian species are best regarded as differing generically, their similarity is sufficient to indicate a subfamilial relationship. In turn they must both be associated with Pseudogibbirhynchia.



Text-fig. S.xxiv

Pseudogibbirhynchia moorei (DAVIDSON). Lower Toarcian;
Dorset. ex. AGER 1962, text-fig.67. x3



Text-fig. S.xxiii

'Rhynchonella' sp.nov. ?Sinemurian; Turnak, E.Bulgaria.
Sections provided by Dr.D.V.AGER. D.V.A. coll. J.1200. x4

Pseudogibbirhynchia was placed in the Cirpinae by AGER (1965 p.607) but the writer is not in favour of maintaining this. The main stock of the Wellerellidae - of which the Cirpinae is a subfamily - is characterised from the early Carboniferous by an entire hinge plate and raised muscle trough, whereas Pseudogibbirhynchia conspicuously lacks this feature (see text-fig. S.xxiv, from AGER 1959). It may nevertheless be argued that the relationship to the Cirpinae is indicated by the prefalcifer crura and that the septum has merely retreated from the apex of the valve leaving the muscle trough sessile. A similar retreat is in fact found in Prionorhynchia (see AGER 1959, text-fig.26), a genus externally markedly reminiscent of Cirpa, in which the muscle trough is only slightly raised by a low median septum. However whilst it is possible that Pseudogibbirhynchia may ultimately be descended from a wellerellid ancestor it seems inadvisable to stretch this speculation to the extreme of including Pseudogibbirhynchia in, what is in effect, the Mesozoic equivalent of the type subfamily. In the writer's opinion Pseudogibbirhynchia and its Liassic allies evolved with the development of prefalcifer crura from a late Triassic stock represented by Vindobonella, and that the whole complex is sufficiently distinctive to warrant recognition as a subfamily. However, in view of the comprehensive study of the evolution of the Mesozoic rhynchonellids being carried out by Dr.D.V.AGER, Dr.A.CHILDS and the writer, its establishment is delayed for discussion and agreement.

Vindobonella katzeri sp.nov.

Plate 8, figs. 1-7; plate 9, figs. 1-8; text-figs. S.xxv, S.xxvi;
text-plate. S.6

- 1854 Rhynchonella subrimosa SCHAFHÄUTL spec.; SUESS, p.26, pl.4, figs.5-11
1880 Rhynchonella subrimosa SCHAFH.; ZUGMAYER, p.37, pl.4, figs.22-28
var.globosa p.37
var.complanata p.37
var.trigonalis p.37
1905 Rhynchonella subrimosa SCHAFH.; von ARTHABER, pl.50, figs.2,3
1917 Rhynchonella subrimosa SCHAFH. sp.; GOETTEL, p.107, pl.7, figs.3,4
var.complanata p.108, pl.7, fig.4
var.globosa p.108, pl.7, fig.3
var.trigonalis p.108.
1958 Rhynchonella subrimosa (SCHAFHÄUTL); MAHEL, p.131, pl.4, figs.1-4
1958 Rhynchonella nov.sp., aff.subrimosa (SCHAFHÄUTL); MAHEL, p.132, pl.4,
figs. 5-7

Holotype:

According to the ICZN Rec. 73b. the holotype of V.katzeri should be chosen from the misidentified material of the authors listed in the synonymy above, but unfortunately none of it is suitable: SUESS's and GOETTEL's has been lost, von ARTHABER gave no descriptions and his specimens cannot be identified. MAHEL's material is not amenable to serial grinding and collecting of topotypes from his localities is very difficult. Although ZUGMAYER's specimens are preserved in the Pal.Inst.Univ.Vienna and would normally be acceptable for holotypic designation, none of them are sufficiently typical in form to be desirable, therefore a specimen from the Geol.Bundes.Vienna has been chosen and is figured here on plate 8, fig.7. A paratype showing the muscle scars on the brachial valve is also figured.

Type Locality:

The type specimen is from a box labelled 'Rhynchonella subrimosa SCHAFH. Küssener Schichten. Hirtenberg unweit südl. des Kalkofens am rechten Triesting Ufer, links vom Fussteir nach Enzesfeld', and numbered 3 rot 9/5. Seventeen other specimens associated with it are designated paratypes.

Range and Distribution:

As for genus above.

Diagnosis:

10-16 ribs present, otherwise as genus.

Derivation of name:

Named with grateful thanks after Herr Ernst KATZER of Waldegg, an amateur geologist and local historian of very great assistance to the writer in tracing ZUGMAYER's localities in the Piesting Tal.

Description:

Vindobonella katzeri comprises medium sized, equi-biconvex rhynchonellids with a subcircular to transversely oval outline, and variably globose or depressed in profile. All specimens are characterised by a posterior smooth area of greater or lesser extent, and between 10 and 17 barely rounded ribs on the anterior part of the shell. The anterior commissure is plicate, involving 3,4 or rarely 5 brachial ribs, and produces a slightly sunken subtrapezoidal ligule. No true fold or sinus is ever developed. The beak is low, broad, suberect and the ridges which accompany it are sharp apically but rapidly lose their emphasis when traced laterally. The brachial valve is only slightly pinched but in thick, gerontic individuals planareans may be simulated. The pedicle opening is submesothyrid in position and the deltidial plates are conjunct. Pyriform dorsal adductor muscle scars lie on either side of the median ridge and the pallial sinuses show a saccate pattern, (see pl.8 figs.5 and 6).

The delthyrial cavity is rounded in transverse section and the adductor muscle impressions are noticeable as shallow grooves. A thin delthyrial lining is present and in the ground Austrian specimen the deltidial plates are very thick, (see text-fig.S.25.). The outer socket ridges are large and project into the groove on the edge of the teeth.

The muscle trough lies sessile on the floor of the valve and the median ridge plays no part in the formation of the hinge plate (see text-plate S.6). Small inner socket ridges clearly separate the broad socket plates from the outer hinge plates. The crura are rooted on the outer slopes of the walls of the muscle trough, and in transverse sections their development is reflected in the sigmoidal deflection of the growth lines. The crural bases are bluntly calcate and the crura themselves are of the radulifer type.

Remarks:

V.katzeri has been long recognised and several times described as 'R.subrimosa' (SCHAFHÄUTL), (= Calcirhynchia subrimosa herein), but the original figures (1851 pl.7, figs.3,4) very clearly show specimens ribbed to the apices of the umbones, and in fact SCHAFHÄUTL remarked on this feature (p.411). SUESS, however, felt that SCHAFHÄUTL's description of 'R. subrimosa' fitted more closely to the present species than to any other he included in his monograph, and after some hesitation applied this name to posteriorly smooth specimens, (1854 pl.4, figs.5-11). Although WINKLER (1859 p.25) understood the character of SCHAFHÄUTL's species, ZUGMAYER (1880) and all later revisors followed SUESS's misinterpretation.

Although SCHAFHÄUTL named his species Terebratula subrimosa, by ICZN Art. 49 subrimosa cannot be retained for the species to which it was wrongly applied by SUESS even though they were placed in different genera.

The wide variation in this species was already noted by SUESS (1854 p.27) who illustrated specimens with between 2 and 6 brachial ribs in the fold, as a preliminary to the distinction of separate species. ZUGMAYER (1880 p.37) then distinguished and figured three 'Gruppe' - based on external shape which he designated 'durch den Beinamen globosa' for the typical form, (here pl.8 fig.1), complanata (pl.8 fig.2) and trigonalis for a trigonal form. He also noted the appearance of ribs close to the umbones of some individuals and referred to 'der Uebergang von Rh.subrimosa zur fissicostata'. GOETEL (1917 p.107) used a similar phrase for specimens from Hybe and a paratype series of specimens from there, kindly lent by Dr. Miloš SIBLÍK, is shown on plate 9, figs. 1-4: of which fig.4 is the most remarkable. Specimens showing the opposite extreme of very restricted anterior ribbing were separated by MAHEL (1958 p.132) as Rh.nov.sp.aff.subrimosa and a series of examples is also shown on plate 9. However at both MAHEL's source localities more typical specimens occur together with those of his new species and the writer believes that the latter are young specimens and variants which may all be included within V.katzeri. Each locality in fact, has some peculiarity of size or extent of ribbing, and this is better understood under one name than as a host of local and unusable subspecies.

GOETEL (1917 p.108) referred to var.complanata forms as characteristic of a Tatra 'Kolonie' but this cannot be given wide significance for his

material came from only one locality (Hybe) and is simply a reflection of the populations (or assemblages) he happened to collect from; one certainly would not draw his conclusion from the paratype series figured here.

ZUGMAYER cannot be considered to have clearly established globosa, complanata and trigonalis as subspecies, and they may therefore be interpreted as infrasubspecific.

Significantly V.katzeri has neither been found in the Caucasian or Crimean upper Triassic, nor in the associated eastern Balkans, and it may therefore prove to be a purely North Alpine and Carpathian species.

The possible relationship of V.katzeri to an undescribed species from the Bulgarian Liassic and to Pseudogibbirhynchia has already been discussed under the generic description of Vindobonella.

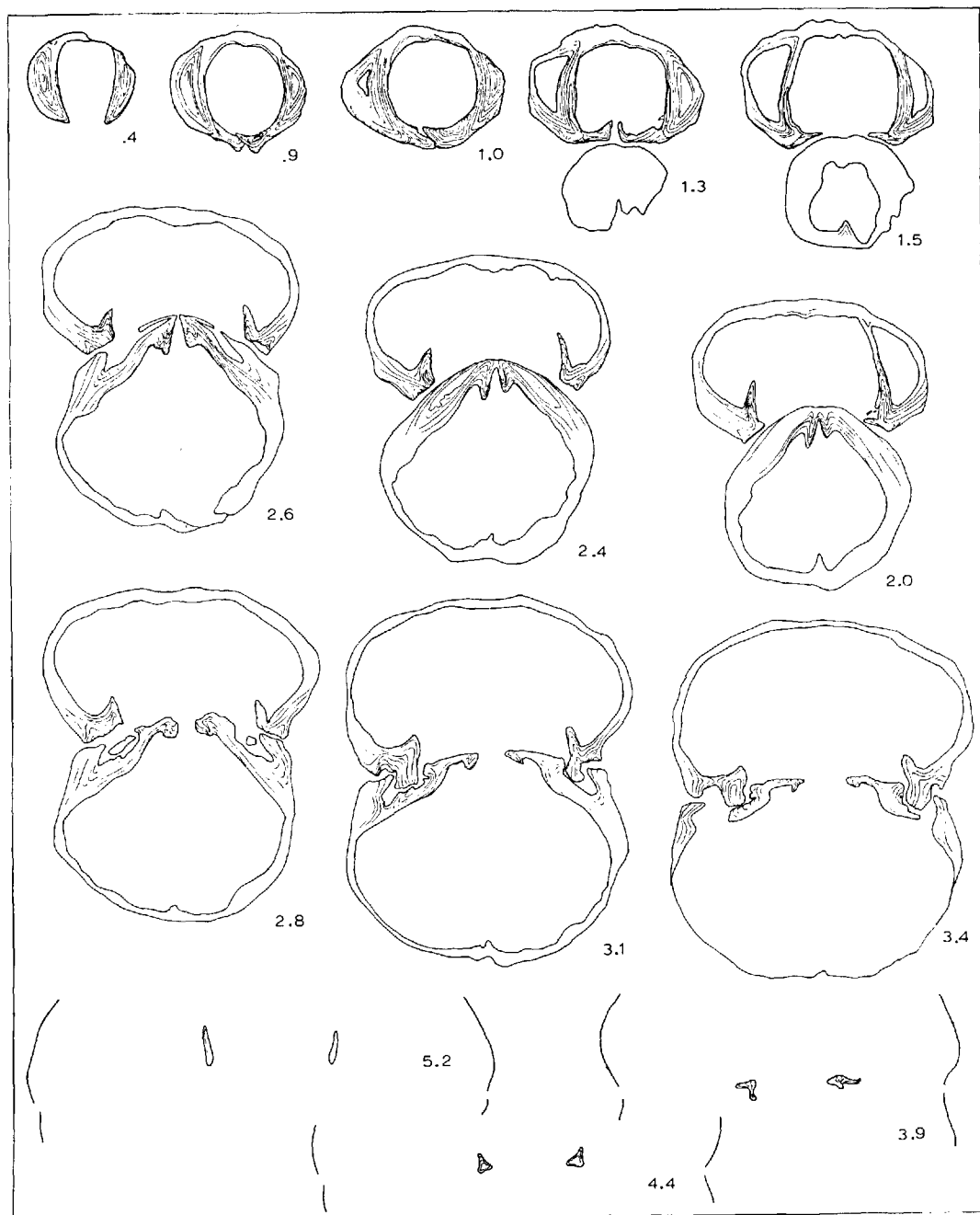
Dimensions of Figured Specimens:

	length	breadth	thickness
8/1	14.2	15.0	13.1
8/2	15.4	16.6	9.6
8/4	15.6	15.1	14.3
8/5	19.5	20.0	14.6
8/6	21.4	26.2(r)	16.1
8/7	12.7	19.8	14.3
9/1	14.3	15.7	9.6
9/2	15.6	16.9	11.9
9/3	16.2	16.9	13.3
9/4	16.4	16.4	13.2
9/5	14.2	14.8	9.0
9/6	12.8	15.0	9.6
9/7	14.0	15.0	9.7
9/8	15.8	19.1	12.1

Material:

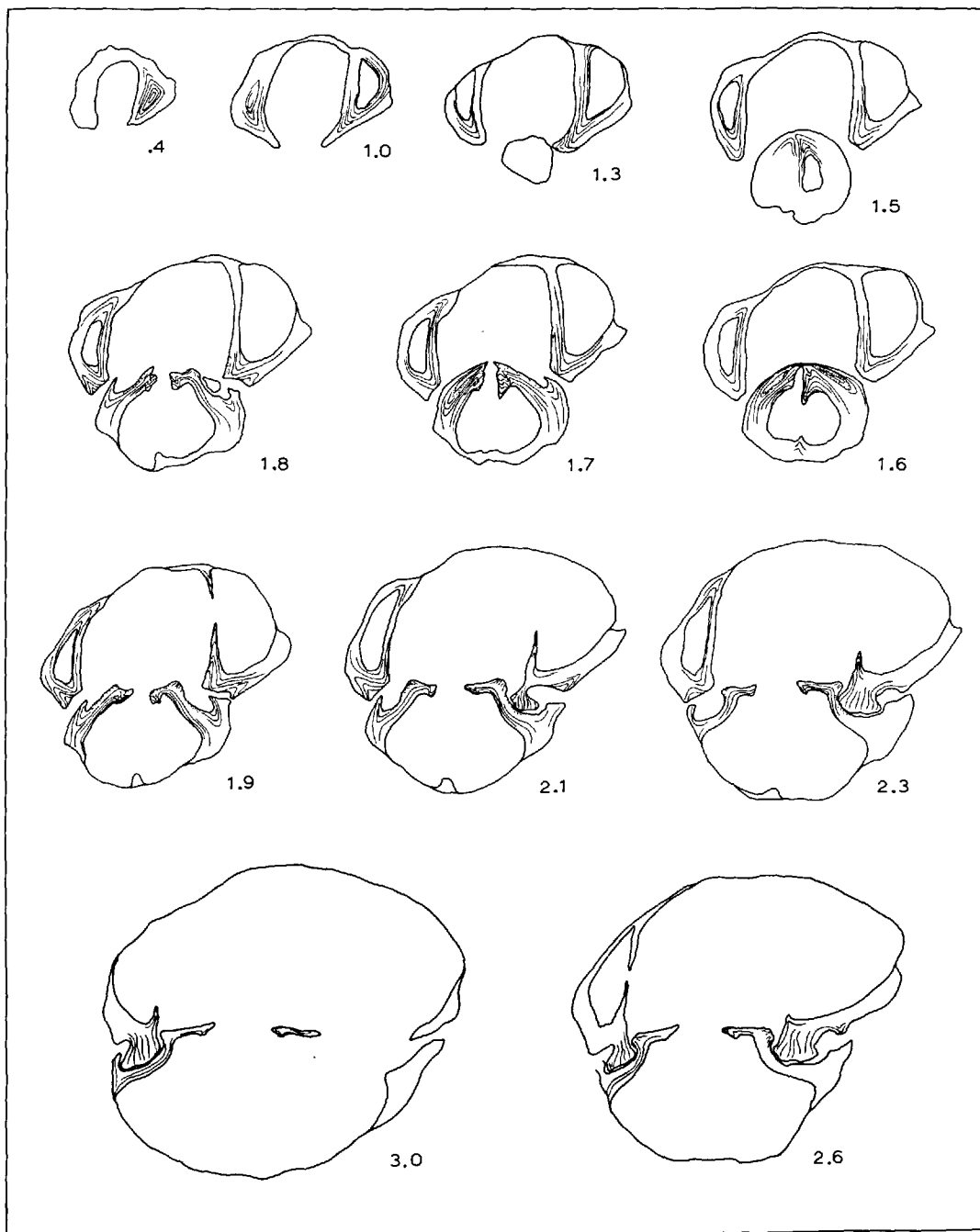
Type locality, (see above), Geol.Bundes.Vienna, (3) rot 9/5 - 18; type locality, Geol.Bundes.Vienna, (2) rot 9/5 - 22; 'Rechtes Gehänge des Kaltengang Geol.Bundes.Vienna, (9) rot 19,5 - 41; 'Mandlinger Wald', Piesting Tal, B.M.N.H. B 39205 - 6; Hohe Mandling, forest path 630 - 670m. - 5, T.32; Vorder Mandling by Waldegg - 5, T.33; Kitzberg by Neusiedl -

4, T.34; Axelstein by Jachensau, Walchensee - 1, T.35; Kendelbachgraben
- 3, T.36; Hybe, N.Slovakia - 6, T.37; as T.37, kindly lent by
Dr.M.SIBLIK - 8. Val Frunsi, Ferice (Aneseni sheet), N.W.Rumania - 3;
Tarcaita (Moneasa sheet) N.W.Rumania - 2.



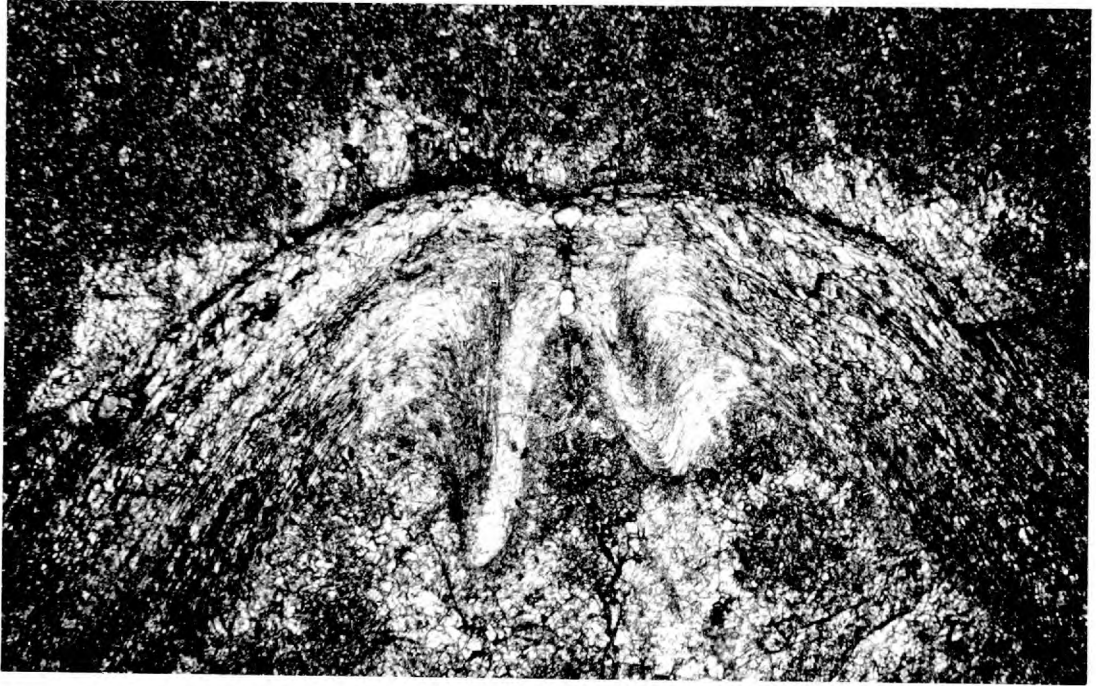
Text-fig. S.xxv

Serial transverse sections of Vindobonella katzeri sp.nov. Rhaetian; specimen from the Geol. Bundes. Vienna, (collector Dr.B.PLÖCHINGER) Kitzberg, by Neusiedl, Piesting Tal, Lower Austria. x5 Crura end 5.3mms. Total length of specimen 14.3mms. PC.Nr.18.



Text-fig. S.xxvi

Serial transverse sections of Vindobonella katzeri sp. nov.
 Rhaetian; Tarcăița, north west of Vascau, N.W. Rumania; $46^{\circ}32'30''$ N. $22^{\circ}19'15''$ E. Harta Geologica a R.P. R. - length of specimen 13.3mm. PC.Nr.32.



Text-plate. S.6

Transverse section of the brachial umbo of Vindobonella
katzeri sp.nov. showing the walls of the sessile muscle
trough. Detail of section 2.0, text-fig. S.xxv x75

?Family Wellerellidae LICHAREV in RZHONSTITSKAYA, 1956

Subfamily uncertain

Genus Osmarella gen.nov.

Type species:

Rhynchonella Starhembergica ZUGMAYER, 1880 p.38, pl.4, figs. 19 - 21.

Range and Distribution:

Norian of S.Slovakia (Drnava).

Rhaetian of the Northern Alps (Vienna area).

Liassic ?Pliensbachian of the Northern Alps (Hierlatz).

Diagnosis:

Small to medium sized rhynchonellids; many low, rounded ribs, may be smooth posteriorly. Beak and area very small. Sulcus and fold poorly developed. Dorsal median septum low. Hinge plate entire. Crural bases bulbous, crura prefalcifer - like.

Included species:

Apart from the type species, of which O.laevicosta may be a junior synonym (see below), or a separate species within the genus, only O.sp.nov. can be assigned to Osmarella.

Derivation of Name:

Osma - is an arbitrary combination of letters, and ellus -a -um, a diminutive commonly used for rhynchonellids.

Remarks:

The structure of the hinge plate found in this genus appears to be quite unlike anything yet found in the Mesozoic rhynchonellids and there are no obvious related genera. It has been provisionally placed in the Wellerellidae only because the hinge plate is entire. Further genera of this nature may be usefully grouped as a new subfamily.

Osmarella starhembergica (ZUGMAYER), 1880

Plate 2 figs. 3-7; text-figs. xxvii, xxviii; text-plates S.7, S.8

- 1880 Rhynchonellen Starhembergica ZUGMAYER, p.38, pl.4, figs. 19-21
 ?1889 Rhynchonella laevicosta nov.sp. STUR m.s., GEYER, p.66, pl.7, figs. 20-21
 1890 Rhynchonella Starhembergica ZUGM.; BITTNER, p.280
 ?1893 Rhynchonella laevicosta STUR. m.s.; BÖSE, p.644, pl.15, fig.1

Lectotype:

The originals of ZUGMAYER pl.4, figs.19 and 21 are preserved in the Pal. Inst. Univ. Vienna, and are refigured here pl.2, figs.3 and 4. That of fig.19 is here selected as lectotype.

Dimensions of Lectotype:

Length 12.0mm., breadth 13.2mm., thickness 7.3mm.

Type Locality:

All ZUGMAYER's material came from Brand by Waldegg in the Piesting Tal, Lower Austria. This locality is almost certainly that indicated on the Hohe Wandgebietes map, Geol. Bundes. Vienna, at 47°51'50"N. 33°43'45"E., where specimens are still easily obtainable.

Range and Distribution:

Norian of S.Slovakia (Drnava).

Rhaetian of Northern Alps (Vienna area).

Possibly also present in the Liassic of Hierlatz -?Pliensbachian, as 'R'.laevicosta'.

Diagnosis:

Beak tiny. Anterior commissure broadly plicate; no fold or sulcus. Normally 14-18 shallow ribs. Otherwise as genus.

Description:

Osmarella starhembergica is a medium sized rhynchonellid, transversely oval to subcircular in outline and equibiconvex in profile. The ribs, commonly numbering between 14 and 18 are low, rounded, faint posteriorly and may be absent on the vertical ligule of thick, anteriorly flattened individuals. One exceptional specimen collected has 24 ribs. The beak is tiny and no beak ridges are distinguishable. Plane fields adjacent to the cardinal margin are conspicuous in both valves; in young depressed individuals they are divided by the acute opposition of the valves but in

gerontic specimens they simulate planareas. No fold or sulcus is ever developed for the anterior commissure is rarely more than sinuate and only becomes broadly plicate in old, anteriorly flattened individuals.

The dental lamellae are low and there is no thickening present in the delthyrial cavity. The teeth are stubby, transversely quadrate, and crenulated. In immature specimens the inner socket ridge is clearly distinguishable, but later the hinge plate becomes arched and the socket ridge is less prominent. The inner hinge plate is entire and only faintly keeled by the very low median septum (see text-plates S.7 and S.8). The crural bases are bulbous and the crura themselves are prefalciifer-like.

Remarks:

'Rh'.laevicosta was first described by GEYER (1889) but attributed by him to STUR m.s.; BÖSE (1893) followed this. GEYER, however, must be given the authorship, for although STUR may have coined the name it was GEYER who cast the description and thereby made it available. GEYER's specimen of his pl.7, fig.20, from the ?Pliensbachian of Hierlatz, has a more rectangular plication than the Rhaetian specimens, but is otherwise very similar. Pending further investigation it is regarded as a probable junior synonym of O.starhembergica.

Although ZUGMAYER (1880 p.39) wrote that the species was quite common in the 'Starhemberg Schichten' this has not been confirmed. ZUGMAYER's preserved material is wholly from the type locality where it is still rich, but the environment here appears to have been distinctive (see under Ecology) and in the immediate neighbourhood it is rare and known only from single specimens.

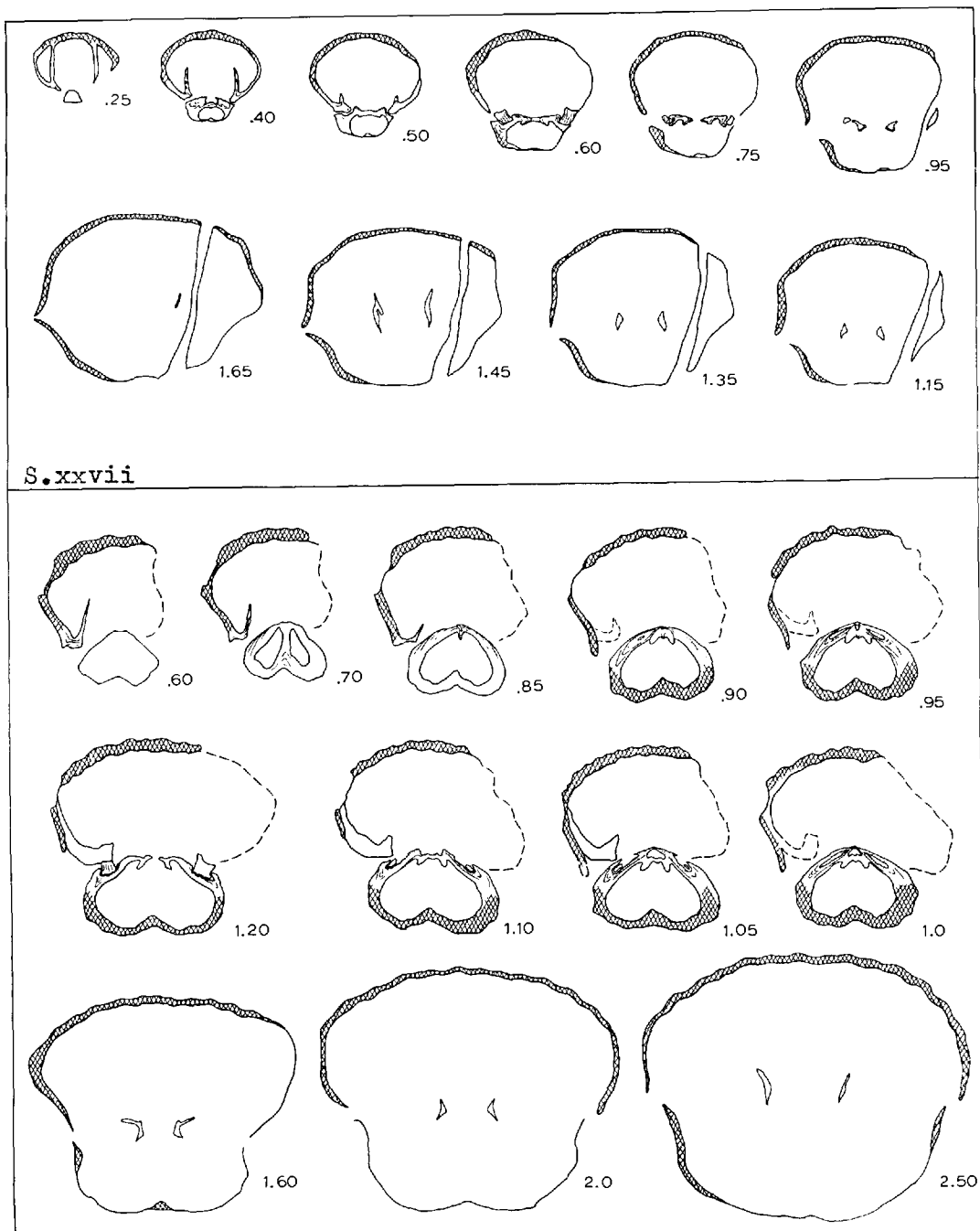
BITTNER (1890) found two examples in the late Norian of Drnava, (Slovakia) and his record has been confirmed by collecting.

Dimensions of Figured Specimens:

	Length	Breadth	Thickness
2/3	13.5	13.8	9.1
2/4	12.0	13.2	7.3
2/5	12.0	13.9	7.9
2/6	13.0(d)	14.1	11.2
2/7	13.6	16.0	8.9

Material:

Brand, Piesting Tal (type locality, see above) - 14, T.2;
'Mandlinger Wald' - Vd.Mandling by Waldegg, Piesting Tal - 1, B.M.N.H.,
BB 43204 ex. B 39204; Ob.Kaisersteffel, Piesting Tal - 1, T.3;
Drnava, Slovakia - 3, T.4.



Text-figs. S.xxvii and S.xxviii

Serial transverse sections of Osmarella starhembergica (ZUGMAYER). Rhaetian; Brand, Piesting Tal, Lower Austria; 47°51'50''N. 33°43'45''E. - locality indicated on Hohe Wandgebietes, Geol. Bundes. Vienna. Both x5; S.xxvii - Crura end 1.75mms. Total length of specimen 11.7mms. CP.Nr.31. S.xxviii - Crura end 2.7mms. Specimen too damaged to be accurately measured. CP.Nr.28 Topotypes.

TEXT-PLATES S.7 and S.8

Osmarella starhembergica (ZUGMAYER)

Text-plate S.7

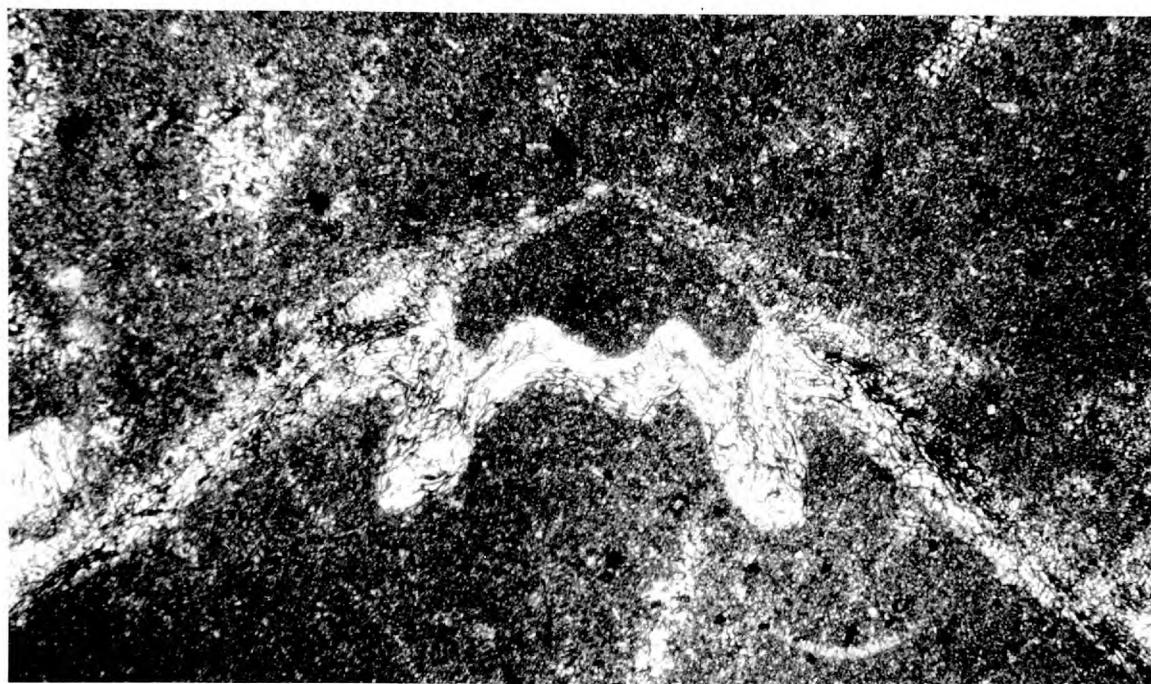
Transverse section of the brachial umbo of Osmarella
starhembergica, showing the notothyrial pit, the
large, bulbous crural bases and the posterior por -
tion of the sockets. Detail of section .95, text -
fig.S.xxviii x75

Text-plate S.8

Transverse section of the apex of the brachial umbo
of O.starhembergica, showing the form of the hinge
plate. Text-fig. as above, section 1.05 x75



Text-plate. S.7



Text-plate. S.8

Osmarella sp.nov.

Plate 3, fig.8

Range and Distribution:

This species is recognised through only one specimen from the Rhaetian of Ober Kaisersteffel, near Waldegg, in the Piesting Tal, Lower Austria.

Description:

The specimen described here is a small rhynchonellid, rounded pentagonal in outline, and dorsi-biconvex in lateral profile. 13 barely discernible ribs are present on the anterior part of the valves which are posteriorly smooth. The shallow brachial valve has a relatively high, broad, subtrapezoidal ligule as a result of the plication of the anterior commissure, which involves seven of the brachial ribs. No true fold or sulcus is developed, but a slightly depressed median field can be seen in the ventral valve. The beak is not preserved but was obviously minute and the remains of a tiny area delimited by short beak ridges are still present.

Of the internal structure only dental lamellae are known.

Remarks:

The very low rounded ribs, the trapezoidal plication, and the tiny beak all indicate this species as a member of Osmarella. It has not been named in case further collecting, possibly in the Norian, reveals a richer and more suitable type locality from which a new species can be more accurately and fully described.

Dimensions of Figured Specimen:

	length	breadth	thickness
3/8	10.8	11.8	6.9

Family Dimerellidae BUCKMAN, 1918

Remarks:

The Dimerellidae was established by BUCKMAN (1918 p.72) and its contents were discussed at length by AGER (1959) when he erected the two subfamilies Rhynchonellinae and Norellinae, and recognised the Dimerellinae. Subsequently (1965) AGER created the Halorellinae and Peregrinellinae. All these groupings are accepted here but several of the genera in the Rhynchonellinae are transferred elsewhere. Additionally it is thought that Norella may have some affinity with a subfamily founded on Piarorhynchia where it is discussed. It certainly appears to be less closely allied to Dimerella than the type genera of the remaining subfamilies which form a close knit group. Even as early as 1890 BITTNER (p.191) suggested that Rhynchonellina and Halorella were genetically connected.

It is suggested below in a detailed consideration of the genera here accepted in the Rhynchonellinae, that a further subfamily may be useful for the distinction of Sulcirostra and its relations.

Subfamily Rhynchonellinae AGER, 1959Remarks:

The genera listed below are here recognised as belonging to the Rhynchonellinae. Each is discussed in turn together with the other genera placed in the subfamily by AGER (1965).

Rhynchonellina GEMMELLARO, 1876

Carapezzia TOMLIN, 1930

Sulcirostra COOPER and MUIR-WOOD, 1951 (for the present).

Rhynchonellina was first described by GEMMELLARO (?1876 p.29) from the Liassic of Sicily (not from the Tithonian as he thought and FISCHER - 1887 - repeated, see also BITTNER 1894 p.558). Although the type species, R.suessi, is a smooth form, he included within Rhynchonellina a strongly ribbed species, 'R'.seguenzae' (see GEMMELLARO's pl.5, here text-plate 12). BÖSE (1894) noted this and divided the genus into two

main groups: Gruppe A - Laeves, and Gruppe B Costatae. Subsequently de GREGORIO (1930) gave nomenclatural recognition to the costate species as the subgenus Rhynchonellopsis, a junior homonym later changed to Sulcirostra by MUIR-WOOD and COOPER (1951).

The internal structure of Rhynchonellina is not known in detail. GEMMELLARO (1876) in his original description of the type species illustrated three preparations of the interior. The most informative of these is a longitudinal section (pl.5, fig.2; here on text-plate 12) which shows the crus with a short ventrally directed crural process. EICHENBAUM (1883 p.716) also noted processes but BÖSE (1894 p.59) disputed this observation and from EICHENBAUM's own specimen drew a figure with simple crura. However, he noted that it was a young individual and possibly the process was too small to be observed. Crural processes are also found in R.bilobata, (GEMMELLARO pl.5, fig.4; here on text-plate 12 and BÖSE 1894 p.60, fig.4) and in R.neumayeri, (CARAPEZZA and SCHOPEN pl.2, fig.12; here on text-plate 11). All three of these species are externally smooth. In his full generic diagnosis of Rhynchonellina, BÖSE (1894 p.53) wrote only that in some species crural processes are present but he did not show them in his reconstructions (figs.1a,b,c) which formed the basis of later figures (e.g. AGER 1959, and 1965). Nevertheless, from the information available Rhynchonellina may be regarded as characterised by short, ventrally directed crural processes. Poor preservation is possibly responsible for their apparent absence in some species.

The median septum, the presence or absence of which has also been the subject of some dispute (see BÖSE 1894 p.53 and BITTNER 1894 p.559) and p.568-9) is merely a ridge between more or less deep muscle scars and of little significance. Weak dental lamellae may be present in some species. GEMMELLARO's figure of the delthyrium of R.suessi showing a round foramen and deltoidal plates is inaccurate, and the true open delthyrium is shown by BÖSE (1894 p.59, fig.3) on a well preserved specimen.

Carapezzia is a very close ally of Rhynchonellina. It is also externally smooth and has apparently identical crural processes.

The relationship is discussed in more detail under Carapezzia below.

Sulcirostra was also included in the Rhynchonellinae by AGER (1965) and shares with Rhynchonellina a similar outline, delthyrial character, tendency to opposite sulcation, and very long crura but it is easily distinguished by the radial ribbing of its species. Internally two dorsal septa are present and sections figured and discussed here (all kindly provided by Dr.D.V.AGER) show that a great deal of variation exists in their positioning and development.

The equation of Rhynchonellina juvavica BITTNER from the Ramseider Scharte of the Steinernen Meeres (Austria with Sulcirostra seguenzae GEMMELLARO - the type species - made by BOSE (1894 p.62) and followed by AGER (1959 text-fig.3) was strongly denounced by BITTNER (1894 p.549-51). S.seguenzae was described from Sicily and in view of BITTNER's remarks it is uncertain whether the internal structure shown by AGER is representative of this species or not. Identical subparallel dorsal septa occur in silicified material from south east Switzerland (presented to Dr.AGER by Dr.BERNOULLI) and both these and the Austrian specimens are referable to Sulcirostra on external grounds. The structure they show can be considered part of the Sulcirostra complex, and AGER's figure is reproduced here (text-fig.S.xxix).

Dorsal septa are also seen in 'S'alpina' (text-fig.S.xxx) also from the Liassic of Switzerland. In this case they are differently placed and form the walls of very deep sockets. A new genus will be useful to contain this and similar species.

Anarhynchia AGER (in press, fig.7; here text-fig.SxxxI) from the ?Callovia of California is most probably a late member of the Sulcirostra complex as AGER suggests. Its two septa are medial as in 'S'alpina' but they serve only as an insertion point for the crura, and have no connection with the sockets.

In 'S'.paronai' from the Liassic of Oregon (presented by Dr.A.HALLAM and sections kindly made available by Dr.D.V.AGER) the two septa have become obsolete but two slight though obvious ridges remain (text-fig. S.xxxiii sections 2.5 and 2.7). A similar loss has occurred in 'S'.n.sp.' a coarsely ribbed external homeomorph of Anarhynchia also from the

Liassic of Oregon (text-fig.S.xxxii) but unfortunately the apical portion of the brachial valve of the ground specimen had been eroded and no traces of ridges can be seen. However, the hinge plates are identical in form to those of 'S'. paronai and the two species are certainly close relatives.

Thus amongst the four postulated Liassic relatives of Sulcirostra considerable functional variation is found in the homologous dorsal septa: in ?S.seguenzae they strengthen the sockets and hinge plate and in 'S'alpina they form the sockets, whereas in 'S'paronai and 'S'.nov.sp. the septa have become obsolete (or are incipient) leaving their traces as two low ridges. In Anarhynchia from the ?Callovian the septa only anchor the crura and are different in function yet again.

To few species are known to detail the course of reduction or development of the dorsal septa in Sulcirostra but it may well be similar to that found by WILLIAMS (1951) and AMSDEN (1966). Both these authors observed a progressive reduction in the 'outer plates' (= inner hinge plates herein) of early Silurian stricklandiids, but AMSDEN noted that 'care must be exercised in using this shell structure in taxonomy and correlation because the outer plates show considerable intraspecific variation'. A similar caution will be needed in the case of Sulcirostra and its allies. However, new genera in addition to Anarhynchia and a subfamily, perhaps best founded on Sulcirostra, may be found useful.

It is noteworthy that in no nominal Sulcirostra species have crural processes been discovered and this feature therefore remains diagnostic of Rhynchonellina.

Reasonable speculation on the relationship between Sulcirostra and Rhynchonellina is still hazardous, for although their similarity makes it likely that one is the ancestor of the other it is difficult to say which. Sulcirostra is at present known from lower in the late Triassic than Rhynchonellina but first records have only limited validity in view of the incompleteness of collecting in the Triassic. The microstructural differentiation of the crural bases of the North American specimen of Sulcirostra probably indicate that this genus and its closest allies are the more advanced and are descended from the Rhynchonellina group.

Apart from Sulcirostra three other Mesozoic rhynchonellid genera are known to have twin dorsal septa: Septocrurella, Caucasella and Crurirhynchia. The first two have their crura supported by crural plates (septifer crura) and Caucasella is probably part of a Bathonian - Callovian lineage directly ancestral to Septocrurella from the Oxfordian, although the genera themselves are somewhat dissimilar externally. In Crurirhynchia from the late Triassic of the Caucasus, the crura arise from oblique septa partly fused with the sockets. However, these genera are totally different from Sulcirostra externally and they do not fit in the pattern of internal variation now known for Sulcirostra. Their septa in fact appear to be analogous rather than homologous with those of Sulcirostra and they are therefore rejected as members of the Rhynchonellinae.

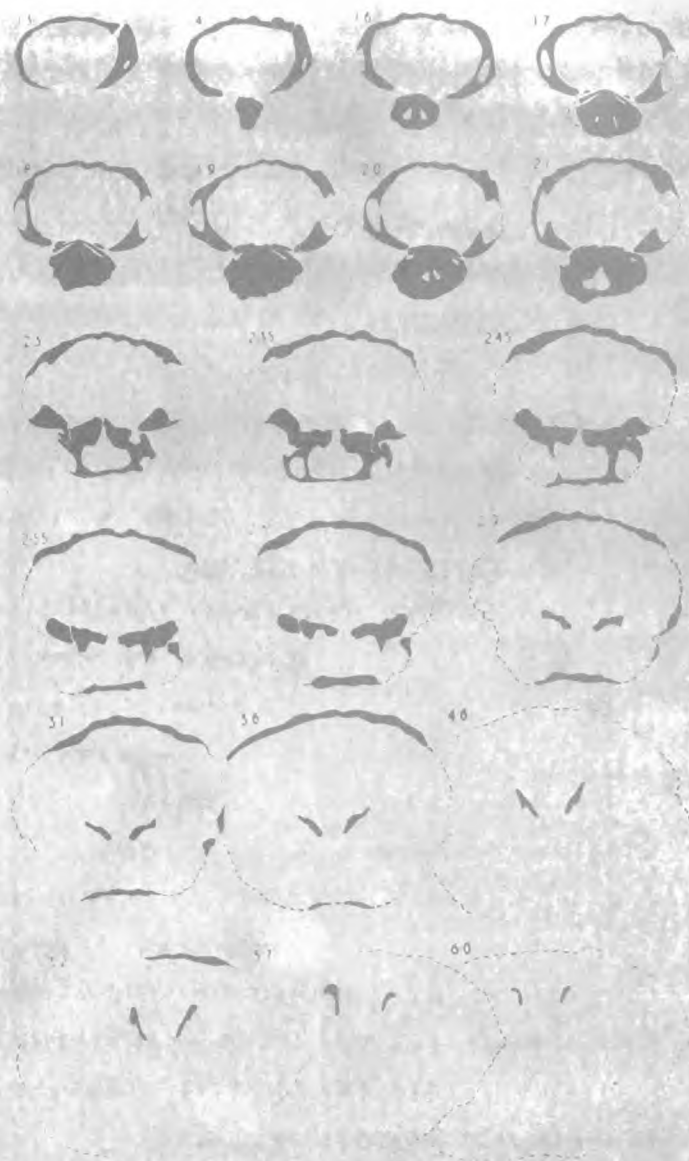
Omolonella has also been placed in the Rhynchonellinae but the 'septata' which might associate it with Sulcirostra are simply very long socket plates and the genus is placed with Cuneirhynchia and discussed above under a possible new subfamily based on Piarorhynchia.

Holcorhynchia was placed in the Rhynchonellinae because of its slight dorsal sulcation. It is an obscure genus founded by BUCKMAN (1918) on a lower Toarcian species which has not received modern investigation. As interpreted by AGER (1959a) it is ancestral to Monticlarella and was included in the Monticlarellinae CHILDS, by CHILDS (1966). According to DAGIS's (1965) view of the genus it appears to be related to Piarorhynchia and is discussed under that genus herein.

Gnathorhynchia is only known from very few specimens of its type species, G.liostraca of which G.securiformis is probably a senior synonym. The remainder of the species which BUCKMAN (1918) assigned to the genus were removed to Caucasella by MOISSEIEV (1934). Externally the type bears little resemblance to Rhynchonellina and needs to be reinvestigated.

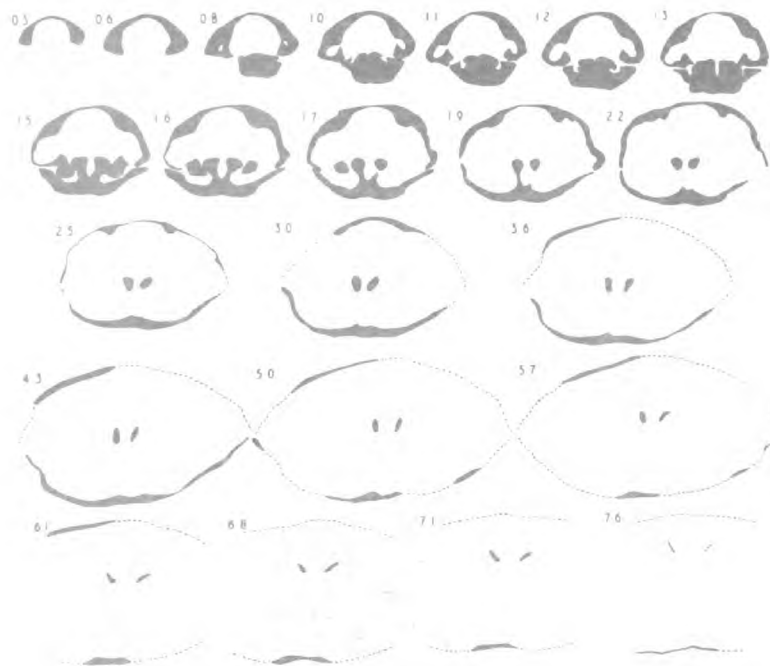
Capillirostra was proposed by COOPER and MUIR-WOOD (1951) as a nom.nov. for Rhynchonellopsis BÖSE, a provisional subgenus of Rhynchonellina founded to include ?Rhynchonellina finkelsteini which BÖSE suspected might have short crura and therefore require separation from Rhynchonellina. Together with this Upper Jurassic species he

associated 'Rhynchonella' loricata from the Upper Triassic, a seemingly disparate union which was received with astonishment by BITTNER (1894 p.570) who had remarked previously (1890 p.168) that 'R'.loricata probably belonged to Halorella. Certainly the presence of C.finkelsteini in the Upper Jurassic makes it unlikely that it can be associated with the predominantly Lower Jurassic Rhynchonellina. In fact it may well be connected with Monticlairella, and BÖSE's remark that QUENSTEDT had provisionally assigned specimens to M.striocincta supports this.



Text-fig. S.xxvix

Sulcirostra seguenzae (GEMMELLARO). Liassic; Ramseider Scharte, Steinernes Meer, nr. Salzburg, Austria. ex. AGER 1959, text-fig. 3. x3



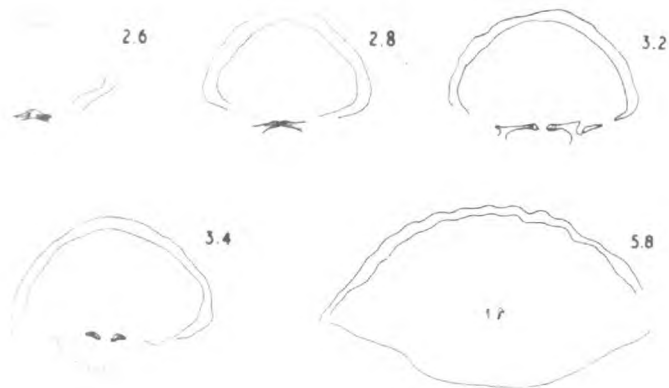
Text-fig. S.xxx

'Sulcirostra' alpina (PARONA). Sinemurian,
Arzo, Switzerland. Specimen presented by Prof.
R.TRUMPY. Sections provided by Dr.D.V.AGER.
D.V.A. colln. A.26. x2.5



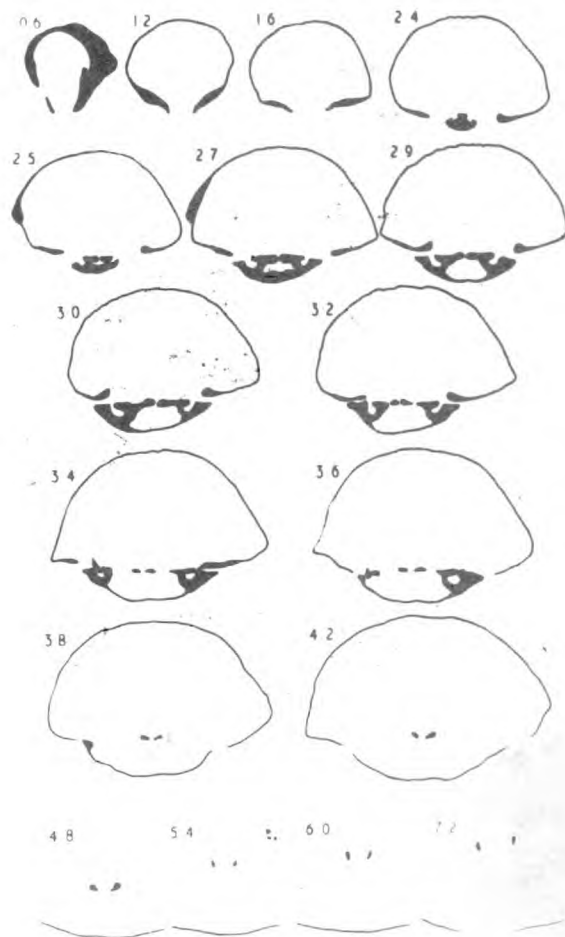
Text-fig. S.xxxi

Anarhynchia gabbi AGER. ?Callovian; Calif. ex.
AGER - 'Halorella and its relations,' in press. x1.5



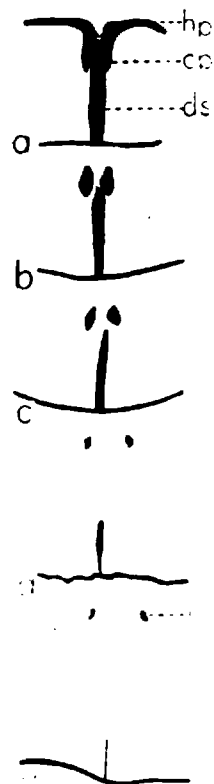
Text-fig. S.xxxii

'Sulcirostra' sp.nov. Liassic; Oregon. Specimen presented by Dr.A.HALLAM. Sections provided by Dr.D.V.AGER. x3.5



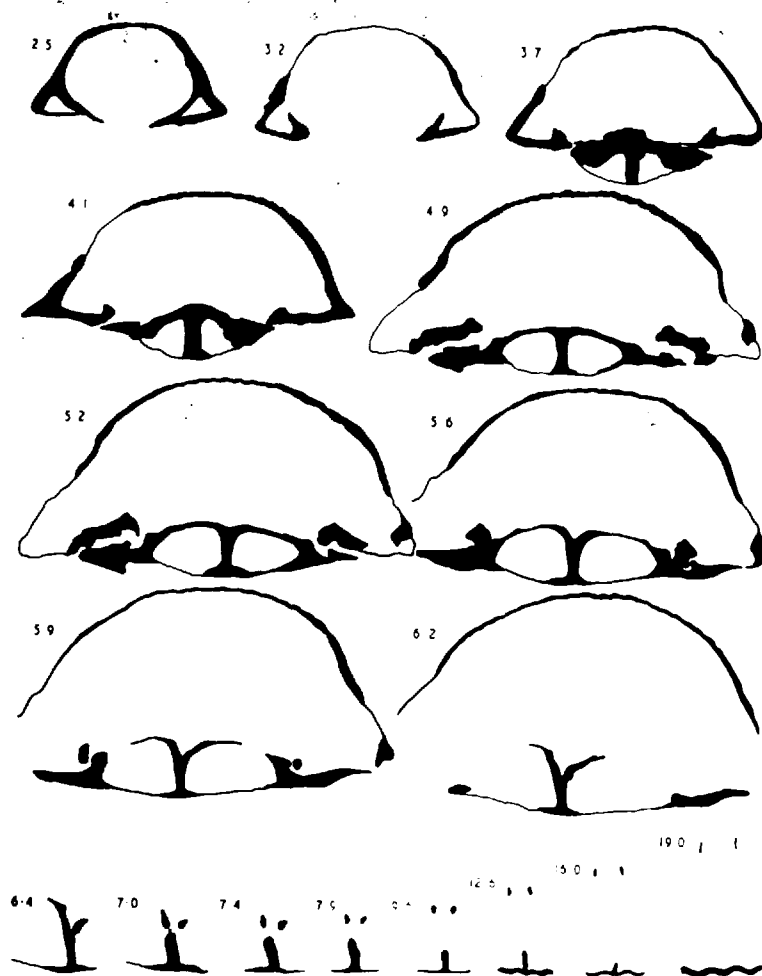
Text-fig. S.xxxiii

'Sulcirostra' paronai (BÖSE). Liassic; Oregon. Specimen presented by Dr.A.HALLAM. Sections provided by Dr.D.V.AGER. x3



Text-fig. S.xxxiv

Peregrinella multcarinata (LAMARCK). Polish specimen. Ex.BIERNAT 1957, text-fig.3. x5
hp - hinge plate; cp - crural base; ds - dorsal septum; c - crura.



Text-fig. S.xxxv

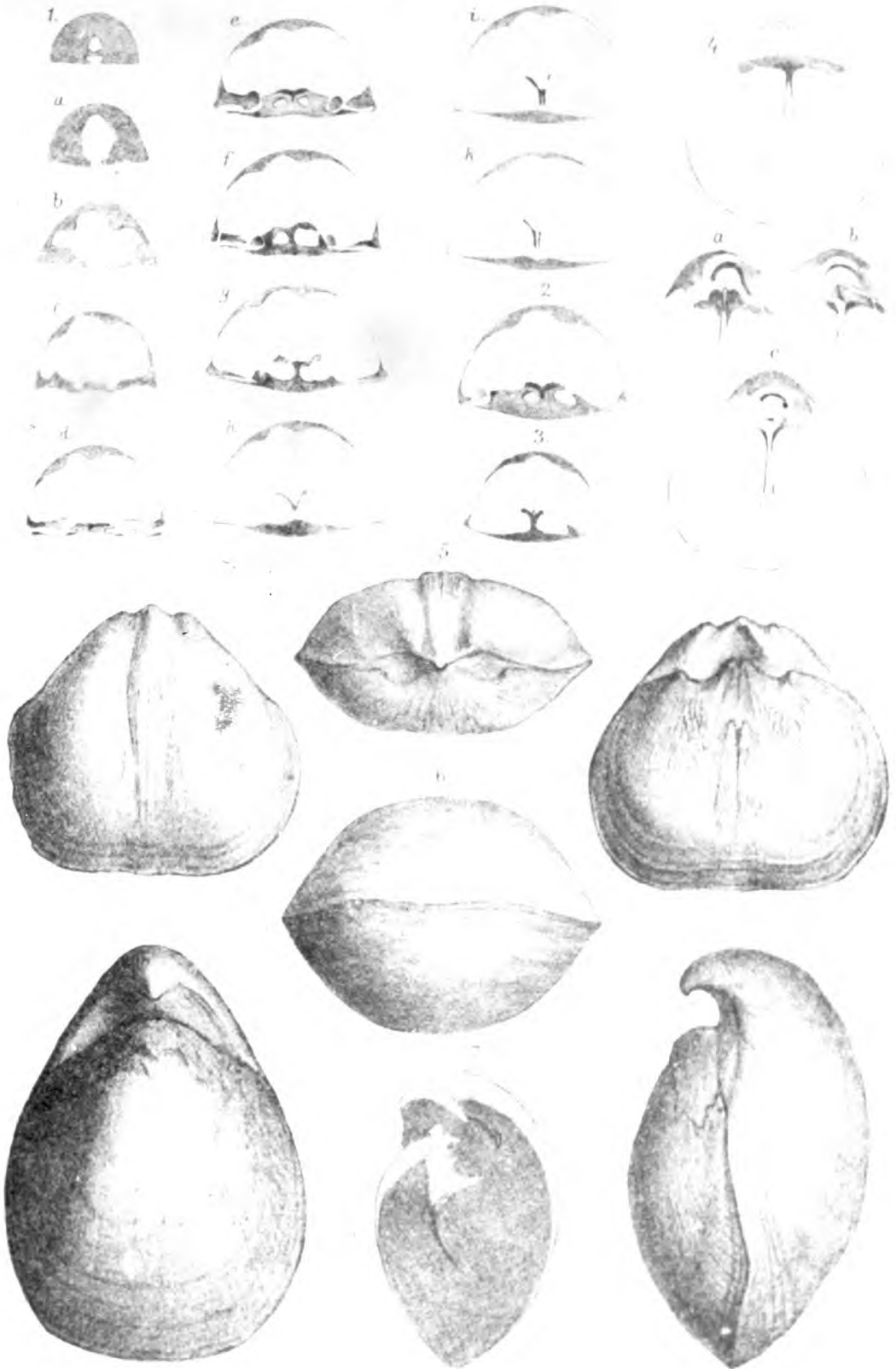
Peregrinella multcarinata (LAMARCK). Hauterivian; Chatillon-en-Diois, Drome, France. Sections provided by Dr.D.V.AGER. D.V.A. colln. Cr.293. x3

Text-plate A

Original plate 12 of BITTNER (1898) showing Carapezzia
geyeri. The serial sections are probably the best produced
in the nineteenth century.

A. Bittner: *Rhyzonellina Geyeri* n. sp.

Taf. XII. 113



A. Sweboda (Nat. ger.)

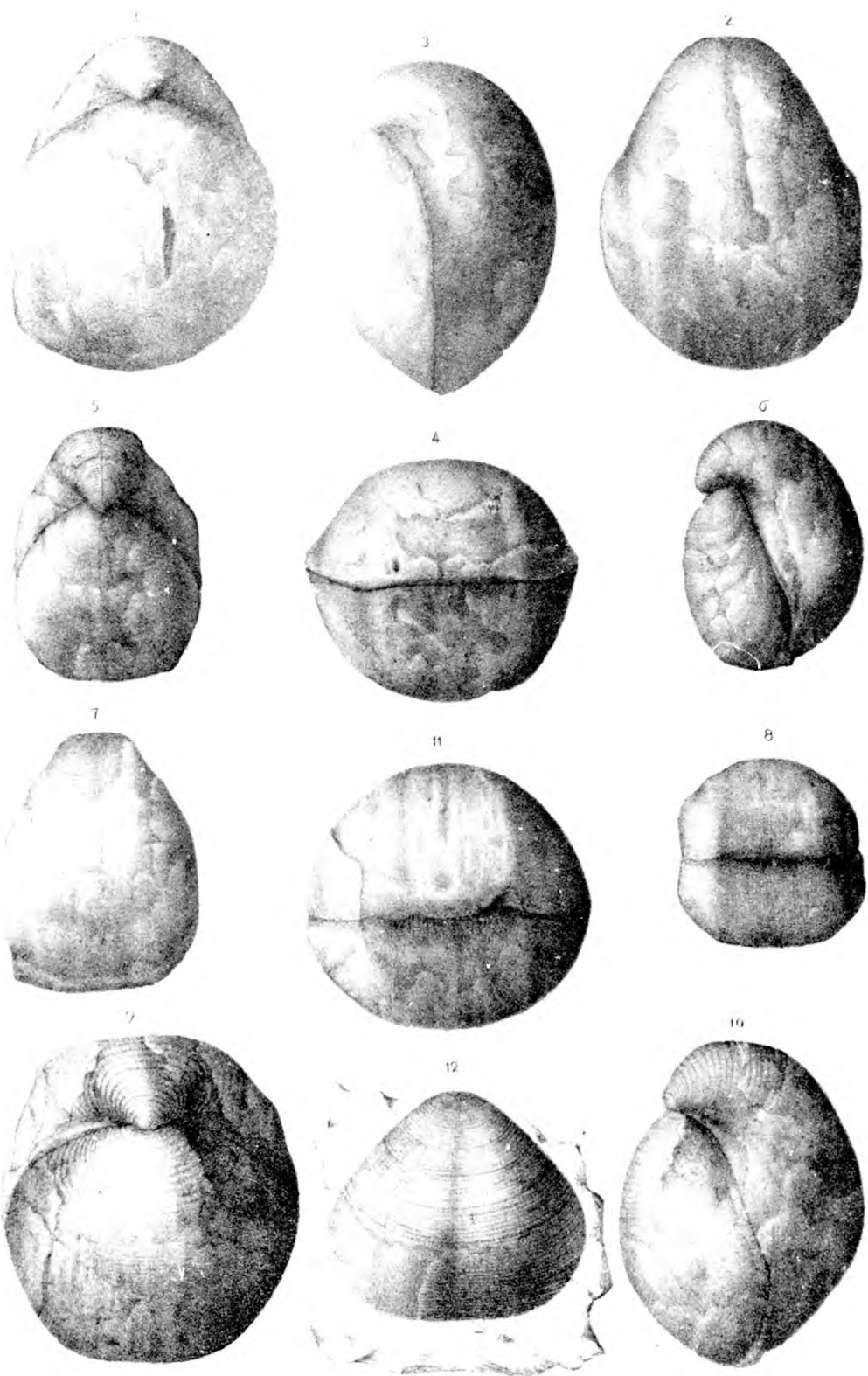
Jahrbuch der k. k. Geologischen Reichsanstalt Band XLV 1897

Verlag der k. k. Hof- und Landesdruckerei Wien

Text-plate B

Original plate 1 of CARAPEZZA and SCHOPEN (1899) showing
Carapezzia globosa - the type species of the genus.

TAV. I

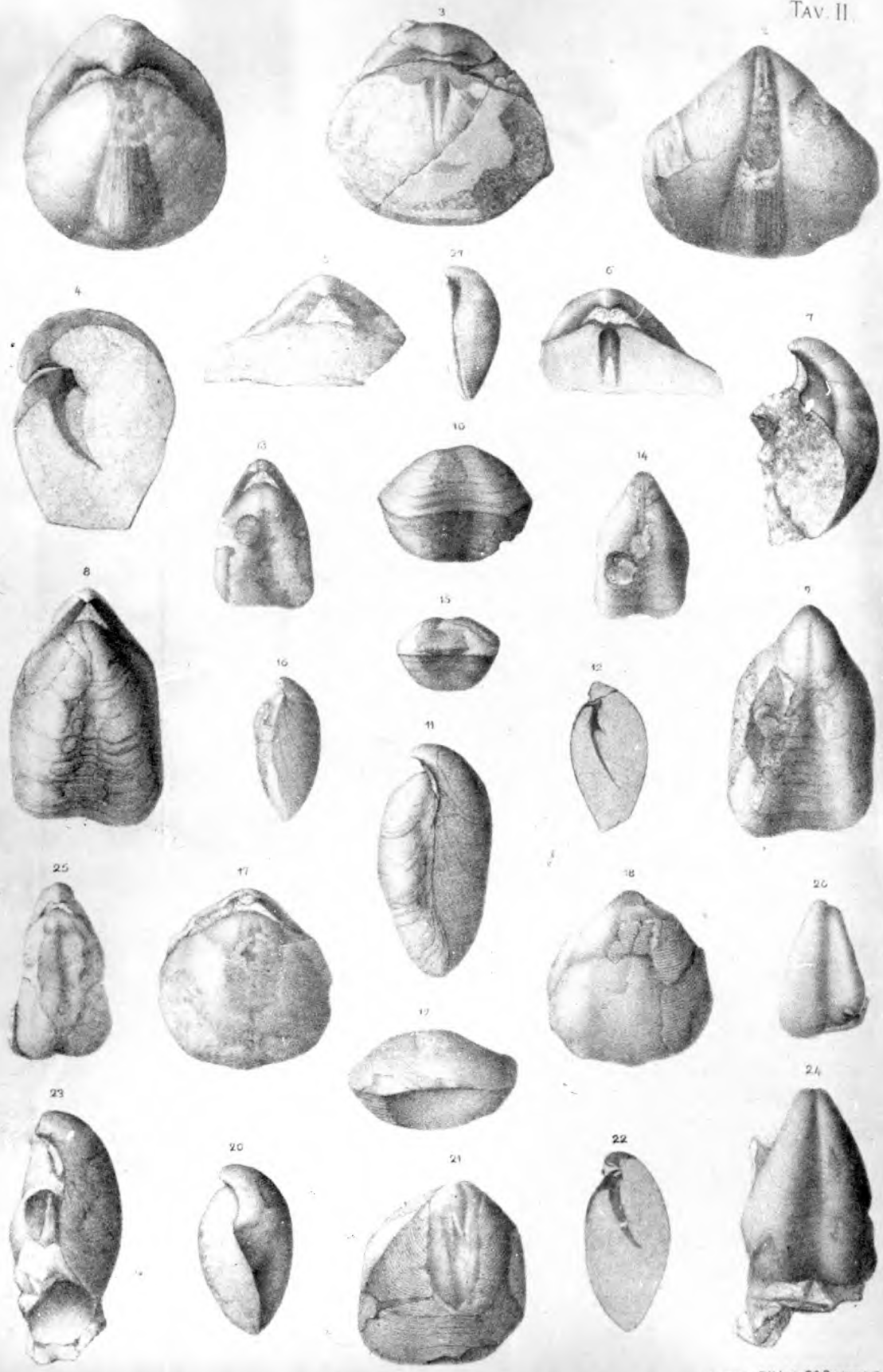


W. J. A. D. S.

W. J. A. D. S. & C. P. P. P. P.

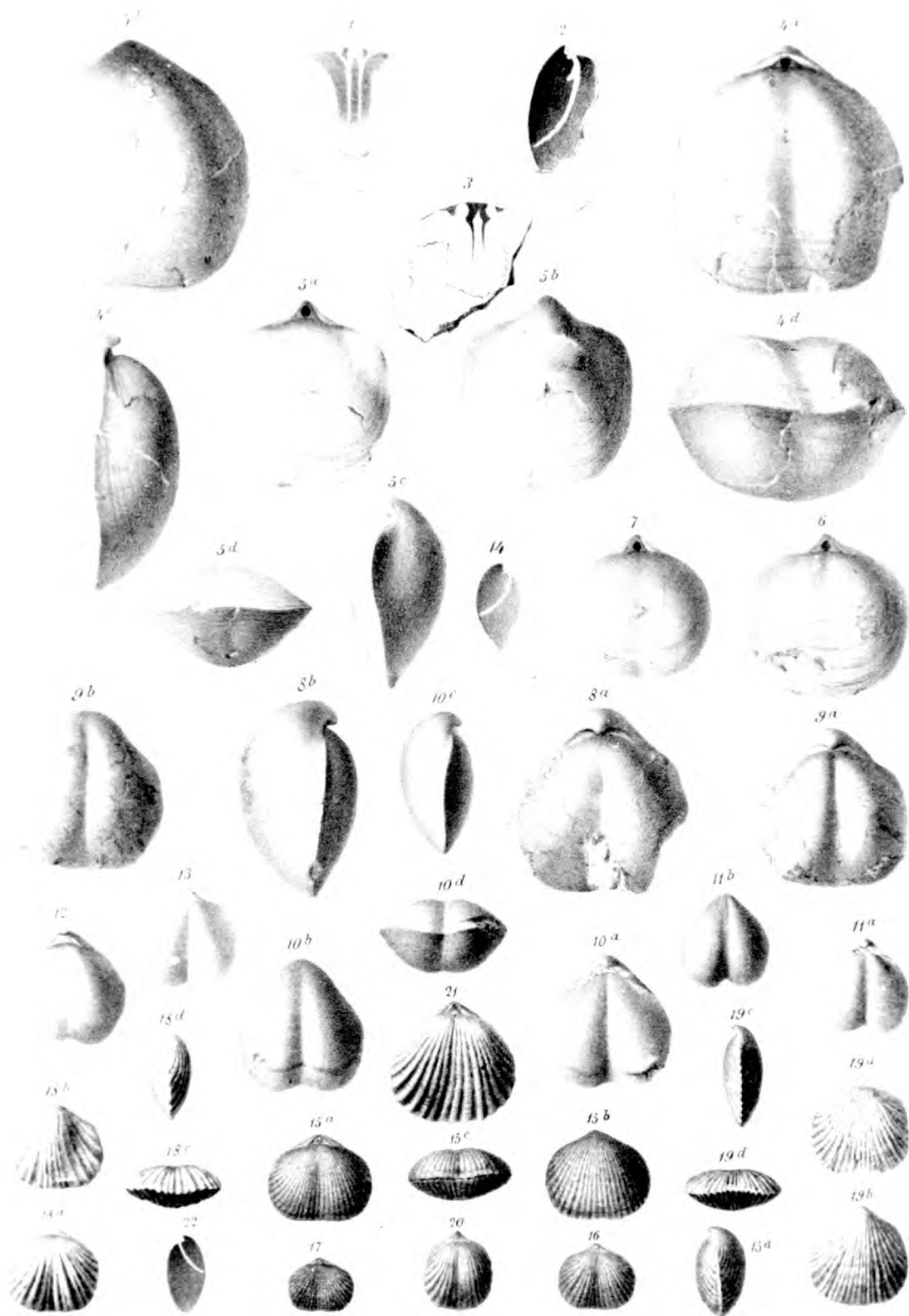
Text-plate C

Original plate 2 of CARAPEZZA and SCHOPEN (1899) showing
Carapezzia globosa (figs.1-7), Rhynchonellina neumayeri
(figs.8-16), Rhynchonellina filostriata (figs.17-22); and
Rhynchonellina adunca (figs.23-27).



Text-plate D

Original plate of GEMELLARO (?1876) showing
Rhynchonellina suessi (figs.1-7) - the type species of the
genus; Rhynchonellina bilobata (figs.8-14); and Sulcirostra
seguenzae (figs.15-22) - the type species of the genus.



Genus Carapezzia TOMLIN, 1930

1899 Rhynchonellina (Geyeria), CARAPEZZA and SCHOPEN, p.248

1930 Carapezzia TOMLIN, p.24

1965 Carapezzia TOMLIN; AGER, p.603

Type species:

Rhynchonellina (Geyeria) globosa CARAPEZZA and SCHOPEN, 1899;
SD. AGER 1965 p.603

Range and Distribution:

Rhaetian of the Gailtaler Alps.

Liassic of Sicily.

Doubtfully also in the Liassic of the Gailtaler Alps (see C.geyeri below).

Diagnosis:

Large, smooth, biconvex rhynchonellids; outline ovate. Rectimarginate or slightly plano-plicate. Beak massive, may be strongly incurved. Dental lamellae absent. Crura long, blade like, fused apically to divide valve; short crural processes on ventral side of crura.

Included species:

Only the type species and C.geyeri, described below, have been recognised as members of this genus.

Remarks:

CARAPEZZA and SCHOPEN (1899 p.248) proposed Geyeria as a subgenus of Rhynchonellina, and their name was changed as a junior homonym, to Carapezzia by TOMLIN (1930 p.248). It was regarded as a full genus within the Rhynchonellinae by AGER in the brachiopod volume of the Geol.Soc.Amer. treatise (1965).

CARAPEZZA and SCHOPEN founded their subgenus on Rhynchonellina (Geyeria) globosa and remarked at length on its close internal and external resemblance to 'Rhynchonellina' geyeri and in fact chose their original subgeneric name as a tautonym of that species. Their two plates of globosa and one of BITTNER's of geyeri (1898) are included here for comparison (text-plates 9-11). Despite the absence of external striations on geyeri (those on BITTNER's pl.12, fig.7 are caused by the fibrosity of the shell), there can be no doubt that they are congeneric, and the detailed internal structure known for BITTNER's species may be considered

as representative of Carapezzia.

Carapezzia was originally distinguished from Rhynchonellina on internal character (CARAPEZZA and SCHOPEN 1899 p.215) but no details were given. Both have identically positioned crural processes and the supposed differences are caused by the massiveness of the umbones in Carapezzia, possibly coupled with unsophisticated means of observation. Distinguished only by its massive beak, Carapezzia is retained here as a full genus pending further investigation of Rhynchonellina. The most satisfactory position for it may well be its original one as a subgenus.

The types of both genera - C.globosa and R.suessi - are preserved in the Ist. e Mus.Geol. Univ.Palermo (Dr.G.BUCCHERI, personal communication 1965), but it has not yet been possible to examine them or to obtain specimens for grinding. The character of Rhynchonellina so far as it may be deduced, is detailed in a discussion of the Rhynchonellinae.

At first sight the brachial structure of C.geyeri appears very close to Peregrinella, but in that genus the crural bases lie characteristically on the inner edge of the flat hinge plates above a prominent median septum (text-figs. S.xxxiv and S.xxxv). In Carapezzia the blade shaped crura themselves fuse apically to divide the valve and in structural detail are quite different to Peregrinella.

Since Dzieduszyckia (?=Eoperegrinella AGER 1965a p.159, and in press) from the Devonian has been found to have an internal structure almost identical with the Cretaceous P.multicarinata (AGER in press), the Peregrinellinae can be regarded as a long ranging subfamily of conservative internal character and quite distinct from the Rhynchonellinae exemplified by Carapezzia.

Carapezzia geyeri BITTNER, 1898

Plate 10, figs.1-4; text-figs. S.xxxvi, S.xxxvii

1898 Rhynchonellina Geyeri BITTN.; GEYER, p.355

1898 Rhynchonellina Geyeri BITTNER, p.387, pl. 11, figs.1-9, pl.12, figs. 1-7

1899 Rhynchonellina Geyeri BITTNER; CARAPEZZA and SCHOPEN, p.249

1963 Rhynchonellina geyeri BITTN.; SCHLAGER, p.69, 71

Lectotype:

All of BITTNER's originals except those of pl.12, figs. 4,7 are preserved in the Geol.Bundes.Vienna. That of pl.12, fig.6 is here chosen as lectotype and refigured on pl.10, fig.1

Dimensions of Lectotype:

Length 56mms., breadth 42mms., thickness 32.5mms.

Type locality:

All BITTNER's figured material came from the Stadelwiese above Oberpirkach, Drautal, in the Gailtaler Alps. The writer was able to find specimens at 1860m. and 45°46'55''N. 12°53'10''E. and these are regarded as topotypes. SCHLAGER (1963) thought the locality to be Liassic (see below).

Range and Distribution:

Rhaetian and ?Liassic of the Gailtaler Alps, (S.Austria).

C.geyeri is known only from the two closely neighbouring localities mentioned by GEYER (1898 p.355) and BITTNER (1898 p.392). GEYER gave the age of these as 'probably Rhaetic'. SCHLAGER (1963 p.69) confirmed the Pirkner Graben occurrence as Rhaetian but recorded the type locality as Liassic (p.69 - 71). Unfortunately the field contacts are obscure but the limestone in which Carapezzia is found is typical of the Rhaetian whilst wholly unlike the fissile shales forming the ammonite bearing Liassic in this area. In view of this and the complex tectonic situation the writer prefers to regard as artificial the intercalation supposed by SCHLAGER and places the type locality in the Rhaetian.

Diagnosis:

Massive beak suberect in young specimens but later strongly recurved; area well developed. Otherwise as genus.

Description:

Carapezzia geyeri is a large, equi-biconvex rhynchonellid, individuals being up to 70mm. long. Young specimens are subcircular in outline and become elongate-ovate with growth. The anterior commissure may be rectimarginate, as in the majority of younger individuals, or broadly and flatly flexed in older specimens when it is commonly accompanied by a slight median sulcation of both or either valve. The beak is very prominent and massive, becoming increasingly incurved with age but never making the well developed area difficult to distinguish as in C.globosa. The delthyrium is triangular, open and bordered by prominent tooth tracks (well seen in BITTNER's pl.1, fig.7).

The shell surface, which is rarely preserved, is smooth but for fine growth lines, and the shell itself is fibrous and thick particularly at the umbones.

The delthyrial cavity is large and a thin, partially detached lining is present; dental lamellae are absent. A marked puckering of the growth lines in the middle part of the apex of the pedicle valve is followed by a deep depression indicating the muscle fields.

A flat cardinal pad lies on the hinge plate and spills over into the unused portion of the sockets, which are almost without inner socket ridges. The valve is divided medianly by the fusion of the blade like crura, somewhat rectangular lateral cavities being formed. The crura themselves are extremely long, almost reaching the pedicle valve, and on their ventral side they bear short crural processes.

Remarks:

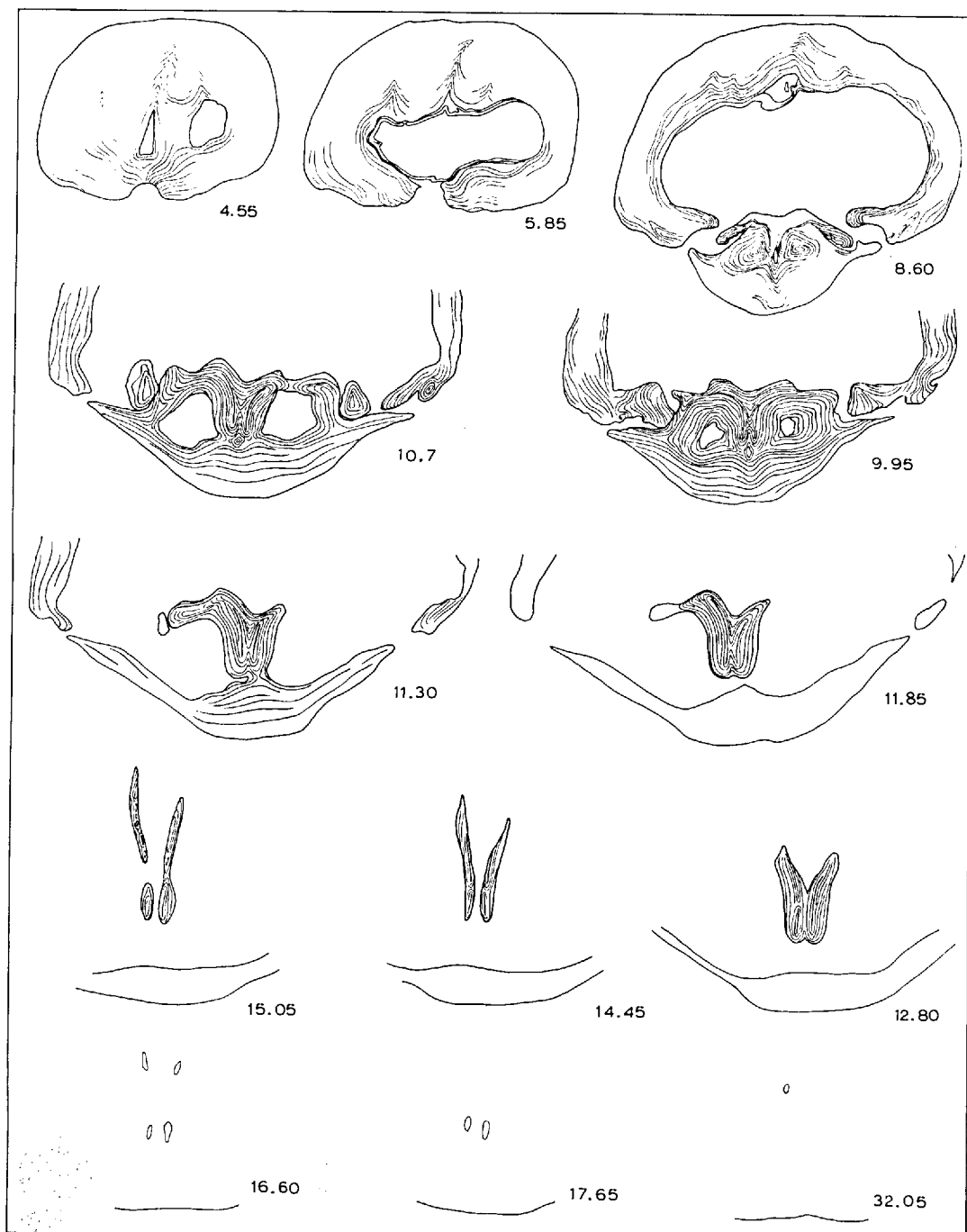
C.geyeri is remarkable in that there is neither any differentiation of the hinge plate elements nor of the shell layers seen in normal rhynchonellids. This together with the lack of deltidial plates suggests that it is one of the last members of a primitive and conservative stock. Further collecting may well reveal Palaeozoic predecessors equally comparable in their similarity as Dzieduszyckia (?=Eoperegrinella AGER, in press) and Peregrinella.

Dimensions of Figured Specimens:

	length	breadth	thickness
10/1	56.0	42.0	32.5
10/2	32.1	29.5	26.7
10/3	29.0	29.1	16.0
10/4	----	40.0	26.0

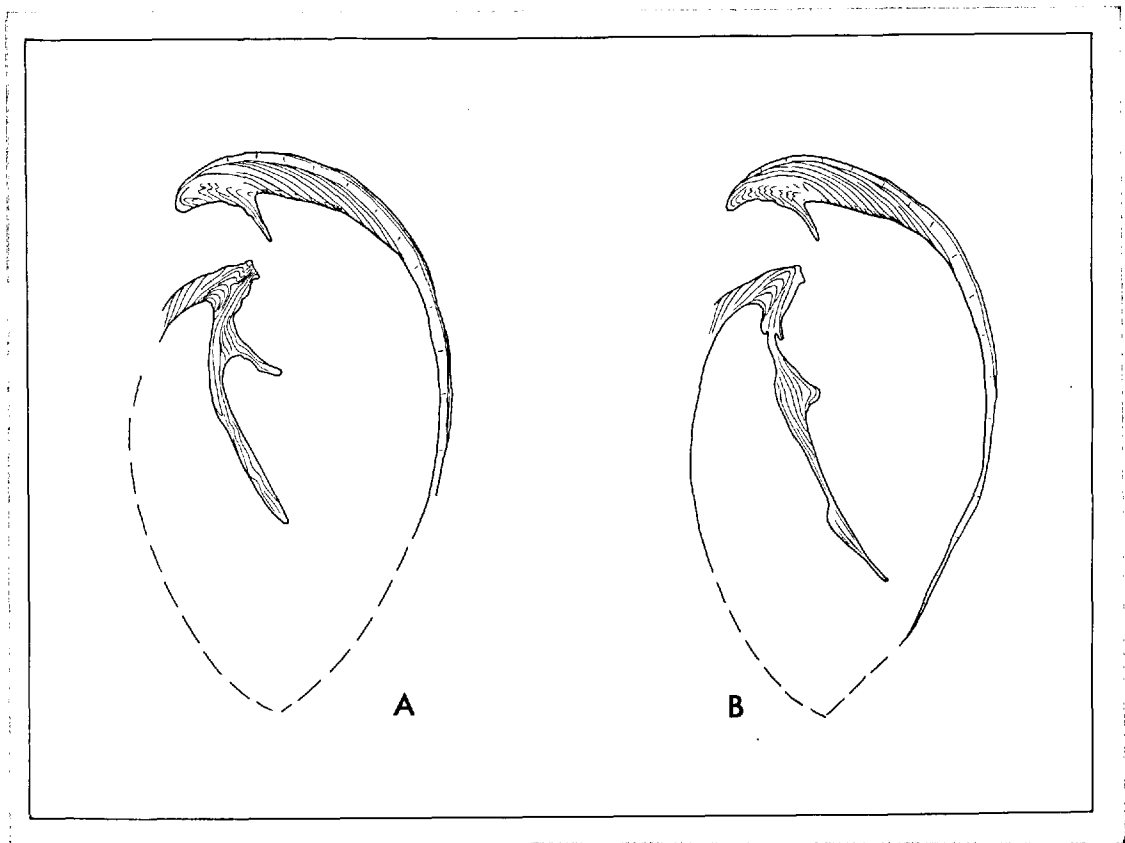
Material:

Stadelwiese, by Oberpirkach (type locality, see above) - 150, T.1
 The Pirkner Graben specimens are very poorly preserved and cannot be
 extracted from their limestone matrix.



Text-fig. S. xxxvi

Serial transverse sections of Carapezzia geyeri (BITTNER).
 Rhaetian, (Liassic of SCHLAGER 1963, p.69 - see text);
 Stadelwiese above Oberpirkach, Drautal, Gailtaler Alps;
 45°46'55''N. 12°53'10''E. 1860m - 180 Winklern. x3 Crura
 end 33.5mm. Total length of specimen 40mm. CP.Nr.6 Topotype.



Text-fig. S. xxxvii

Longitudinal sections of Carapezzia geyeri ground almost parallel to the plane of symmetry to show the full length of the crura. Topotypic specimen from the Gailtaler Alps, S. Austria, locality as text-fig. S. xxxvi. The interval between A and B is .25mms. x2 PC.Nr.6a Topotype.

Other Rhynchonellida reported from the Rhaetian.

Five further rhynchonellid species have been described from supposedly Rhaetian beds. They occur in small, isolated outcrops far from the main alpine chain and the writer has been unable to collect material for investigation. Therefore only the following brief notes are given for each species.

'Rhynchonella' colombi RENEVIER, 1864.

1864 Rhynchonella Colombi RENEVIER, p.46, pl.3, figs. 6,7.

1885 Rhynchonella Colombi RENEVIER; HAAS, p.22, pl.1, figs. 17-19.

1926 Rhynchonella Cartieri OPPEL; PETERHANS, p.366, pl.2, figs. 1-4

RENEVIER (1864) described this species from loose, supposedly Rhaetian material, found at Villeneuve close to the south east shore of L.Léman. (L.Geneva). HAAS (1885) revised this material regarding it as doubtfully Rhaetian and appending a personal communication from RENEVIER who admitted that he also was uncertain. PETERHANS (1926), revising the stratigraphy of many of HAAS's localities, stated that the Rhaetian, Hettangian and Sinemurian are missing at Villeneuve and that 'R.colombi' must be at least Lotharingian (Upper Sinemurian) in age. He regarded it as a junior subjective synonym of 'R.cartieri' OPPEL.

'Rhynchonella' nov.sp. HAAS, 1885

1885 Rhynchonella nov.sp. HAAS, p.21, pl.2, fig.1.

One poorly preserved specimen was figured and described by HAAS (1885) but not named. It has a sharp median fold and is closely similar to Homeorhynchia, known in the continental Lower Liassic (see AGER 1956, p.28). The specimen came from a quarry near Meillerie in the Haute Savoie, on the southern shore of L.Léman. HAAS described Rhaetina gregaria and Zugmayerella uncinata from the same quarry but did not say whether the rhynchonellid was an immediate associate of this typical Rhaetian assemblage. PETERHANS (1926) did not consider Meillerie and its stratigraphy requires revision.

HAAS's original is apparently no longer present in the Musée Geologique Lausanne, (Mme Dr.A.SCHNORF personal communication 1966; the writer is also indebted to Dr.SCHNORF for the reference to PETERHANS).

'Rhynchonella' pillae CAPELLINI, 1862

- 1851 Rhynchonella sp., SAVI and MENECHINI, p.92
 1862 Rhynchonella Pillae MGH.; CAPELLINI, p.55
 1866 Rhynchonella Pillae MGH.; CAPELLINI, p.413, pl.6, figs. 15,16.

The authorship is here given to CAPELLINI, 1862 (as it is in DIENER, 1920) since he was the first author to describe and name the species, although the name may well be from a manuscript by MENECHINI.

The specimen figured by CAPELLINI is small, depressed, and multicostate with a rounded sinus. It was apparently crushed and is too poorly preserved to be compared with other species. The only known locality lies in the Gulf of Spezia, N.W.Italy. CAPELLINI's 1862 specimen was said to be in the 'Museo di Pisa', but most of his collection and probably his 1866 material is in the Museo Capellini, Istituto di Geologia, Università di Bologna, (Dr.M.GAETANI - Milan - verbal communication 1965).

'Rhynchonella' portuenerensis CAPELLINI, 1862

- 1851 Rhynchonella sp., SAVI and MENECHINI, p.91
 1862 Rhynchonella portuenerensis CAPELLINI, p.55
 1866 Rhynchonella portuenerensis CAP. p.414, pl.6, figs.17,18
 1908 Rhynchonella portuenerensis CAP.; PRINCIPI, p.199, pl.7; fig.11

CAPELLINI's material of this species also came from the Gulf of Spezia and seems to be very little different from 'R.'pillae'. PRINCIPI's specimens from near Perugia are almost certainly of a separate species.

'Rhynchonella' umbra PRINCIPI, 1908

1908 Rhynchonella umbra PRINCIPI, 1908, p.199, pl.7, fig.10

This species has only been described from its type locality near Perugia and is quite without recent investigation.

SYSTEMATIC PALAEONTOLOGY

2

SPIRIFERIDA

Order Spiriferida WAAGEN, 1883

Suborder Spiriferidina WAAGEN, 1883

Superfamily Spiriferinacea DAVIDSON, 1884

Family Spiriferinidae DAVIDSON, 1884

Remarks:

ZUGMAYER (1880) distinguished two groups within Spiriferina d'ORBIGNY: Gruppe A (Tripartitae) containing species in which the ventral median septum and the dental lamellae are separate, and Gruppe B (Dimidiatae) in which they are joined to form a spondylium-like structure. The first group he regarded as typical Spiriferina and in it placed two Rhaetian species - 'Spiriferina' emrichi and 'S'.praecursor. DAGIS (1963) investigated 'S'.emrichi and used it as the type of his genus Sinucosta, assigning it to the Spiriferininae. 'S'.praecursor is _____ species and has not been found since its original description; it may be a senior synonym of 'S'.dernoensis BITTNER from the late Norian of Drnava, and is here provisionally referred to Mentzelia.

Subfamily Spiriferininae DAVIDSON, 1884

Genus Sinucosta DAGIS, 1963

1963 Sinucosta DAGIS, p.104

1963 Guseriplia DAGIS, p.107

1965 Sinucosta DAGIS; PITRAT, p.714

Type species:

Spirifer Emrichi SUESS, 1854 p.24, pl.2, fig.7; OD.

Range and Distribution:

Norian of Slovakia (Drnava, Stratenska hornatina), the Crimea, Caucasus and Pamirs; probably N.E.Turkey (Balik maden).

Rhaetian of the Northern Alps, Slovakia (Hybe) and N.W.Rumania (Apuseni Mts.)

Included species:

The following species are included in Sinucosta:

S. frondescens BITTNER, 1890 p.74, pl.40, fig.2

S. gregaria SUESS. (For figure - BITTNER, 1890 p.145, pl.28, figs. 14-19)

S. lipoldi BITTNER, 1890 p.74, pl.28, figs.20-21 all from the Carnian.

S. meridionalis BITTNER, 1903 p.519, pl.26, fig.11,12 from the Anisian.

S. pectinata BITTNER, 1890 p.31, pl.35, fig.24,25 occurring in both the Anisian and Ladinian.

Diagnosis: (Internals after DAGIS 1963)

Medium sized spiriferinids; transversely elongate, hinge line shorter than maximum width, cardinal margins round. Brachial valve shallow, pedicle valve moderately convex; beak pointed, incurved. Area unornamented. Delthyrium open. Ribbing rounded, multitudinous; fold and sulcus ribbed as lateral slopes. Median septum present; dental plates divergent. Low, striate cardinal process lies between hinge plates. Jugum present.

Remarks:

DAGIS based his genus Sinucosta on SUESS's species Spirifer emmerichi, and Guseriplia on G. multicostata, a Caucasian species of his making. He used finer ribbing and the presence of 'septalial' plates in Sinucosta to distinguish the two genera. However, as discussed at length below, the density and strength of the ribbing is so variable as to be a hazardous specific character and quite inapplicable at generic level. Moreover, any contrast between the sections of Sinucosta emmerichi (DAGIS 1963 fig.47) and Guseriplia multicostata (fig.48) is quite acceptable as internal variation within one species. The greater prominence of the 'septalial plates' in Sinucosta emmerichi is due to the camouflage in G. multicostata by the larger cardinal process of what appears to be an older specimen (no magnifications are given). Differing angle of section may add to the apparent discrepancies; moreover, the brachial valve of G. multicostata seems to have been sectioned separately, so aggravating this problem.

Therefore in common with PITRAT (1965 p.714) the writer regards Guseriplia as a junior subjective synonym of Sinucosta.

Sinucostra emarichi (SUESS), 1854

Plate 11, figs. 1-4

- 1853 Spirifer imbricatus SCHAFHÄUTL, p.310, pl.6, fig.5
 1854 Spirifer Emarichi SUESS, p.24, pl.2, fig.7
 1859 Spirifer Emarichi SUESS; WINKLER, p.25
 1871 Spirifer Emarichi SUESS; QUENSTEDT, p.523, pl.54, figs.68-70
 1880 Spiriferina Emarichi SUESS; ZUGMAYER, p.24, pl.4, figs.1-3
 1890 Spiriferina Emarichii SUESS; BITTNER, p.283,
 var. acerrima pl.26, figs.9,10
 ?var. subtilicostata pl.26, fig.11
 ?1891 Spiriferina cfr.Emarichii SUESS; BITTNER p.108, pl.1, fig.12
 ?1892a Spiriferina cfr.Emarichii WINKL; BITTNER p.80
 1917 Spiriferina Emarichi SUESS; GÖPFEL, p.96, pl.8, fig.2
 1958 Spiriferina emarichi SUESS; MAHEL, p.136-7,
 Spiriferina emarichi acerrima BITTNER p.137 pl.5,
 figs. 3,4
 Spiriferina emarichi subtilicostata BITTNER p.138
 1962 Spiriferina emarichi SUESS; PRIEDA, p.62
 1963 Sinucostra emarichi SUESS; DAGIS, p.104, pl.13, figs.8-11
 1963 Guseriplia multicostata DAGIS, p.107, pl.14, figs.1-9
 1963 Guseriplia bittneri DAGIS, p.109, pl.14, figs.10-12

Holotype:

The original of SUESS is no longer present in the Geol.Bundes.Vienna (Prof.R.SIEBER, verbal communication 1965), and must be presumed lost.

The plesiotype of ZUGMAYER is preserved in the Pal.Inst.Univ.Vienna and is refigured here on plate 11, fig.1

Dimensions of Holotype:

From SUESS's figure - length 23.2mm., breadth 26.3mm., thickness 25.7mm.

Type locality:

Given by SUESS as 'Kitzberg'. This lies near the village of Neusiedl in the Piesting Tal, Lower Austria.

Range and Distribution:

Norian of Slovakia (Drnava, Stratenska hornatina) the Caucasus, Crimea and Pamirs.

Rhaetian of the Northern Alps, Slovakia (Hybe), and N.W. Rumania (Apuseni Mts.).

Diagnosis:

Ribbing very variable in intensity; fold and sulcus shallow. Jugum has median trough. Otherwise as genus.

Description:

Sinuocosta emrichi is a medium sized spiriferinid, transversely elongate, with smoothly rounded lateral and cardinal margins. The hinge line is shorter than the greatest width. The brachial valve is shallow, and the pedicle valve moderately convex in both outline and profile, with the pointed beak recurved at right angles over the anaclyne area in mature individuals. Horizontal growth lines are prominent on the area, but the fine vertical striations noted by BITTNER on SUESS's holotype have not been observed, possibly because of unsuitable preservation. The apical lateral slopes are rounded and the beak ridges variably accentuated, but in fully shelled specimens the area is clearly delimited. The delthyrium is triangular and open, with no sign of bordering ledges. The anterior commissure is only gently flexed and the sulcus, although long and distinguishable to the ventral umbo, is broad and shallow passing smoothly into the curvature of the valve.

Considerable variation is shown by the ribbing in both coarseness and concomitant intensity: up to forty fine, rounded and somewhat sinuate ribs may be present but individuals with as few as twenty markedly more accentuated corrugations are, in the writer's opinion, within the range of the species.

Well preserved specimens bear a dense network of fine spines which have been observed up to one mm. long. On breaking they leave a pustulose surface, seen well on pl.11 fig.3.

The internal structure was not examined and the diagnosis for the genus above was prepared from the sections figured by DAGIS (1963).

Remarks:

In distinguishing the weak and strongly ribbed varieties of S. emmrichi, var. subtilicostata and var. acerrima BITTNER (1890 p.283-284) recognised that between the two extremes lay a full range of intermediates from which SUESS had chosen his holotype. He remarked at length on the parallelism of the range at Drnava and that noted by ZUGMAYER (1880 p.24-25) in specimens from Austrian localities. MAHEL (1958 p.138) found similar variation in examples from individual Slovakian localities. Therefore whilst admitting, though with a little doubt, that the almost smooth var. acerrima may be a separate species, the writer cannot accept DAGIS's (1963) further division of the species and certainly not their assignation to separate genera.

DAGIS included the finest ribbed of his specimens in Sinucostra emmrichi as the type of that genus and listed in synonymy SUESS (1854), ZUGMAYER (1880), and GOETEL (1917). The original of ZUGMAYER's figure is refigured here on pl.11, fig.1, and a specimen from GOETEL's locality alongside in fig.2. A specimen similar to SUESS's holotype and from near the type locality is shown in fig.3. These specimens undoubtedly belong to one species. It may, moreover, be argued that fig.2 is closely comparable to BITTNER's (1890) fig.10 from Drnava and that his fig.9 is only a laterally compressed form of the same species. Ten personally collected specimens convincingly demonstrate this and the separation of individuals like fig.9 as members of another species and genus - Guseriplia bittneri - is unacceptable.

The differences in rib density, size, recurvature of the beak and development of the sinus and fold which DAGIS notes between his species are, in the writer's view, explained by adult intra-specific variation and contrasting juvenile and adult form. As mentioned above the internal differences between Sinucostra and Guseriplia also appear superficial and all three nominal species of these genera are here regarded as synonyms.

Dimensions of Figured Specimens:

	length	breadth	thickness
11/1	25.0	13.0	17.7
11/2	20.8	24.8	14.3
11/3	----	31.3	----
11/4	18.8	13.0	17.7

Material:

Bleskovy pramen, Drnava, Slovakia - 10, T.53; Hybe, Slovakia - 3, T.54; Ober Kaisersteffel, Piesting Tal - 2, T.55; Vorder Mandling - 1, T.56, Kitzberg - 3, T.57.

?Family Spiriferinidae DAVIDSON, 1884

Subfamily Laballinae, DAGIS, 1962

Included genera: (after DAGIS, 1963).

Laballa MOISSEIEV; Spondylospira COOPER; Lepismatina WANG;

?Psioidea HECTOR; Zugmayerella DAGIS.

Diagnosis: (after DAGIS, 1963)

Ventral septum and dental lamellae united to form spondylium - like structure. No delthyrial cover known.

Remarks:

ZUGMAYER (1880) based the second of his divisions of Spiriferina, the Dimidiatae, on the Rhaetian species Laballa suessi, Zugmayerella koessenensis, Z. uncinata and 'S. austriaca' subsequently this group has received considerable attention culminating in the work of DAGIS (1962a and 1963).

Although ZUGMAYER felt that the internal structure of the Dimidiatae was sufficiently similar to Spiriferina to make generic separation unnecessary he noted that if they were to be differentiated then they would be best combined with the Palaeozoic genus Cyrtina. He thus followed QUENSTEDT (1870 p.523) who ground Z. uncinata and noticed the internal resemblance to Cyrtina. Subsequently ZITTEL (1880), HAAS (1885) and HALL and CLARKE (1890) placed one or all of the Rhaetian Dimitidae in Cyrtina. However BITTNER (1890 p.293) pointed out the importance of the absence of a deltidium in the Rhaetian species and reasserted their relationship to Spiriferina.

The situation remained confused until the 1962 when DAGIS published MOISSEIEV's manuscript name and diagnosis of the genus Laballa for 'S. suessi' and assigned 'S. austriaca' to Lepismatina WANG. For these genera plus Spondylospira COOPER and Psioidea HECTOR, DAGIS (1962a) created a new subfamily, the Laballinae within the Spiriferinidae. In 1963 he added the remaining Rhaetian 'Dimidiatae' species, 'S. koessenensis' as the type of a new genus Zugmayerella.

In discussing the relationship of the Laballinae, DAGIS noted the absence in its species of the deltidium, tichorhinum and jugal processes found in Cyrtina (see IVANOVA 1959 and 1960 p.279, fig.403) and the identity of this condition to that in the true spiriferinids. Additionally he made the suggestion that the spondylial structure seen in the Laballinae is a 'variant of the spiriferined apical structure produced through the approximation of the dental plates to the septum and their eventual coalescence with it, together with an elongation of the valve possibly due to adhesion of the valve to the substrate' (NLL transl.). DAGIS postulated his genus Pseudocyrtina as a morphological intermediate in this sequence. In this genus the dental lamellae are markedly flexed towards the median septum in their central part forming a delthyrial chamber, then diverge again to join the ventral shell wall. He thus emphasised the affinity of the Laballinae and the Spiriferininae. However, in 1965 he chose to stress the distinctness of his subfamily by raising it to family level and including in it a further subfamily, the Thecocyrtellinae for BITTNER's (1890) genus which has a delthyrial plate but no tichorhinum or jugal processes.

Neither Laballa nor the Laballinae were considered by PITRAT (1965) in the brachiopod volume of the Geol.Soc.Amer. treatise, but the remaining genera included by DAGIS in the subfamily were again associated with Cyrtina in the Cyrtinidae. Here the Laballinae is recognised, for the lack of a tichorhinum is in itself sufficient to support a subfamily. However, the ledges on the margins of the delthyrium of L.suessi suggest the former presence of a delthyrial cover (see e.g. pl.11, fig.5) and indicate that the exact character of a grouping around Laballa remains uncertain. Moreover, the writer is unconvinced of the derivation of the laballinid apical structure from Spiriferina. For these reasons the Laballinae is retained as a subfamily to await further investigation.

Lepismatina austriaca is here regarded as a junior subjective synonym of Zugmayerella uncinata and no Ehaetian representative of Lepismatina is recognised.

Genus Laballa MOISSEIEV in DAGIS, 1962 a1962a Laballa MOISSEIEV in DAGIS, p.511963 Laballa MOISSEIEV, DAGIS p.87Type Species:Spiriferina Suessi ZUGMAYER, 1880 p.29, pl.3, figs.14-19; OD.Range and Distribution:Carnian of N.E.Siberia and possibly New Zealand.Norian of Slovakia, E.Bulgarian Balkan Mts., N.E.Turkey, the Caucasus, Crimea and Pamirs.Rhaetian of the Northern Alps.Included Species:Apart from the type four species have placed in Laballa:L.slavini DAGIS, 1962a p.53, pl.7, figs.4,5L.plicata DAGIS, 1963 p.93, pl.11, figs.5,6

from the Carnian of N.E.Siberia.

L.australis TRECHMANN, 1918 p.225, pl.23, figs.13,14

from the Carnian of New Zealand.

Diagnosis: (internals after DAGIS 1962a)

Medium to large spiriferinids. Commonly smooth, may be costate. Sulcus and fold present. Hinge line shorter than greatest width; lateral and anterior margins rounded. Beak may be slightly recurved, area catacline apsacline, smooth, sharply delimited. Ledges border delthyrium possibly indication delthyrial cover. Punctate.

Ventral septum joined to dental lamellae. Cardinal process low, striate. Inner hinge plates present.

Laballa suessi (ZUGMAYER), 1880

Pl.11, figs. 5-7

- 1859 Spirifer Suessi WINKLER, 1859 p.23
 1880 Spiriferina Suessi ZUGMAYER, p.29, pl.3 figs. 14-19
 1890 Spiriferina Suessi WINKL.; BITTNER, p.282
 1891 Spiriferina Suessii WINKL.; BITTNER, p.109
 1892a Spiriferina Suessii WINKL.; BITTNER, p.80
 1947 Cyrtina suessi (WINKLER), MOISSEIEV, p.74, pl.8 fig.7
 1958 Cyrtina suessi WINKLER, MAHEL, p.140 pl.5 fig.11
 1962a Laballa suessi (WINKLER), DaGIS, p.51 pl.7 figs. 1-3
 1963 Laballa suessi (WINKLER), DaGIS, 1963 p.88 pl.9 figs. 4-9
 ?non.1864 Spiriferina Süssi (WINKL); RENEVIER, p.44

Lectotype and Authorship:

WINKLER (1859), who has previously been credited with the authorship of L.suessi, clearly intended his species to include only what he believed to be Rhaetian representatives of 'Spirifer' rostratus and gave only this stratigraphic reason for its separation. However, he applied the name Spirifer Suessi to Spirifer rostratus SUESS, 1854, p.19, pl.4, fig.8 (non SCHLOTH.) from the Liassic Grestener Schichten. Whatever this specimen may be, it is not the Rhaetian species which was fully described and figured by ZUGMAYER (1880) as Spiriferina Suessi and now recognised as Laballa suessi. Therefore Spiriferina Suessi ZUGMAYER, is the first available name for the Rhaetian species. DaGIS's selection (1962a) of one of ZUGMAYER's specimens as lectotype was strictly invalid so long as the authorship was attributed to WINKLER, whose holotype must be the original of SUESS's figure. Now that ZUGMAYER's authorship has been established a lectotype is reselected.

ZUGMAYER's syntypes are preserved in the Pal.Inst.Univ.Vienna, and the original of pl.3, fig.14 is here selected as lectotype. This is the specimen originally chosen by DaGIS.

Dimensions of Lectotype:

Length 22.0mm., breadth 30.3mm., thickness 23.2mm.

Type locality:

ZUGMAYER gave the source of his specimen as 'Kaisersteffel'.

This lies near Waldegg in the Piesting Tal, Lower Austria. Topotypes may still be collected.

Range and Distribution:

Norian of Slovakia (Drnava, Stratenska hornatina), the Caucasus, Crimea and Pamirs.

Rhaetian of the Northern Alps.

Diagnosis:

Not costate. Jugum centrally flattened, spinose. Otherwise as genus.

Description:

Laballa suessi is a medium sized spiriferinid. The hinge line is shorter than the maximum width and the lateral and anterior margins are smoothly rounded. The brachial valve is shallow and bears a strong, rounded median fold bordered near the umbo by two small grooves and angularly raised from the shell for the remainder of its length. The sulcus is correspondingly marked. The pedicle valve is semipyramidal with no beak recurvature in even the largest topotypic or neighbouring examples and the area is then catacline. In contrast DAGIS's (1963) material shows quite strong beak recurvature as well as a shorter hinge line and this may have been caused by the nature of the substrate. Apart from the presence of growth lines the area is smooth and sharply delimited. Narrow ledges border the delthyrium and can be clearly seen on other members of the genus e.g. Laballa bittneri in DAGIS 1963 pl.13, figs. 1b, 2b; L. australis in TRECHMANN 1918 p.225. It is possible that they indicate the original occurrence of a delthyrial cover.

The internal structure has not been examined. DAGIS's investigation was complete and his figures formed the basis of the diagnosis given above.

Remarks:

Laballa suessi does not appear to be easily distinguishable from either Laballa bittneri from the Carnian of Siberia, which seems to constantly show an erect area, or Laballa australis (Spiriferina suessi var.australis TRECHMANN, upgraded by DAGIS, 1963 p.93, = Spiriferina (Psioidea) australis TRECH.; MARWICK 1953 p.40, cum. syn.) from the Carnian of New Zealand. The writer having been kindly shown a specimen of this age from the Slovakian Carpathians (v.BYSTRICKY 1964 p.66-7) by Mme.ANDRUSOVA in Bratislava, is inclined to believe that their separation may not be practicable.

The Spiriferina Süssi (WINKL.) RNV. recorded by RENEVIER from the Lac Léman (L. of Geneva) area was identified before ZUGMAYER's description and is probably a misnomer.

Dimensions of Figured Specimens:

	length	breadth	thickness
11/5	25.3	28.5	24.5
11/6	23.3	31.0	22.3
11/7	28.7	26.7	29.6
11/8	36.5	38.2	----

Material:

Kaisersteffel, Piesting Tal - 2, T.58; Hirtenberg, Triesting Tal - 3, T.59; Lofer Graben, Reit im Winkl - 1, T.60; Drnava - 1, T.61.

Genus Zugmayerella DAGIS, 1963

- 1880 Formenkreis der Spiriferina uncinata ZUGMAYER, p.26
 1917 Formenkreis der Spiriferina jungbrunnensis PETZ., GOETEL p.97
 1963 Zugmayerella DAGIS, p.99
 1965 Zugmayerella DAGIS; DAGIS p.98
 1965 Zugmayerella DAGIS; PITRAT p.679

Type Species:

Spiriferina Kössenensis ZUGMAYER, 1880 p.28, pl.3, figs.2,3,13; OD.

Range and Distribution:

Norian of Slovakia (Drnava), E.Bulgarian Balkan Mts. (Luda Kancia), Caucasus, Crimea and N.E.Siberia.

Rhaetian of the Northern Alps, Slovakia (Hybe), and N.W.Rumania (Apuseni Mts.).

Probably also the Carnian of Spitzbergen (BÖHM 1903, see below).

Included species:

Apart from the type two species have been described in the genus:

Z.eurea DAGIS 1965 p.99, pl.14, figs.3-7

Z.inaequiplicata DAGIS 1965 p.100, pl.15, figs.1-3 both from the Norian of N.E.Siberia.

Diagnosis:

Medium sized semipyramidal species. Beak tall; hinge line shorter than maximum width; lateral margins rounded. Sulcus and fold distinct, unribbed. Lateral slopes bear several rounded ribs. Cardinal margin wholly or partially denticulate, area concomitantly ornamented with denticular ridges. Delthyrium open. Shell surface pustulose; possibly spinose. Dental lamellae fused with median septum forming spondylium - like structure. Cardinal process low, striate. Jugum as simple arch; descending lamellae of spiralia supported by plates. Punctate.

Zugmayerella uncinata (SCHAFHÄUTL), 1851

Plate 12, figs.3-6; text-figs. S.xl - S.xliii; text-plates S.9-S.11

- 1843 Spirifer Jungbrunnensis PETZOLD, p.134, fig. in text.
- 1851 Spirifer uncinata SCHAFHÄUTL, p.135, pl.24, fig.33
- 1853 Spirifer pyramidalis SCHAFHÄUTL, p.310, pl.6, fig.4
- 1854 Spirifer Münsteri DAVIDSON; SUESS (partim), p.22, pl.2, fig.3
- 1854 Spirifer Münsteri DAVIDSON, var.austriaca SUESS, p.23, figs.4,5
- 1859 Spirifer uncinatus SCHAFH.; WINKLER, p.24
- 1861 Spirifer uncinatus SCHAFH.; GÜMBEL, p.401
- 1861 Spirifer Münsteri DAVIDSON; STOPPANI, p.87, pl.17, fig.11-15
- 1863 Spirifer uncinata SCHAFHÄUTL, p.348
- 1863 Spirifer uncinata SCHAFH.; MARTIN, p.253
- 1863 Spirifer uncinata SCHAFHÄUTL; OOSTER, p.37, pl.13, figs.1-8
- 1864 Spiriferina uncinata SCHAFH.sp; DITTMAR, p.151
- 1867 Spiriferina uncinata SCHAFH.,sp; MARTIN, p.253
- 1870 Spirifer uncinatus SCHAFHÄUTL; QUENSTEDT, p.523, pl.54, figs.63-7
- 1880 Spiriferina uncinata SCHAFH.sp.; ZUGMAYER, p.27, pl.3, fig.1
- 1880 Spiriferina austriaca SUESS; ZUGMAYER, p.28, pl.3, fig.6
- 1885 Cyrtina Jungbrunnensis PETZOLDT; HAAS, p.19, pl.2, figs.2-6
- ? 1890 Spiriferina uncinata SCHAFH.; BITTNER, p.283
- ? 1890 Spiriferina austriaca SUESS; BITTNER, p.283
- 1892 Spiriferina uncinata SCHAFH. spec.; BITTNER, (partim) p.80, pl.4, fig.9
- 1909 Cyrtina uncinata SCHAFH. sp.; TRAUTH, p.48, pl.1, fig.1
- 1912 Cyrtina uncinata SCHAFH.; KILLAN and REVIL, p.7
- 1917 Spiriferina uncinata SCHAFH.sp.; GOETEL, p.99
- 1929 Spiriferina uncinata (SCHAFHÄUTL); DOUGLAS, p.642, text figs.1-4
- ? 1938 Spiriferina (?) akdjilgaensis MOISSEIEV, p.222, pl.1, fig.1
- ? 1963 Lepismatina austriaca (SUESS); DAGIS, p.95, pl.11, figs.7-9
- 1963 Zugmayerella uncinata (SCHAFHÄUTL); DAGIS, p.99, pl.13, fig.5

Holotype:

SCHAFHAÜTL's originals were probably in the Bayer.St.Slg.Munich, but a search there through the kindness of the Director, Prof.DEHM, failed to reveal them and they must be presumed lost.

Dimensions of Holotype:

From SCHAFHAÜTL's figure - length 17mm., breadth 17mm., thickness 12mm.

Type locality:

SCHAFHAÜTL gave the source of his material as the 'Gervillien Schichten' of 'Hirschbühl hinter dem hohen Kramer bei Garmisch'. This locality has not been investigated by the writer.

Range and Distribution:

Norian of N.E.Turkey, probably Slovakia (Drnava) and the Pamirs.

Rhaetian of the French Alps (Pas du Roc), Switzerland (Haute Savoie), Northern Alps, Lombardy Alps, Slovakia (Hybo), Polish sub-Tatra, N.W.Rumania (Apuseni Mts.), and E.Iran (DOUGLAS 1929).

Liassic of the Northern Alps (Gresten area - TRAUTH 1909)

Diagnosis:

Ribs angular. Cardinal margin partially denticulate, portion of area adjacent to delthyrium bears denticular ridges. Otherwise as genus.

Description:

Zugmayerella uncinata is a medium sized, semipyramidal spiriferinid with rounded lateral margins and a hinge line shorter than the maximum width. Recurvature of the beak occurs in older specimens and the area is orthocline with denticular ridges covering half its surface adjacent to the open, triangular delthyrium. Slight, blunt growth lines and extremely fine vertical growth lines are present on the unridged part of the area. There is no reflection of the denticular ridges on the inner surface but since the denticulate part lacks punctae, a textural contrast and dividing line is normally visible on weathered casts or decorticated specimens. This phenomena and its importance for the validity of SUESS's var. austriaca and thus Lepismatina austriaca is discussed below.

The ribbing is strong and angular; 2, 3 or rarely 4 ribs are present on the lateral slopes bordering the well developed sulcus and fold.

Fine, $\frac{1}{4}$ mm. spines cover the shell and leave a pustulose surface on breaking.

The dental plates are fused with the median septum exactly as in other members of the genus. There are no inner hinge plates and the striate cardinal process rests on the floor of the valve, bridging the crural bases. The jugum is a simple arch and the descending lamellae of the spiralia are supported by two plates.

Remarks:

As can be seen on text plate 9 there is little doubt that the species described by PETZOLDT in 1843 is that long recognised as 'Spiriferina' uncinata SCHAFHAÜTL 1851. This name has been used extensively in both the zoological and stratigraphical literature, as the synonymy list demonstrates, whereas only HAAS (1885) has correctly used jungbrunnensis. GOETEL (1917) used it as a group name to cover the supposed 'Formenkreis of S.uncinata S.koessenensis, and S.austriaca,' in the sense first suggested by BITTNER (1890 p.283).

There is no doubt of the identity of 'S.uncinata, for although SCHAFHAÜTL's figure does not show the partially striate area, its association with Rhaetina gregaria remarked on by SCHAFHAÜTL (1863 p.348-9), is characteristic.

Therefore Spirifer Jungbrunnensis, having been 'unused as a senior synonym in the primary zoological literature for more than fifty years', is a nomen oblitum by ICZN Art.23(b) and will be referred to the Commission for inclusion on the appropriate Official Index of Rejected Names.

Lepismatina austriaca was distinguished by SUSS (1854) as a variety of 'Spirifer' muensteri (non DAVIDSON). Subsequently ZUGMAYER (1880) raised it to binomial status as an 'abart' of his 'Formenkreis der Spiriferina uncinata', and DAGIS (1963) placed it in Lepismatina. Unfortunately the holotype is no longer present in the Geol.Bundes.Vienna (Prof.R.SIEBER, verbal communication 1965) and must be presumed lost. However, ZUGMAYER's original is preserved in the Pal.Inst.Univ.Vienna and is a decorticated cast on which a division of the area is quite clear on close examination. It matches exactly the appearance of decorticated

TEXT-PLATE S.9

Zugmayerella uncinata (SCHAFHAUTL)

Text-plate S.9

- a-c Zugmayerella uncinata (SCHAFHAUTL).
Ochsenberghütte by Hindelang, Bavaria
B.M.N.H. - BB 43208 ex B 39170 x2
- d Partially decorticated Z.uncinata
Axelstein by Jachenau, Bavaria. x2
- e Original of ZUGMAYER 1880 pl.3, fig.6
- Spiriferina austriaca SUESS. x2
- f Spirifer Jungbrunnensis PETZOLDT, 1843 p.134

Note the identity of Zugmayerella uncinata (a - c) and the specimen depicted in PETZOLDT's figures (f)

The textural division of the area of ZUGMAYER's original of L.austriaca is clearly seen in fig.e, and is identical with the appearance of the decorticated area of Z.uncinata in fig.d. It is argued in the text that these two nominal species are synonymous.



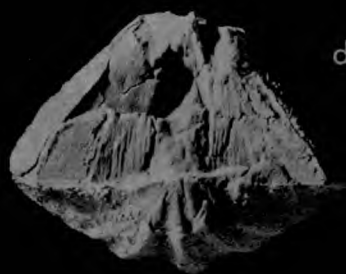
a



b



c



d



e

f

letzteren sind mit kleinen Warzen bedeckt. Wir werden ihn vorläufig nach seinem Fundorte *Spirifer Jungbrunnensis* nennen.



examples of Z.uncinata broken from a hard limestone. Moreover, the distinction made by SUESS of var.austriaca as 'wenig gefalteten Formen' must be read in the context of his inclusion of the prolifically ribbed Z.koessenensis in his description. ZUGMAYER (1880) was unable to use it as a diagnostic feature. In the absence of the holotype the evidence points to L.austriaca being a junior synonym of Z.uncinata and it is regarded as such here.

Of the figures given by DAGIS (1963) for L.austriaca it seems likely that at least the originals of figs. 7 and 8 also belong to Z.uncinata, (that of fig.9 seems like a young Z.koessenensis).

Spiriferina cf.austriaca from the Ladinian of New Zealand (TRECHMANN 1918, p.224, pl.24, fig.5; see also MARWICK 1953) certainly lacks denticular ridges and may well belong in Lepismatina.

Although Lepismatina is not now recognised in the Rhaetian species related to L.hsui - the type - are certainly present in the Norian. A specimen of L.arctica, kindly lent to the writer by Dr.D.PATRULIUS, from the Rumanian Norian is definitely devoid of denticular ridges and several species described by BITTNER (1890 and 1899) show a close external similarity to it. Many of these species are alate and the suggestion of PITRAT (1965 p.678) that WANG's Lepismatina is synonymous with HECTOR's Psioidea, the type of which is the alate and nondenticulate P.nelsonensis, requires investigation.

Dimensions of Figured Specimens:

		length	breadth	thickness	
	12/3	16.3	23.2	20.0	
	12/4	13.6	21.7	16.0	
	12/5	15.8	20.2	18.0	
	12/6	16.5	25.2	22.9	
text-plate	9/a-c	11.8	17.7	14.9	BB 43208
	9/d	as12/4			
	9/e	as12/5			

Material:

Ochsenberghütte by Hindelang - 11, B.M.N.H., B 39169; loc.cit. - 7, B 39170; loc.cit. - 18, B 39172; loc.cit. - 29, B 24623; loc.cit. - 1, BB 39208; Hochalpthütte by Pfronten - 12, T.45; Bodenschneid Gipfel by Schliersee - 1, T.46; Wildfellalm by Spitzingsee - 2 plus many fragments, T.47; Axelstein by Jachenau, Walchensee - 20, T.48; Ampelsbach by Achenkirch - 13, T.49; Steinplatte by Waidring - 35, T.50; Bystry potok by Gombas, Ruzomberok, Slovakia - 20, T.51; Mała Swinica by Zakopane, Poland - 2, T.52.

TEXT-PLATES S.10 and S.11

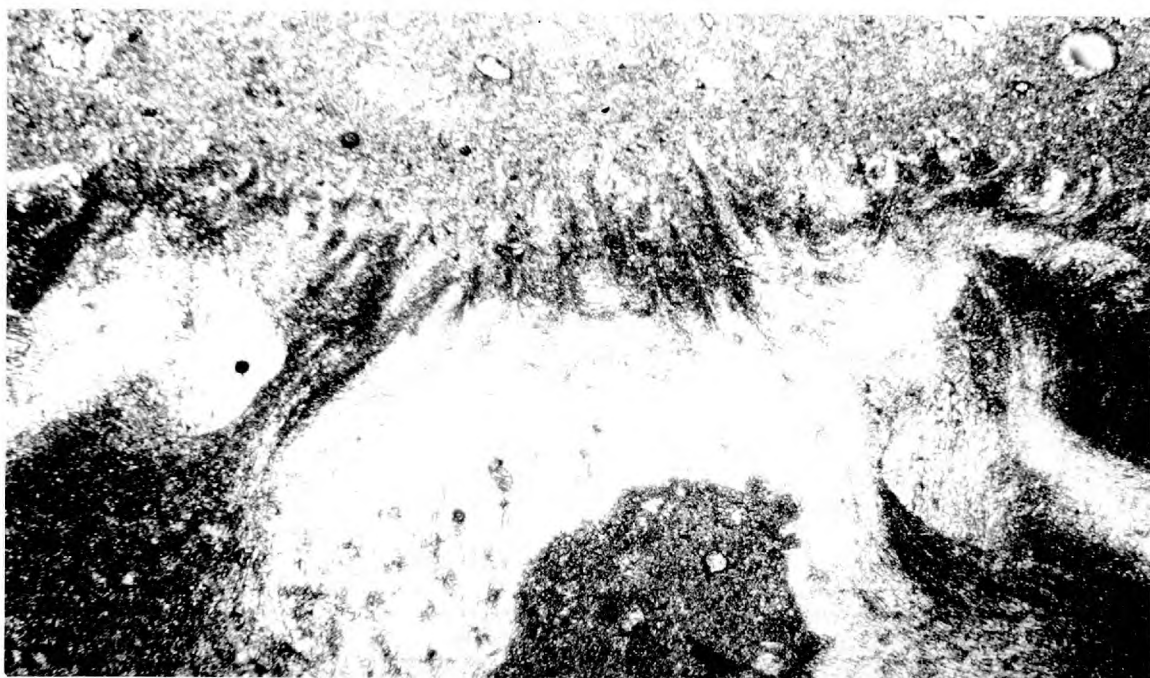
Zugmayerella uncinata (SCHAFHAUTL)

Text-plate S.10

Transverse section of the cardinal process of
Zugmayerella uncinata. Detail of section 0.6,
text-fig. S.xIii x10

Text-plate S.11

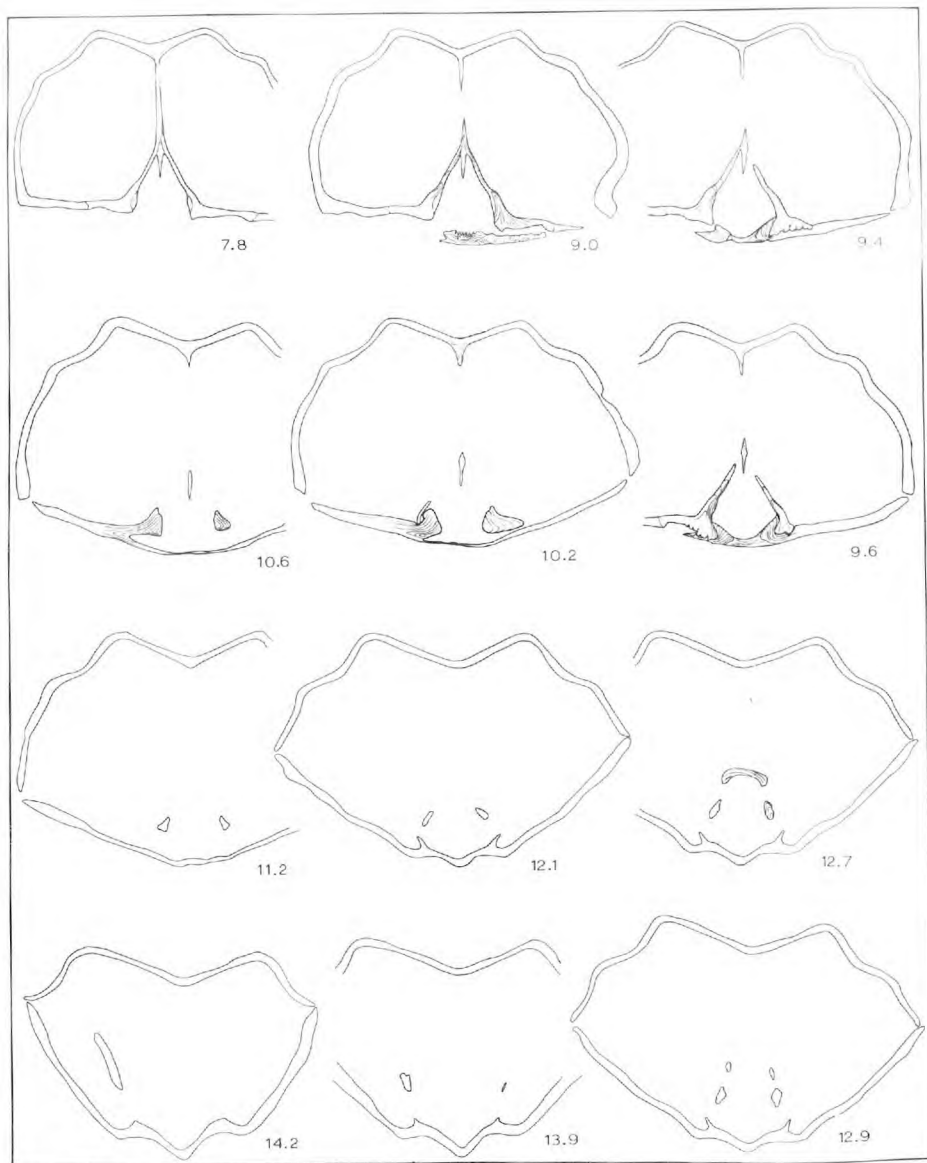
Transverse section of the junction between the
impunctate denticulate and the punctate non -
denticulate parts of the area of Zugmayerella
uncinata. Detail of text-fig. S.xI x15



Text-plate S.10

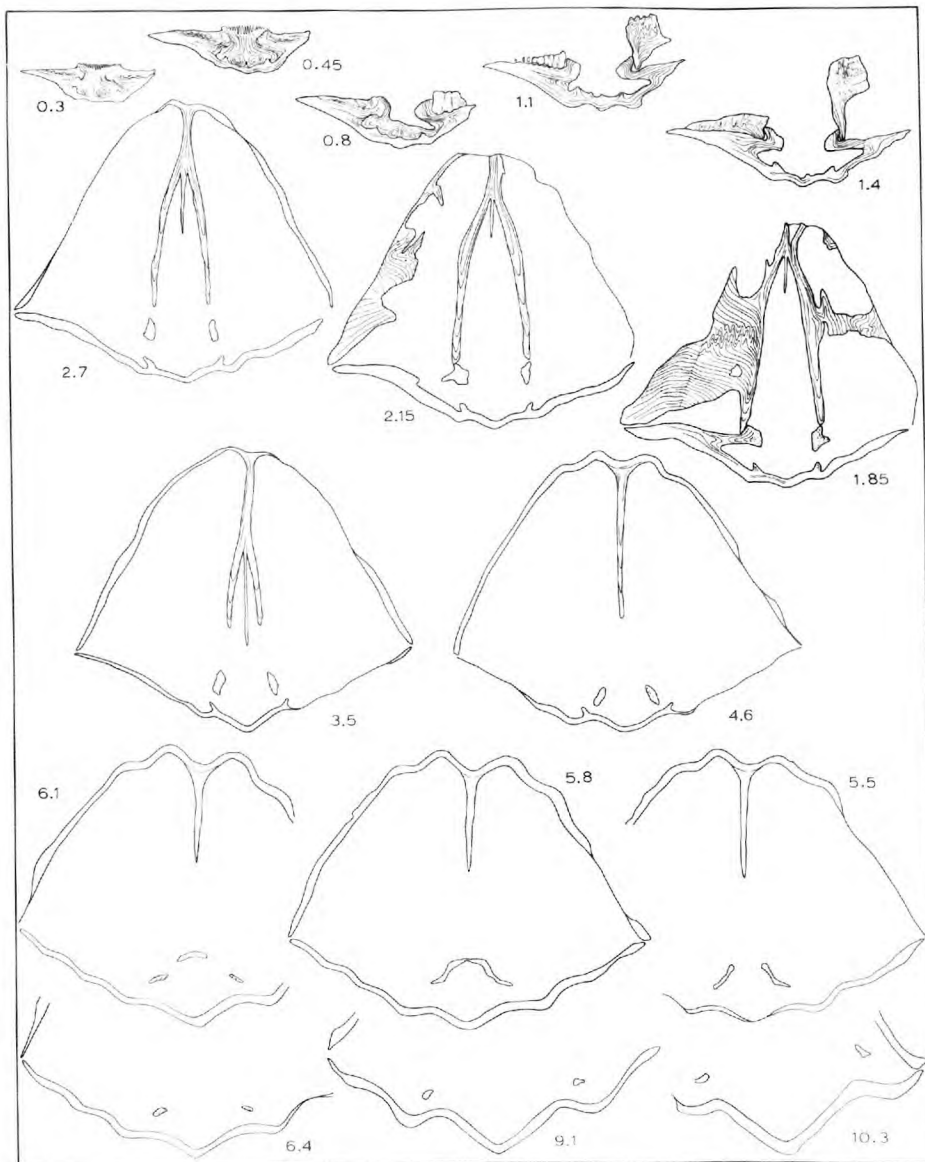


Text-plate S.11



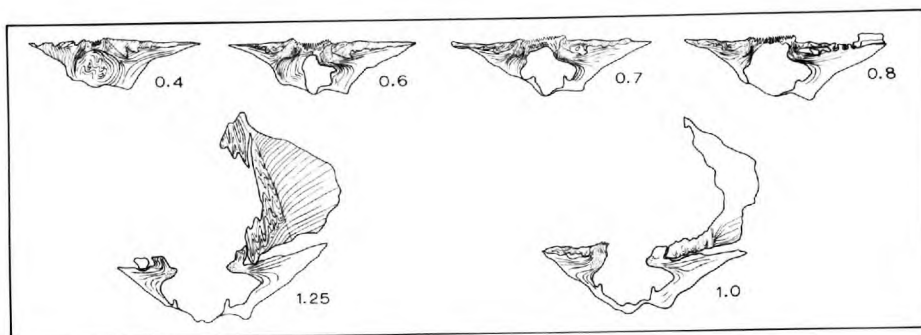
Text-fig. S.x1

Serial transverse sections of Zuercherella uncinata
 (SCHAFERLUTL). Rhaetian; Ochsenberghütte by Hindelang, Bavaria.
 B.M.N.H. - B 39169 x3 Total length of specimen 18.9mm.
 Specimen ground normal to the plane containing the greatest length.
 PC.Nr.62.



Text-fig. S.xli

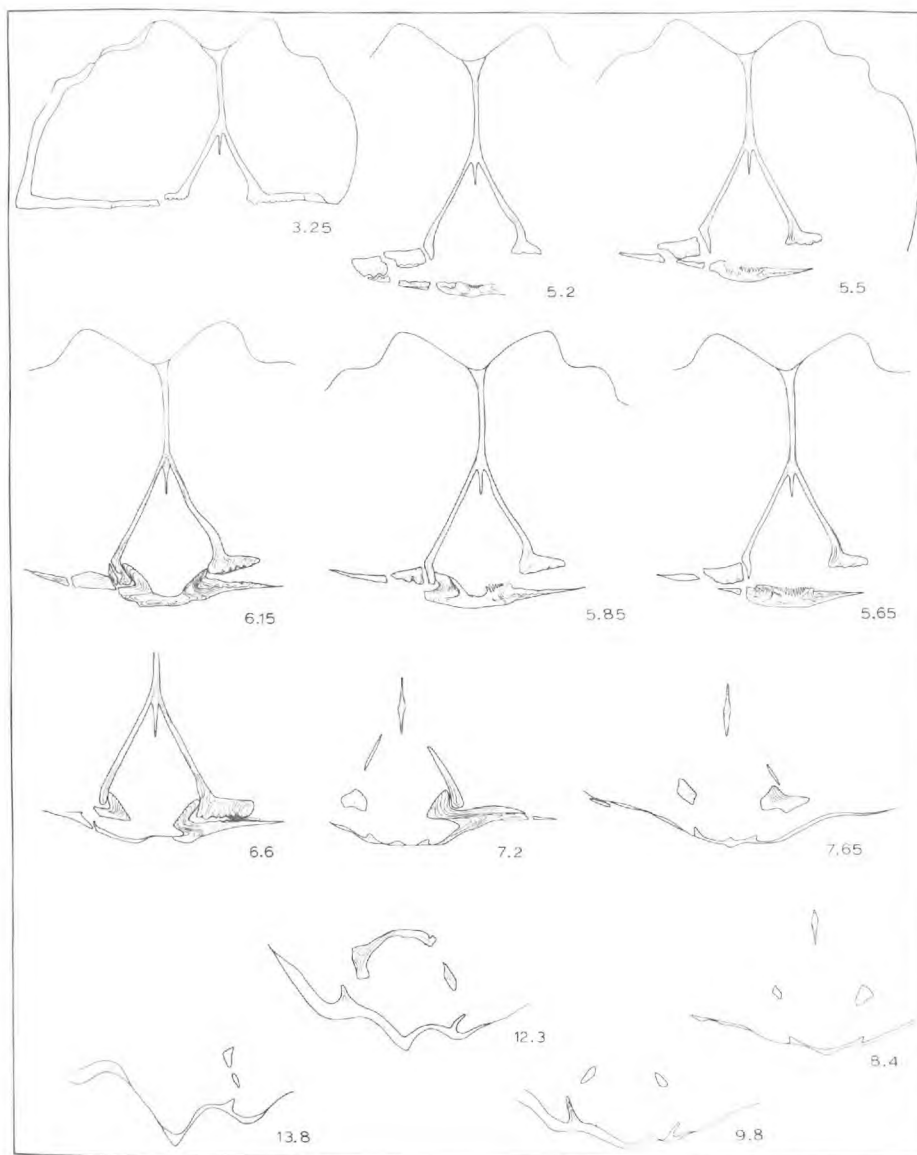
Serial transverse sections of Zugnayerella uncinata
 (SCHAFHÜTL). Locality and spec.no. as text-fig. S.xl x3
 Specimen ground normal to the commissural plane. PC.Nr.61



Text-fig. S.xlii

Serial transverse sections of Zugmayerella uncinata
(ZUGMAYER). Rhaetian; Steinplatte by Waidring, Tirol, Austria;
47°37'10''N. 12°34'10''E. - 91 St.Johann in Tirol. x3
Specimen sectioned normal to commissural plane. PC.Nr.59

This specimen was ground as a possible Lepismatina austriaca.
Half of the area was stripped of shell and showed no trace of
denticular ridges, the remainder was concealed by matrix and
only revealed its structure on grinding.



Text-fig. S.xliii

Serial transverse sections of Zugmayerella uncinata (SCHAFHÄUTL). Rhaetian; Steinplatte by Waidring, Tirol, Austria; 47°37'10''N. 12°34'10''E. - 91 St.Johann in Tirol. x3
Specimen sectioned normal to the plane containing the greatest length. Total length of specimen 18.4mm. PC.Nr.60

This specimen, with its area buried in matrix, was ground as a possible Lepismatina austriaca.

Zugmayerella koessenensis (ZUGMAYER), 1880

Plate 12, figs.1 and 2; text-figs.S.xxxviii and S.xxxix

- 1854 Spiriferina Munsteri DAVIDSON; SUESS (partim), p.22, pl.2, figs.1,2
 1880 Spiriferina Kossenensis ZUGMAYER, p.28, pl.3, figs.2,3,13
 1890 Spiriferina Kossenensis ZUGMAYER; BITTNER p.283
 1917 Spiriferina Kossenensis ZUGM.; GOETEL, p.100, pl.8, fig.3
 1917 Spiriferina nov.sp. GOETEL, p.102, pl.8, fig.5
 1932 Spiriferina sp.; MOISSELEV, p.594, pl.1, figs.1-3
 1932 Cyrtina nov.sp.indet.; MOISSELEV, p.594, pl.1, figs.4,5
 1963 Zugmayerella koessenensis (ZUGMAYER); DAGIS, p.100, pl.13, figs.1-4

Lectotype:

ZUGMAYER's syntypes are preserved in the Pal.Inst.Univ.Vienna. Both are typical of the species but as the original of fig.3 is a young specimen that of pl.3, fig.3 is here chosen as lectotype. It is refigured on pl.12, fig.1.

Dimensions of Lectotype:

Length 15.3mm. breadth 16.2mm. thickness 19.3mm.

Type locality:

ZUGMAYER gave the type locality as 'Kitzberg'. This lies near the village of Neusiedl in the Piesting Tal, Lower Austria.

Range and Distribution:

Norian of Slovakia (Drnava), E.Bulgarian Balkan Mts. (Luda Kamcia), Caucasus and Crimea.

Rhaetian of the Northern Alps, Slovakia (Hybe), and N.W.Rumania (Apuseni Mts.).

Diagnosis:

Fold and sulcus medianly flattened. Lateral slopes bear 4-6 rounded ribs. Cardinal margin wholly denticulate, area completely ornamented with denticular ridges. Otherwise as genus.

Description:

Zugmayerella koessenensis is a somewhat compressed, medium sized spiriferinid. The lateral margins are smoothly rounded and the hinge

line is shorter than the greatest width. When fully developed both valves are characteristically elongate in outline, the brachial valve being shallow and the pedicle valve tall with recurvature of the beak in gerontic individuals. The cardinal margin is wholly denticulate and the area fully covered with prominent longitudinal denticular ridges. The delthyrium is open. The fold and sulcus are prominent and medianly flattened in all but the youngest individuals, enabling isolated valves to be identified with ease. The narrow, rounded ribs also differentiate the species from others in the Rhaetian, at least four being present on the lateral slopes of even very young individuals which lack the median flattening of the fold. Fully grown specimens may have six.

The surface of the shell is pustulose and the spines, if any, were probably very short. Rough growth lines are present.

The dental plates are fused with the median septum forming a spondylium-like structure. The cardinal process is low and striate and may spread well along the hinge margin in older specimens. Inner hinge plates (crural plates of DAGIS) do not appear to be present, contrary to the observation of DAGIS (1963 p.101). The jugum is in the form of a simple arch, but the jugal spinules found by DAGIS appear to have been destroyed in both the specimens ground, in one of which the spiralia are also absent. Plates support the descending lamellae of the spiralia.

Remarks:

Z.eurea described by DAGIS (1965) from the Norian of north east Siberia only differs from Z.koessenensis in having 7 or 8 ribs on the lateral slopes in contrast to 6 in the Rhaetian species. Additionally the marked dorsal median ridge apparent in DAGIS's figures of Z.eurea (which was not ground) may indicate well developed inner hinge plates.

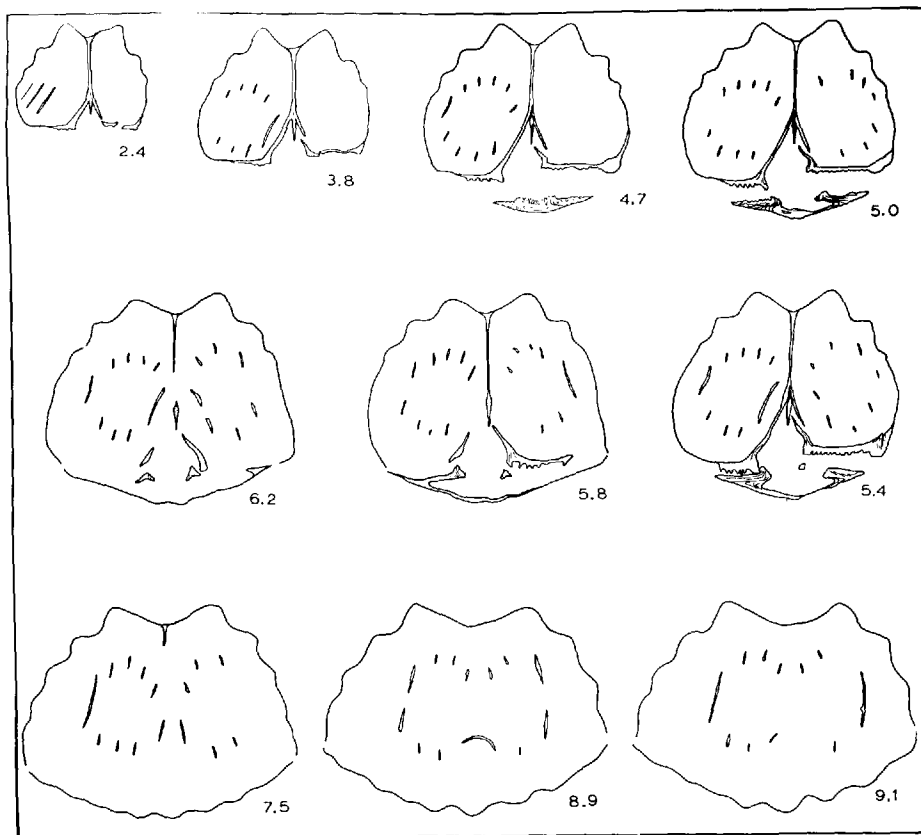
The species BÜHM recorded as Spiriferina sp.ex aff.Sp.koessenensis ZUGM. (1903 p.12, pl.1, figs.33,34) from the Carnian of Spitzbergen can be placed in Zugmayerella but his figured specimens are ^{not} well enough preserved to be specifically determinable.

Dimensions of Figured Specimens: (Originals of ZUGMAYER, 1880)

	length	breadth	thickness
12/1	15.3	16.2	19.3
12/2	11.5	16.0	11.8

Material:

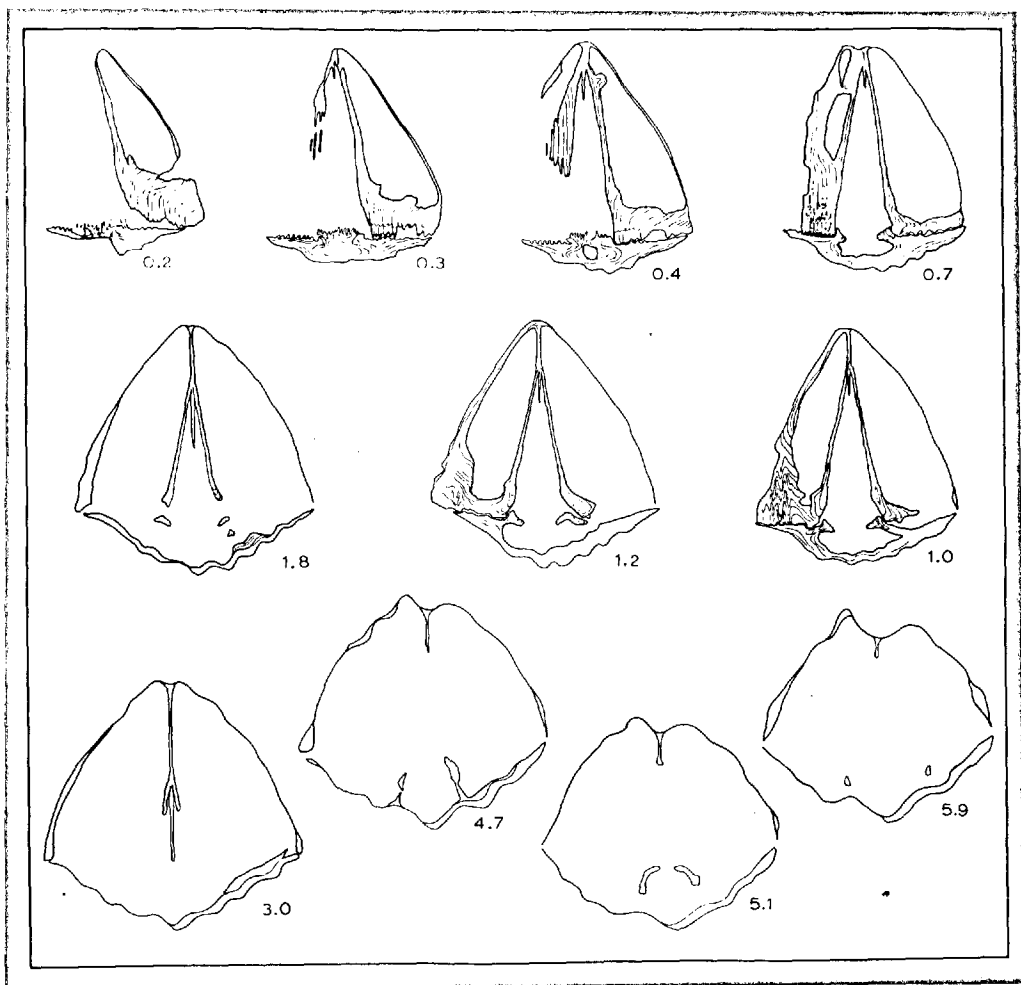
Kitzberg by Neusiedl, Piesting Tal -3, T.42; Kressenberg,
 Piesting Tal (collector Herr E.KATZER) -2, T.43; Hybe, Slovakia -1, T.44;
 plus isolated valves from many localities - see Distribution.



Text-fig. S.xxxviii

Serial transverse sections of Zugnayerella koessenensis (ZUGMAYER). Rhaetian; Kressenberg Wiese, head of Steinbach Graben, Piesting Tal, Lower Austria; collector Herr E.KATZER; 47°50'30''N. 33°40'45''E. - 75 (Pr) Puchberg am Schneeberg.

x3 Specimen ground normal to the plane containing the greatest length. PC.Nr.64



Text-fig. S.xxxix

Serial transverse sections of Zugmayerella koessenensis (ZUGMAYER). Rhaetian; specimen from the Pal.Inst.Univ.Vienna - 'Kaisersteffel', ?Ober Kaisersteffel herein, Piesting Tal, Lower Austria. x3 Total length of specimen 11.7mm. Specimen ground normal to the commissural plane. PC.Nr.4.

Suborder Retziidina BOUCOT, JOHNSON, and STATON, 1964

Superfamily Retziacea WAAGEN, 1883

Family Retziidae WAAGEN, 1883

Genus Neoretzia DAGIS, 1963

Type species:

Waldheimia superba SUESS, 1856 p.48, pl.1, fig.7 (= Retzia superbescens BITTNER, 1890 p.281 pl.26, figs, 13-15; OD).

Range and Distribution

Middle and Upper Triassic of the Alpine-Carpatho-Balkan chain and the Himalayas; Upper Triassic of the Crimea and Caucasus, possibly also of New Zealand.

Neoretzia is the only genus of the family so far recognised in the Mesozoic. Externally, and to some extent internally, it closely resembles the type genus from the Lower Devonian and Hustedia from the Carboniferous and Permian. It will quite certainly prove to include many, if not the majority of the 20 or so nominal Triassic species, in particular the widespread 'Retzia'schwageri group of 'varieties'.

Diagnosis: (Internals after DAGIS 1963)

Species elongate-oval in outline; beak tall, variably recurvate. Area apsacline to orthocline. Deltidial plates conjunct. Ribs angular. No dental lamellae. Pedicle collar present. Cardinal process bilobed, massive. Median septum thin, tall. Jugum complex, jugal processes bear W-shaped plate on ventral side which re-unites with primary lamellae. Apices of spiralia directed laterally.

Remarks:

Retzia superbescens BITTNER, designated as the genotype by DAGIS (1963), is here regarded as a junior subjective synonym of Waldheimia superba SUESS. This species is retained as the type despite the possibility discussed below that DAGIS may have been mistaken in attributing his Caucasian and Crimean material to it. If, after further investigation, it is proved that this is the situation, then the genotype must be considered in the light of ICZN Art. 70a, in which case DAGIS's own rich material will be most suitable for selection.

Neoretzia superba (SUESS), 1856

Plate 13, figs.6-8

- 1856 Waldheimia superba SUESS, p.48, pl.1 fig.7
 1880 Retzia superba SUESS sp.; ZUGMAYER, p.34-36, pl.4 figs.6-11
 1890 Retzia superbescens BITTNER, p.281, pl.26 figs.13-15
 ?1927 Retzia Schwageri BITT. n.var.taurica; MOISSEIEV, p.751, pl.23, figs. 17-20
 ?1947 Retzia caucasica MOISSEIEV, p.74, pl.8, fig.9
 ?1963 Neoretzia superbescens (BITTNER); DAGIS, p.131-4, pl.20, figs.4-10
 pl.21, figs.1-2

Holotype:

The original of SUESS, originally in the Geol.Bundes.Vienna, cannot be found (Prof.R.SIEBER, verbal communication 1965).

The plesiotype of ZUGMAYER (1880 pl.4, figs.6-11) is preserved in the Pal.Inst.Univ.Vienna and is refigured here on plate 13, fig.6.

Dimensions of Holotype:

SUESS's figure was not measured.

Type Locality:

Hirtenberg, Triesting Tal, Lower Austria.

Range and Distribution:

Norian of Slovakia (Drnava).

Rhaetian of the Northern Alps (Vienna area).

Diagnosis:

Beak long, only slightly recurved; area apsacline. 9-12 sharp ribs, may branch on larger specimens. Internally apparently as genus (from ZUGMAYER figs. 9-11).

Description:

Neoretzia superba, exceeding 20mm. in length is a little larger than most species which may be assumed to belong to the genus. It is strongly ovate in outline, with a short, straight hinge line, a very extended beak and a smoothly rounded anterior margin. The area is apsacline, gently recurved in profile, and sharply divided from the lateral slopes. Conjoint deltidial plates are present, and on well preserved specimens the suture is clear. DAGIS's observation that the plates cover the entire surface of the area in addition to the delthyrium has not been confirmed.

The exact position of the pedicle foramen was not to be seen on the material consulted, but must be apical as in other members of the family. Between 9 and 12 sharp ribs are present and secondary ribs may occur on their slopes near the anterior margin. At the dorsal umbo the central rib is somewhat weaker than its neighbours and flattening, or even a slight sulcation is apparent in anterior view.

Removal of the shell reveals markedly flattened inter-rib troughs and radially striated rib flanks on the internal cast. The striations are not present in the inter-rib troughs.

Growth lines are present but not strongly marked. Fine punctation is visible on partially decorticated surfaces.

Lack of material prohibited serial grinding and the internal structure of the species is only certainly known from the figures of ZUGMAYER (1880 pl.4, figs. 9-11). These show all the important elements found by DAGIS in his Caucasian material and whether the Soviet and Austrian specimens are conspecific or not, there can be very little doubt that internally they are in all essentials identical. ZUGMAYER shows dental lamellae to be absent, a massive cardinal process and a thin dorsal septum. The flat jugum is evident in his fig. 10, and the laterally directed spiralia in fig.11. In addition DAGIS found a pedicle collar and illustrated the jugum in detail. The jugal plate is flat and two jugal processes unite to form an anteriorly directed tube. This tube gives rise to two broad, ventrally directed branches which unite with the primary lamellae. Between them is a further plate which bears a low median blade giving a W-shape in cross-section. Such an arrangement appears to be unique in the retziids, for although Retzia itself and Eumetria have somewhat similar jugal processes, their arrangement is much simpler: they point posteriorly ventrally and do not join the primary lamellae (see BOUCOT et.al.1965 fig.531, 2a, 8f and 8g).

Remarks:

The specimens from the Norian of Drnava described by BITTNER as Retzia superbescens cannot at present be separated from those representing SUESS's species from the Rhaetian of Lower Austria. BITTNER (1890p.281)

in attempting to distinguish them remarked that the ribs of two of his four Drnava specimens 'sind einfach, nicht dichotomirend wie bei der rhatischen Form', and used this to distinguish the species. However, in the other two he noted the appearance of secondary ribs and spoke of one as 'eine Vermittlung zwischen beiden Arten', and the other as 'eine wahre Uebergangsform'. Moreover, on directly comparing four Austrian specimens of 'Retzia superba' from Hirtenberg with his material he declared one to be 'vollkommen identisch' with the typical Drnava form. At the end of his description he was forced to narrow the distinction between the species to irregular rib branching in superbescens in contrast to regularity in superba. However, as ZUGMAYER (1880 p.35) noted in fully describing the rib branching of superba, its extent and development depend on the size and maturity of the individual and it cannot be used to distinguish two species. That this is not practicable is clearly seen on plate 13 where figs.6 and 7 show specimens from Drnava (superbescens) and Hirtenberg (superba) having identically developed assymetrical rib branching and which are, indeed, perfect mirror images of one another. Therefore Neoretzia superbescens (BITTNER) is here thought to be a junior subjective synonym of Neoretzia superba (SUESS).

Some doubt, however, must remain attached to the identity of the specimens described by DAGIS and used by him the foundation of Neoretzia. A characteristic feature of N.superba appears to be the high, markedly apsacline area. In contrast the Caucasian and Crimean specimens have a lower more recurvato beak and an area 'lying roughly in the plane of the commissure' DAGIS (1963 p.131 - NLL transl.). In this they closely resemble the many members of the complex of 'varieties' of Neoretzia schwageri figured by BITTNER (1890, 1892, 1899) and the specimens from the Norian of Slovakia described and figured by MAHEL (1958 p.143-4) as Retzia schwageri fastosa (pl.5, figs. 8-10) and Retzia superbescens (pl.5, figs.5-7). It is with the N.schwageri complex that the writer prefers to place the Soviet and Slovakian N.'superbescens'. A specimen from the Norian of Rumania kindly loaned by Dr.D.PATRULIUS, and almost certainly of the species figured by DAGIS, has been used to reinforce this view. Only a thorough examination of both the Middle and Upper Triassic retziids as

a whole will reveal the species boundaries within this complex of closely allied forms, and, in particular, the status of the type species of Neoretzia.

Suborder Athyrididina BOUCOT, JOHNSON, and STATION, 1964

Superfamily Athyridacea M'COY, 1844

Family Athyrididae M'COY, 1844

Remarks:

BITTNER gave much attention to the Triassic athyrids and founded a total of eleven 'Untergattungen', now considered as nominal genera. Seven of these - Tetractinella, Pentactinella, Anomactinella, Amphitomella, Dioristella, (1890), Pomatospirella (1892), Stolzenburgella (1903), are still without satisfactory subfamilial status. Four - Diplospirella, Pexidella, Anisactinella, and Euractinella (1890), were grouped by SCHUCHERT (1894) in his Triassic subfamily the Diplospirellinae. It is curious that although these genera, comprising more than thirty nominal species are widespread in the Middle and Upper Triassic of the Alps, they have not been found in either the Rhaetian of this area or the Middle and Upper Triassic of the Soviet Union.

Subfamily Athyridinae M'COY, 1844

Genus Oxycolpella DAGIS, 1962

1854 Spirigera ORBIGNY; SUESS, p.17

1880 Spirigera d'ORB; ZUGMAYER, p.31

1890 Spirigera 'Glatte Formen' BITTNER, p.296 (pars)

1962 Oxycolpella DAGIS, p.68

1963 Oxycolpella DAGIS; DAGIS, p.120

1965 Oxycolpella DAGIS; DAGIS, p.132

Type species:

Spirigera oxycolpos SUESS, 1854 p.17, pl.1, figs. 1-20 (For discussion of the changed authorship of this species see under Oxycolpella oxycolpos below.)

Range and Distribution:

Upper Triassic of the Alpine-Carpathian-Balkan chain, the Crimea and Caucasus, N.E.Siberia and almost certainly the Middle and Upper Triassic of New Zealand.

Included species:

Apart from the type four species are known to belong in Oxycolpella:

O. robinsoni DAGIS, 1962 p.72, pl.4, fig.1

O. guseriplica DAGIS, 1962 p.73, pl.4, figs.2-4

O. kunensis DAGIS, 1963 p.127, pl.20, figs.1-3

from the Norian of the Caucasus.

O. ochotica DAGIS, 1965 p.132, pl.24, fig.1

from the Norian of N.E. Siberia.

Additionally 'Athyris'eurycolpos is certainly a member of the genus and its distinction from O. guseriplica seems uncertain.

The following species are probable oxycolpellids:

?O. wreyi SUESS in ZITTEL, 1864 p.28, pl.7, fig.3

?O. manzavinoides TRECHMANN, 1918 p.232, pl.25, fig.7 from the Carnian of New Zealand.

?O. kaihikuana TRECHMANN, 1918 p.231, pl.25, fig.5 from the Ladinian of New Zealand.

Diagnosis:

Large athyids; hinge line short, curved; outline transversely oval to rounded pentagonal. Beak small, pointed, markedly incurved; pedicle foramen round, tiny. Area barely distinguishable. Dental lamellae present but often obscured by heavy callus. Cardinal process large, bilobed. Hinge plate unpierced. Jugal saddle present; accessory lamellae from jugal stems, semi-circular fimbriate.

Remarks:

Oxycolpella is one of the youngest known athyrid genera. It is accompanied in the Upper Triassic by two other members of the subfamily, Majkopella MOISSEIEV in DAGIS 1962, and Clavigera HECTOR 1879. Both are distinguishable from Oxycolpella by their long, straight hinge lines, and Clavigera is in addition characterised by a shallow sulcus in both valves. Majkopella is found in the Norian of the Caucasus, Crimea and Turkey, and its internal structure is essentially identical with Oxycolpella. Clavigera is interesting in being recorded from the Liassic

of New Zealand (TRECHMANN 1918 p.237, also MARWICK 1953 p.46) and is therefore the only athyrid known in the Jurassic.

DAGIS (1962b and 1963) made a detailed comparison of Oxycolpella with the type species of the subfamily, Athyris concentrica from the Devonian, pointing out the very poorly developed cardinal process and the pierced hinge plate in A.concentrica. Externally members of the two genera are extremely similar.

Oxycolpella oxycolpos (SUESS), 1854

Plate 13, figs. 1-5; text-figs. S.xliv, S.xlv

- 1851 Spirifera mesoloba PHIL.; SCHAFHÄUTL, p.134
- 1853 Spirigera oxycolpos EMMRICH, p.356
- 1854 Spirigera oxycolpos EMM. sp.; SUESS, p.17, pl.1, figs. 1-20
- 1870 Terebratula oxycolpos SUESS; QUENSTEDT, p.461-5, pl.51, figs.103-10
- 1880 Spirigera oxycolpos EMMRICH sp.; ZUGMAYER, p.31-4, pl.3, figs.20-28
- ?1890 Spirigera spec. aff. oxycolpos EMMRICH spec.; BITTNER p.273
- 1882 Spirigera oxycolpos EMMR.sp; ZUGMAYER, p.353-4, text figs. 1-3
- 1905 Spirigera oxycolpos EMMR.; ARTHABER, pl.50, fig.6
- 1917 Spirigera oxycolpos EMMR. sp.; GOETEL, p.103-4
- ?1927 Spirigera oxycolpos EMMR.sp.; MOISSELEV, p.750, pl.23, figs.12-15
- ?1947 Athyris oxycolpos EMMR.sp.; MOISSELEV, pl.9, fig.9
- ?1958 Spirigera cf. oxycolpos EMMRICH; MAHEL, p.141-2, pl.7 fig.3
- 1962 Oxycolpella oxycolpos (EMMRICH) DAGIS, p.69-72, pl.3, figs.4&5
- 1963 Oxycolpella oxycolpos (EMMRICH) DAGIS, p.121-3, pl.18, figs.1-6

Lectotype and Authorship:

EMMRICH has hitherto been credited with the authorship of this species, but when using the name Spirigera oxycolpos (1853 p.356) he gave no description or figure. In the course of a clear account of the Lofer Graben between Reit im Winkl and Küssen he wrote only of 'die grosse ausgezeichnete Spirigera oxycolpos', and repeated a similar phrase later in the same paper (p.377). The ICZN is clear in stating that mention of a type

locality does not constitute an 'indication', (Art.16b) and Spirigera oxycolpos ~~LENIRICH~~ therefore does not satisfy Art.12 and is not an available name. SUESS's description is the first to satisfy the conditions of availability and he is here credited with the authorship.

The originals of SUESS pl.1 figs. 1-12,14,15,17-20, of which 11-20 are polished sections, are preserved in the Geol.Bundes.Vienna, and the specimen depicted in figs.1-4 is selected as lectotype. It is refigured here on pl.13 fig.1.

Dimensions of Lectotype:

Length 45mm., breadth 47.1mm., thickness 27.2mm.

Type Locality:

SUESS gave the source of his specimen as the 'Kössener Schichten von Kössen'. This locality lies in the Lofer Graben between Reit im Winkl and Kössen on the Bavarian - Austrian border. Topotypic specimens are still obtainable.

Range and Distribution:

Norian of the Caucasus and Crimea; probably also of the Northern Alps (BITTNER 1890 p.273); possibly Slovakia (Stratenska hornatina).

Rhaetian of the Northern Alps, Slovakia (Hybe), N.W.Rumania (Apuseni Mts.).

Diagnosis:

Outline transversely oval. Otherwise as genus.

Description:

Oxycolpella oxycolpos is a large athyrid, one of SUESS's specimens (pl.1, figs.10,11) being 60mm. long. It differs from other members of the genus in being transversely oval in outline. The hinge line is short and curved, the lateral margins rounded and the anterior margin barely flattened. The valves are equally convex with a low, broad, markedly incurved ventral beak below which the area is hardly distinguishable. The pedicle opening is extremely small and permesothyrid in position. The delthyrial cover is a single internally deposited plate associated with a delthyrial lining. A broad furrow like sinus divides the pedicle

valve, and if the median accentuation is sharp it may be traced to the umbo. The dorsal fold is less obviously differentiated from the shell curvature and is only distinctive in the anterior part of the valve. The precise form of the sulcus, fold and resultant ligule varies: it may be angular or flattened (see plate 13, figs.4,5b, and a similar variation is seen in other oxycolpelliids (see DAGIS 1963)).

The growth lines on well preserved specimens are coarse and tend to be laminate. Stripping of the surface layer reveals radial striations.

The shell is extremely thick towards the umbones and the lateral cavities are filled with callus, fusing the dental lamellae to the shell wall. The delthyrial cavity is also constricted by callus, which closes the base of the delthyrium with a single plate. In its lower part this plate is medianly ridged, but farther towards the apex of the beak it shares in the thickening of the cavity and serves as the dorsal part of a pedicle collar. Deltidial plates are present but play no apparent role. The teeth are thick and stubby in shallow sockets. The cardinal process is bilobed and luxuriantly developed in contrast to the type genus of the subfamil in which it is very small (see DAGIS 1963 p.121, fig.54) It overlaps the delthyrial cover and invades the obsolete portions of the sockets. Anteriorly the lobes embodied in the massive hinge plate, and serve as inner socket ridges. The crura are incorporated on the inner side of the lobes.

Unfortunately the specimen ground was not taken far enough to expose the jugum, and DAGIS's sections do not show it either. However, ZUGMAYER (1882 text figs.1-3) clearly illustrated the cardinalia following a reinterpretation of his original (1880) figures. Text fig.45 is of ZUGMAYER's reconstruction. The jugum can be seen to be united to form an anteriorly bifurcating saddle, and the jugal stem gives rise to two semicircular, fimbriate accessory lamellae. It is identical in all essentials to Athyris.

ZUGMAYER shows the mantle canal system as saccate rather than pinnate as in Athyris (see WILLIAMS 1956, fig.7). The diductor muscle scars on

the pedicle valve are elongate and run for almost half the length of the valve. Posteriorly they enclose the adductor scar, and have a pattern very similar to Athyris (see PITTMAT 1965 fig.537.4c). The brachial valve shows narrow, elongate anterior and posterior adductor scars. The ovarian impressions are prominent bands on either side of the muscle scars in both valves.

Dimensions of Figured Specimens:

	length	breadth	thickness
13/1	45.4	47.1	27.2
13/2	21.2	21.9	11.1
13/3	15.0	15.3	8.2
13/4	35.2	40.9	20.8
13/5	39.5	41.8	21.3

Material:

Lofer Graben by Reit in Winkl - 30, T.62; Marmorgraben by Mittenwald - 2, T.63; Vorder Mandling, Piesting Tal - 2, T.64; Tarkăița, Apuseni Mts. - 1, T.65.



Text-fig. S.xliv

Serial transverse sections of Oxycolpella oxycolpos (SUSS).
 Rhaetian; Lofer Graben between Reit im Winkl (Bavaria) and
 Küssen (Austria); 47°40'35''N. 12°26'55''E. - 91 St.Johann in
 Tirol. Total length of specimen 35.1mm. PC.Nr.69 Topotype.



Text-fig. S.xlv The cardinalia of Oxycolpella oxycolpos (SUESS) from
ZUGMAYER 1882, p.353.

f - Cardinal process
l - Accessory lamellae
L - Primary lamellae

c - Crura
d,s - Jugal stem
v - Jugal saddle

?Oxycolpella sp.nov.

Plate 10, fig.5

Description:

The single specimen described here is subcircular in outline and equibiconvex in profile. The anterior commissure is rectimarginate with only a very slight tendency to ventral flexure. The beak and pedicle opening are typical of athyrids, with a small, round permesothyridid foramen in an erect beak. The area is narrow but clear and the delthyrium deeply sunken and closed. The shell carries coarse growth lines but is otherwise quite smooth.

Remarks:

This species is possibly related to ?Oxycolpella wreyi SUESS, from the Carnian of New Zealand. The complete specimen described and figured by TRECHMANN (1918 p.231, pl.25, fig.6) shows the resemblance most closely (for others see SUESS in ZITTEL 1864, p.28, pl.7, fig.3; also MARWICK 1953, p.44, pl.1, figs.16,17). The New Zealand species differs in having a strong fold. DAGIS (1963 p.120) suggested that it might belong in Oxycolpella and although the internal structure of both it and the present species is unknown, their external appearance supports this. They certainly belong in the Athyridinae.

Dimensions of Figured Specimen:

	length	breadth	thickness
10/5	22.8	22.5	12.9

Material:

Only one specimen, found loose on the Rhaetian profile at Hybe (Slovakia), is known.

Superfamily Reticulariaceae WAAGEN, 1883

Family Reticulariidae WAAGEN, 1883

Remarks:

This family was placed in the Delthyridacea by IVANOVA (1959 and 1960) and DAGIS (1963), but PITRAT (1965) redistributed the genera in this superfamily and recognised the Reticulariaceae for the first time. As the most recent classification this is adhered to here.

Genus Mentzelia QUENSTEDT, 1870

- 1870 Mentzelia QUENSTEDT, p.522
- 1877 Mentzelia QUENSTEDT; DALL, p.47
- 1890 Gruppe Mentzelia; BITTNER, p.291
- 1894 Mentzelia QUENSTEDT; HALL and CLARKE, p.34
- 1963 Mentzelia QUENSTEDT; DAGIS, p.78
- 1965 ?Mentzelia QUENSTEDT; PITRAT, p.727
- non 1940 Mentzelia QUENSTEDT; DOUGLAS, p.332

Type species:

Spirifer Mentzeli DUNKER, 1851, p.287, pl.34, figs.17 - 19, OD.

Range and Distribution:

Middle and Upper Triassic of Western and South East Europe, the Caucasus and Himalayas. Possibly the Liassic of Swabia.

DOUGLAS (1940), in a discussion of the relationship of the genera in the Martiniidae, described and figured what he supposed to be a Mentzelia species, M. persica from the Permian of Iran. He assigned it to Mentzelia solely because of its 'strong median septum' and 'stout dental lamellae'. Unfortunately this emphasis on internal structure overrode any consideration of the external form for the massive, incurved beak, indistinctly limited area and the smooth shell are quite unlike known members of the genus. Therefore DOUGLAS's record of Mentzelia in the Permian is not accepted. His species probably belongs in Martinia.

Diagnosis: (Internals after DAGIS 1963)

Slightly ventri-biconvex. Hinge line shorter than the greatest width; lateral and anterior margins smoothly rounded. Area apsacline, surface with growth lines only; beak pointed, recurvate; beak ridges sharp. Delthyrial cover indicated but not known. Fold and sulcus may be present, may be costate. Bears dense spinules. Impunctate.

Ventral septum long, may be united with low dental lamellae. Inner hinge plates short. Cardinal process striate. Jugum divided.

Remarks:

PITRAT (1965) doubtfully placed Mentzelia in the Martiniidae, probably being misled by DOUGLAS (1940), for he included other spinose genera in the Reticulariidae and members of the Martiniidae are known to lack both spines and deltidial plates. Although Mentzelia may therefore be removed from the Martiniidae and placed with Reticularia the subfamilial link suggested by DAGIS (1963) seems too strong. Reticularia is a lower Carboniferous genus and its relatives have not so far been recognised outside this system, and here Mentzelia is referred only to the Reticulariidae.

The specimens illustrated by QUENSTEDT (1871) as Spirifer cf. verrucosus (pl.54, figs. 117, 118), Spirifer verrucosus villosus (fig.119) and Spirifer verrucosus (figs.138 - 141) from the Lias delta and gamma of Swabia have a microsculpture and shell shape suggesting that they belong to Mentzelia.

Mentzelia cf. M. glabra DAGIS, 1963

Plate 14, figs. 1,2

?1963 Mentzelia glabra DAGIS, p.79 pl.8 figs. 3-5Diagnosis:

Shell not costate; fold and sulcus shallow, anterior commissure flexed. Otherwise as genus.

Description:

The two specimens here described are of a medium sized member of the genus. The hinge line is shorter than the greatest width, and the lateral and anterior margins are smoothly rounded. In lateral profile the pedicle valve is the more convex with a pointed recurved beak. The area, bearing fine growth lines, is broadly triangular and sharply delimited from the lateral slopes. Ledges border the delthyrium and by analogy with Mentzeliopsis cf. M. meridialis (plate 10, figs.6,7) indicate the presence, during life, of a delthyrial cover.

The sulcus in the brachial valve is very shallow, though long and traceable for the length of the valve as a median flattening. The corresponding brachial fold is hardly distinguishable from the lateral shell curvature.

The microsculpture is well preserved on both specimens and consists of dense 1mm. spinules which SCHAUROTH (1855) observed to be as long as 4mms. in the type species. On breaking the spinules leave a pustulose surface, which clearly encroaches on the area in one specimen. Removal of this layer reveals the fine pores of QUENSTEDT's (1871) fig.60a, which he incorrectly interpreted as punctation (see DAGIS 1963). Growth lines are coarse near the anterior margin.

Remarks:

In the absence of DAGIS's distinction of a Norian species, the writer would have had little hesitation in referring these specimens to DUNKER's M. mentzeli which occurs widely in the Middle Triassic. DAGIS stated that his species differs in having a 'more rounded shell form, less inequivalveness, as a rule shorter hinge line with more strongly

rounded angles and considerably larger dimensions' (N.L. transl.). Whether, in fact, the character of DAGIS's eleven specimens from only two localities is sufficient to support their exclusion from the considerable range of forms shown by BITTNER (1890 pl.24 figs. 1-28) is uncertain.

Dimensions of Figured Specimens:

	length	breadth	thickness
14/1	18.2	19.9	11.0
14/2	23.1	24.0	14.9

Material:

2 specimens both found loose associated with typical Rhaetian species on a forest path, Hohe Mandling by Waldegg, 630-670m, 47°53'45''N. 33°39'55''E.

?Mentzelia praecursor (ZUGMAYER), 1880

Plate 14, fig.3

- 1880 Spiriferina praecursor ZUGMAYER, p.25, pl.4, figs. 4,5
 ?1890 Spiriferina dernoeensis BITTNER, p.284, pl.24, fig.12

Holotype:

ZUGMAYER's specimen is preserved in the Pal.Inst.Univ.Vienna, and is refigured here on plate 14, fig.3.

Dimensions of Holotype:

Not measurable.

Type locality:

ZUGMAYER gave the source of his figured specimen as 'Kaisersteffel'. This lies near Waldegg in the Piesting Tal, Lower Austria, and yielded no topotypes when visited.

Remarks:

The writer has been unable to find any material certainly referable to this species and only the holotype of ZUGMAYER's few specimens survives.

ZUGMAYER included the species in his 'Tripartitae', implying, but not mentioning dental lamellae. They are not visible on the holotype, although a ventral median septum is distinguishable. If dental lamellae are indeed absent then BITTNER's suggestion (1890 p.284) that it is a smooth Sinucosta subtilicostata, which he figures with clear dental lamellae, is ruled out. A relationship with 'Spiriferina' dernoeensis from the late Norian of Drnava, with its marked median septum, seems more likely. The writer's sole pedicle valve of this species shows a similar beak character, smoothly rounded lateral slopes and small area. It is impunctate.

The generic status of the species is doubtful and its assignation to Mentzelia is provisional.

Genus Mentzeliopsis TRECHMANN, 1918

- 1918 Mentzeliopsis TRECHMANN, p.229
 1953 Mentzeliopsis TRECHMANN; MARWICK, p.35
 1963 Mentzeliopsis TRECHMANN; DAGIS, p.75
 1965 ?Mentzeliopsis TRECHMANN; PITRAT, p.714

Type species:

Mentzeliopsis spinosa TRECHMANN, 1918, p.230, pl.23, figs.11-16; OD.

Range and Distribution:

Ladinian of New Zealand.

Norian of the Caucasus and N.E.Siberia.

Rhaetian of the Northern Alps.

Included Species:

Apart from the type, found in the Ladinian of New Zealand, three other species have been described:

M.horrida TRECHMANN, 1918 p.230, pl.23, figs.17,18 from the same locality as the type and which MARWICK (1953) could not separate from it.

M.rotunda TUCHKOV, 1956 p.180, pl.1, fig.3

M.meridialis DAGIS, 1963 p.76, pl.7, fig.10, pl.8, figs.1,2, from the Norian of N.E.Siberia and the Caucasus respectively.

Diagnosis:

The genus is fully diagnosed and sections are given in DAGIS (1963).

Remarks:

Mentzeliopsis was included in the Spiriferinidae by PITRAT (1965) but the writer prefers to follow DAGIS (1963) who stressed its relationship to Mentzelia and placed it in the Reticulariinae. The reservation regarding the use of the subfamily, expressed when discussing that genus, also applies here.

Mentzeliopsis cf. M.meridialis DAGIS, 1963

Plate 10, figs.6,7.

?1963 Mentzeliopsis meridialis DAGIS, p.76, pl.7, fig.10, pl.8, figs.1,2

Description:

The two specimens are medium sized members of the genus. The hinge line is shorter than the greatest width and both the lateral and anterior margins are smoothly rounded. The brachial valve is shallow and the pedicle valve semipyramidal with a pointed beak only slightly recurved apically. The catacline area is sharply delimited and flat with clear growth lines and fine pores. On the delthyrial margins are two ledges attached to which, on one specimen, are conjunct deltidial plates open at the base of the delthyrium.

Both the fold and sulcus are well developed and smoothly transitional to the lateral slopes. The ligule is correspondingly high and gently rounded.

A dense layer of ~~thin~~ spinules are present on the shell and leave a pustulose surface on breaking. Minute pores are visible between the pustules.

The internal structure has not been examined.

Remarks:

The two specimens representing this species are clearly very similar to those figured by DAGIS (1963) as M. meridialis, but are very much smaller and pending further investigation are only provisionally referred to it.

The nature of the fine pores noted in the description is uncertain. DAGIS did not comment on them although he figures sections of a specimen with apparently well preserved shell.

Dimensions of Figured Specimens:

	length	breadth	thickness
10/6	18.4	25.6	18.6
10/7	18.8	27.7	18.9

Material:

Only two specimens of this species were found, both in disturbed shale with Oxycolpella oxycolpos in Marmor Graben on the right bank of the Isar, north east of Mittenwald, Bavaria.

SYSTEMATIC PALAEONTOLOGY

3

TEREBRATULIDA

'... for Nondescript, ... read Terebratula ...'

Erratum in FRANCIS (1859).

ERRATUM

For lines 19 and 20 page 264 - 'by MAKRIDIN (1964), who established the Lobothyrinae and the Loboidothyrinae' read 'by MAKRIDIN (1964), who established the Lobothyridinae (nom.correct. pro Lobothyrinae MAKRIDIN, 1964) and the Loboidothyridinae (nom.correct. pro Loboidothyrinae MAKRIDIN, 1964).

Suborder Terebratulidina MUIR-WOOD, 1955

Superfamily Zeilleriacea ALLAN, 1940

Family Zeilleriidae ALLAN, 1940

Remarks:

No subfamilial divisions are at present recognised in the Zeilleriidae. The early members of the family lie in the Middle Triassic and no lines of descent have yet been determined. Indeed major differences still exist regarding the origin of the zeilleriaceans as a whole: STEHLI (1956) believed them to be descended from the Cryptonellidae, and DAGIS (1963) from forms possessing a centronelliform loop.

Genus Zeilleria BAYLE, 1878

- 1878 Zeilleria BAYLE, expl. to pl.8, figs.11, 14; and pl.9, figs.5-13
 1879 Zeilleria BAYLE; DOUVILLÉ p.91
 1879a Zeilleria BAYLE; DOUVILLÉ p.275
 1886 Cornuta-Sippe, ROTHPLETZ (partim), p.83
 1919 Groupe de Z.(M.)perforata et de Z.(M.)numismalis, ROLLIER, (partim)
 1919 Groupe de Z.(M.)cornuta, ROLLIER p.296 p.280
 1965 Keratothyris TULUWEIT, p.76
 1965 Zeilleria BAYLE; MUIR-WOOD p.821
 ---- Waldheimia auctt. (non BRULLÉ 1846)(partim)

Type species:

Terebratula quadrifida LAMARCK, 1819; SD. DOUVILLÉ, 1879 p.275
 (= Terebratula cornuta J.de C.SOWERBY, 1824, p66; see DAVIDSON 1850 p.441, and 1851 p.29, and AGER 1954, p.494, 496-501)

Range and Distribution:

As the genus is at present recognised it is world wide in distribution and ranges from the Upper Triassic to the Lower and possibly the Middle Jurassic.

Included species:

Zeilleria, at times under the guise of Waldheimia, is a catch-all genus in which many dozens of species have been placed. It is greatly in need of division (see Remarks).

Diagnosis:

The genus together with the family is fully diagnosed by MUIR-WOOD (1965 p.821).

Remarks:

AGER (1956 p.1,11) withheld a full discussion of Zeilleria pending a proposed revision by Dr.MUIR-WOOD, but unfortunately this work never appeared. Previously AGER (1954 p.494) had been able on external character to distinguish two groups within the Middle Liassic members of the genus: Group A - Zeilleria sensu stricto, composed of 'rather globose forms with a massive incurved beak, always truncate anteriorly, and usually with indented margins'. Group B consisted of 'much more depressed forms with sharp, non-indented margins, slender sub-upright beaks, and wide interareas', and 'possibly related to Ornithella'.

TULUWEIT (1965) in a revision of the Middle Liassic zeilleriids of North West Germany, cut right across these groups and redistributed several of the species considered by AGER. Although with much the same sort of distinction in mind, he appears to have had a much narrower concept of a useful genus than AGER and erected Keratothyris, with Terebratula cor LAMARCK as type, for 'relatively small species (maximum length 20mm.)' with a 'biconvex stocky' form and 'sharp anterior corners'. He contrasted it (p.77) with Zeilleria which he regarded as having a 'slender shell form' and 'rounded anterior corners', no internal differences were noted.

The numerical weight of TULUWEIT's genus is almost certainly more apparent than real: five of his six new species are founded on less than ten specimens, and many of the total of ten species are very proximate stratigraphically. The writer believes that considerably greater differences are needed than were given by TULUWEIT for the erection of genera and species in as variable a group as the terebratuloids, and that there are no reliable features, either external or internal, which might be accepted as distinguishing Keratothyris from Zeilleria. Keratothyris is therefore placed in synonymy with Zeilleria.

Kolymithyris established by DAGIS (1965 p.148) from the Carnian of Siberia and characterised by a prominent cardinal process, may well prove to be the focus of a group still recognisable in the Jurassic. 'Z'.subnumismalis from the Middle Liassic, placed by AGER in his Group B and by TULUWEIT in Cincta, is probably a late member of this genus.

The monotypic Austrilleria gen.nov. also has a cardinal process, but less luxuriant than Kolymithyris and lying on an otherwise typical zeilleriid hinge plate. This feature was also found by DAGIS in his genus Aulacothyroides which can be separated from Austrilleria through its dorsal sulcation. These two genera are certainly closely related and may well form the basis of a useful subfamily within the Zeilleridae. Zeillerina in the Bathonian is the only other zeilleriid genus known to have a cardinal process and it may be related to the Triassic genera.

All the Rhaetian species described below are only provisionally assigned to Zeilleria. None of them have the strangulate commissure of the type species and so fall in AGER's group B. Division of the genus along the lines suggested by AGER is very evidently necessary but must be based on a broad ranging study of the Jurassic zeillerids and is inappropriate here.

'Zeilleria' austriaca (ZUGMAYER), 1880

Plate 14, figs.4-8; text-figs. S.xlvi,xlvii;text-plates S.12, S.13

- 1880 Waldheimia austriaca ZUGMAYER, p.17, pl.17, figs.12-14
 1890 Waldheimia austriaca ZUGM.; BITTNER, p.279
 ?1892a Waldheimia cfr.austriaca ZUGM.; BITTNER, p.79, pl.4, figs.4,5
 ?1895 Waldheimia (Zeilleria)aff. austriaca ZUGM.; BITTNER, p.250
 ?1917 Waldheimia (Zeilleria)cf.austriaca ZUGM.; GOEPPEL, p.121
 ?1932 Zeilleria austriaca ZUG.; MOISSEIEV, p.599
 1956 Zeilleria austriaca ZUGMAYER; TUCHKOV, p.115, pl.1, fig.5.
 1958 Waldheimia (Zeilleria) austriaca ZUGMAYER; MAHEL, p.150
 non 1927 Waldheimia austriaca ZUGMAYER; MOISSEIEV, p.749, pl.23, figs.4-7

Lectotype:

The originals of ZUGMAYER pl.2, figs.12-14 are preserved in the Pal.Inst.Univ.Vienna, and that of fig.13 is here selected as lectotype, and refigured on plate 14, fig.4.

Dimensions of Lectotype:

Length 28.0mm., breadth 24.8mm., thickness 12.3mm.

Type Locality:

'Kaisersteffel' by Waldegg, Piesting Tal, Lower Austria. Specimens may still be collected there.

Range and Distribution:

Norian of Slovakia (Drnava, Stratenska hornatina), N.E.Siberia, possibly N.E.Turkey and the Crimea.

Rhaetian of the Northern Alps (Vienna area).

Diagnosis:

Compressed; lateral and anterior margins rounded, slight dorsal flexure. Beak suberect. Crural bases wedge shaped, lying on hinge plate; inner hinge plate persistent. Septum high, long. Loop long, laterally compressed.

Description:

'Zeilleria' austriaca is a large, slightly ventri-biconvex zeilleriid. In posterior view the valves are regularly and almost equally convex and this feature is useful in identifying damaged specimens. The lateral commissure is gently flexed dorsally, but there is no trace of a fold or sulcus. The beak is sub-erect and the beak ridges apically sharp, rounding and passing smoothly into the curvature of the lateral margins. The pedicle foramen could not be seen on the specimens examined and it is evidently very small. Striations are present on well preserved internal casts but are by no means restricted to this species and are not diagnostic.

Slender dental lamellae bound the almost circular delthyrial cavity. The teeth are long, laterally inserted and peg like in transverse section. The inner socket ridges are strongly developed on the borders of the shallow hinge plate, and incorporate the wedge shaped crural bases on their ventral surface. There are no outer hinge plates. Apically the inner hinge plate is connected with the long, tall septum, becoming flat and persisting anteriorly. The crural processes are descendent. The loop extends for 80.1 of the total length in the ground specimen and is laterally compressed (see text-fig. S.xlvii).

Remarks:

Although MOISSEIEV (1932) and TUCHKOV (1956) described supposed 'Z'.austriaca' from the Crimea and North East Siberia respectively, DAGIS (1963 and 1965) made no mention of the species, apart from including MOISSEIEV's 1927 record in Rh.taurica.

GOETTEL's report of the species at Hybe (1917) must be considered unproven. He collected only two poorly preserved specimens and figured neither. It seems probable that his identification was based to a large extent on the presence of radial striations which cannot be regarded as diagnostic of 'Z'.austriaca'.

BITTNER's record at Drmava (1890) has been confirmed by personal collecting, but it is not now to be found in the numbers he reported. His Turkish specimens (1892 - 1895) have not so far been re-investigated and the true nature of the curious centronelliform loop shown in his 1892

sections is still a puzzle. Almost certainly it was caused by some freak of preservation.

Dimensions of Figured Specimens:

	length	breadth	thickness
14/4	28.0	24.8	12.3
14/5	31.2	24.7	13.1
14/6	27.7	24.1	12.7
14/7	13.1	12.5	6.2
14/8	10.8	11.2	5.5

Material:

'Brand' Piesting Tal - 13, Pal.Inst.Univ. Vienna, ZUGMAYER colln.;
loc.cit. - 3, B.M.N.H., B 39207; loc.cit. - 10, T.98; 'Hirtenberg,
Triesting Tal - 5, B.M.N.H., B 39191; loc.cit. - 5, T.99; Ober
Kaisersteffel, Piesting Tal - 3, T.100.

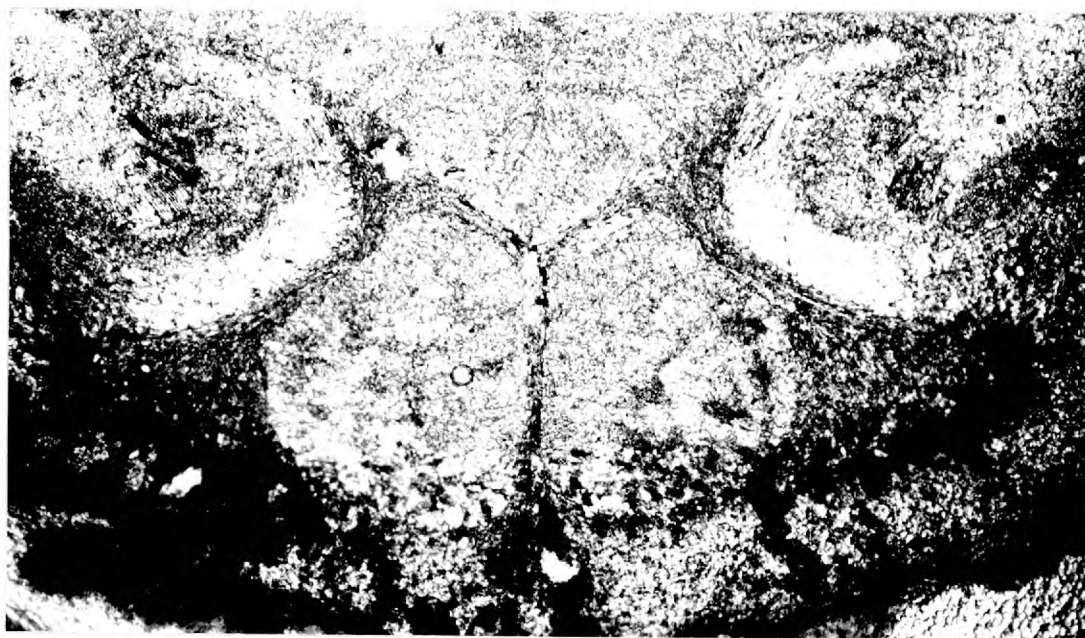
TEXT-PLATES S.12 and S.13
Zeilleria austriaca (ZUGMAYER)

Text-plate S.12

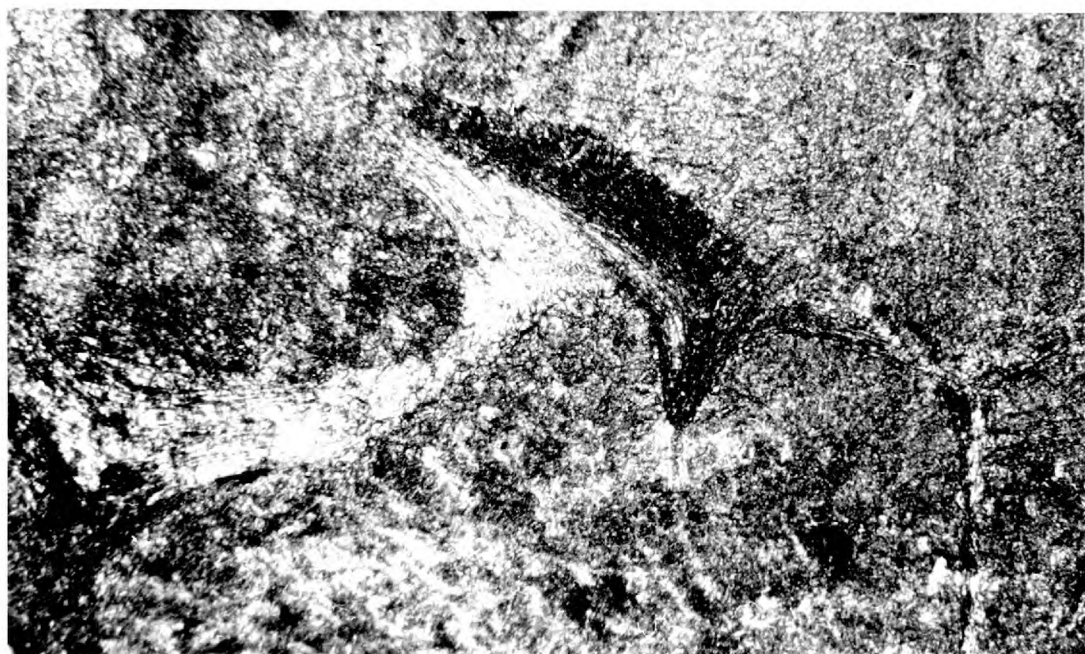
Transverse section of the brachial umbo of Zeilleria austriaca, showing the teeth inserted in the sockets, the crural bases and the delicate hinge plate and median septum. Detail of section 2.5, text-fig. S.xlvi xl0

Text-plate S.13

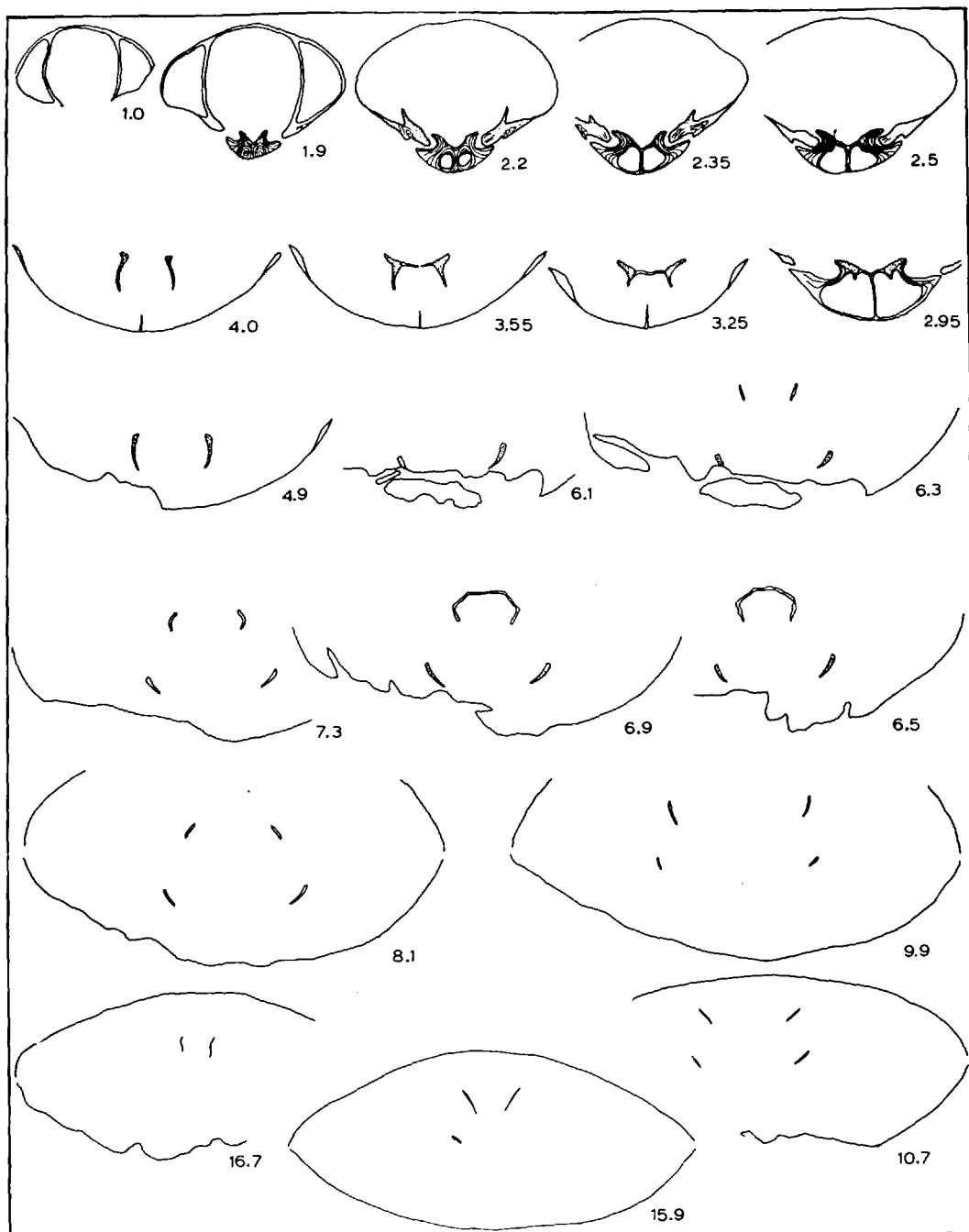
Transverse section of part of the apical structure of the brachial valve of Zeilleria austriaca, showing the position of the crural base on the inner socket ridge. Text-fig. as above, section 2.95 xl5



Text-plate S.12

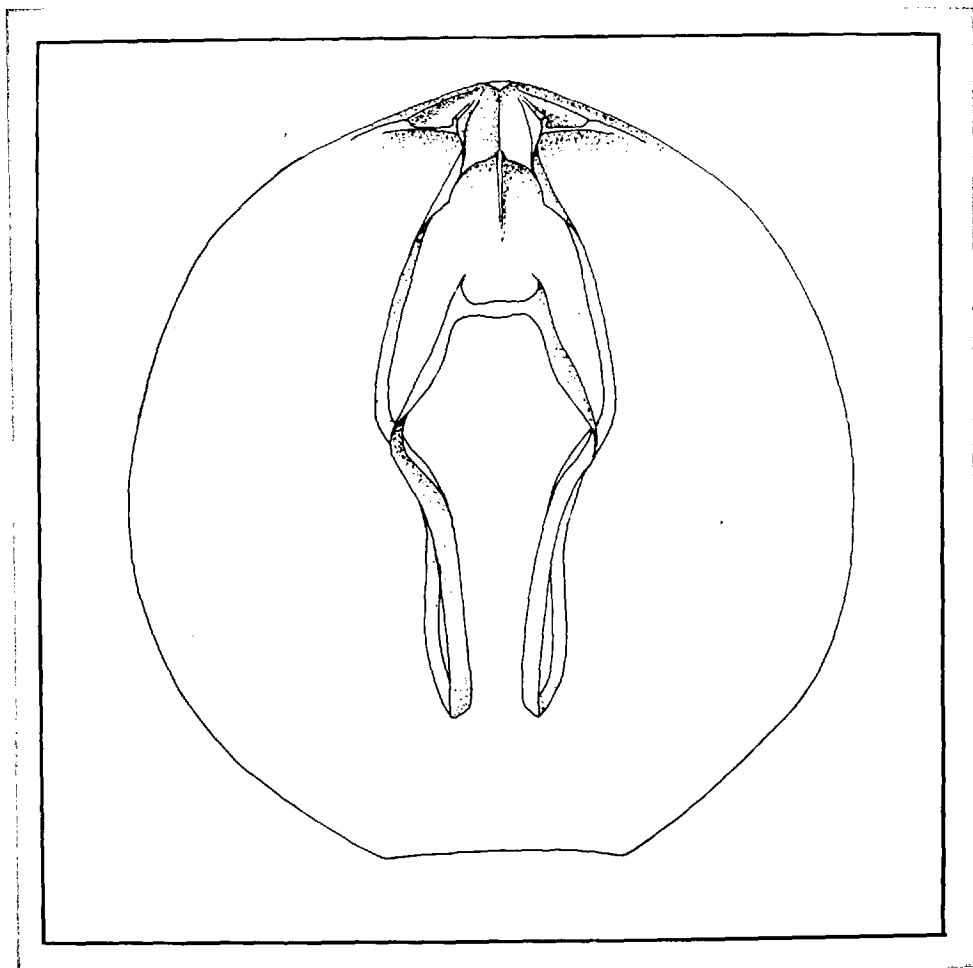


Text-plate S.13



Text-fig. S.xlvi

Serial transverse sections of *Zeilleria austriaca* (ZUGMAYER).
 Rhaetian; Brand by Piesching, Piesting Tal, Lower Austria;
 47°51'45"N. 33°43'45"E. Locality indicated on Hohe Wandgebietas,
 Geol.Bundes.Vienna. x4 Loop traceable to 16.9.mms. Total
 length of specimen 20.9.mms. PC.Nr.46 Loop reconstructed on
 text-fig.xlvii Topotype.



Text-fig. S.xlvii

Reconstruction of the loop of Zeilleria austriaca (ZUGMAYER).
Made from the sections shown in text-fig. S.xlvi.

'Zeilleria' elliptica (ZUGMAYER), 1880

Plate 15 figs.4-8; text-figs.S.xlviii,xlix;text-plate S.14

1880 Waldheimia elliptica ZUGMAYER, p.17, pl.2, figs.6-8,10.

1890 Waldheimia elliptica ZUGM.; BITTNER, p.279.

1917 Waldheimia (Zeilleria) elliptica ZUGM.; GOETTEL, p.120, pl.7, fig.12.

1958 Waldheimia (Zeilleria) elliptica ZUGMAYER; MAHEL, p.150

Lectotype:

The originals of all ZUGMAYER's figures are preserved in the Pal. Inst.Univ.Vienna, and that of pl.2, fig.6 is here selected as lectotype and refigured on pl.15 fig.6.

Dimensions of Lectotype:

Length 22.5mm., breadth 20.0mm., thickness 13.8mm.

Type Locality:

'Kitzberg', by Neusiedl, Piesting Tal, Lower Austria. Material is still obtainable here.

Range and Distribution:

Norian of Slovakia (Drnava, Stratensks hornatina), and the Caucasus.

Rhaetian of the Northern Alps (Vienna area), N.W.Rumania (Apuseni Mts.).

Diagnosis:

Medium sized zeilleriid, lateral and anterior margins rounded. Beak erect, pointed; beak ridges strong. Anterior commissure broadly and flatly flexed. No fold or sinus. Dorsal septum tall, long, united with hinge plate. Crural bases wedge shaped, lying on socket ridges. Complete loop not known.

Description:

'Zeilleria' elliptica is a medium sized zeilleriid varying in outline from elongate oval with smoothly rounded lateral and anterior margins, to somewhat angularly elliptical with a flattened anterior, and obtusely bowed lateral margins. The anterior commissure has a broad, flat dorsal flexure, but there is no trace of a sinus or fold. A marked blunting of the anterior occurs in older specimens and is very evident on ZUGMAYER's originals. The beak is erect and pointed, and has strong, only slightly

rounded beak ridges. The pedicle opening is large and mesothyrid in position.

The dental lamellae are well developed, and some thickening of the ventral wall of the delthyrial cavity may occur. DAGIS (1963 p.193) noted that the umbones of individuals collected from sandy limestones were considerably thickened with callus, presumably in contrast to those from reef limestones. Wedge shaped crural bases lie on the inner socket ridges. The septum is tall and united with the hinge plate and runs for about a third of the length of the valve. The crural processes are descendent, but further details of the loop were not preserved in the specimens sectioned, nor were they shown by DAGIS, (1963 text-fig.92). The curious 'supplementary plate' covering the 'septalium' described by DAGIS (1963) in both this species and 'Z'.bukowski, was not observed.

Remarks:

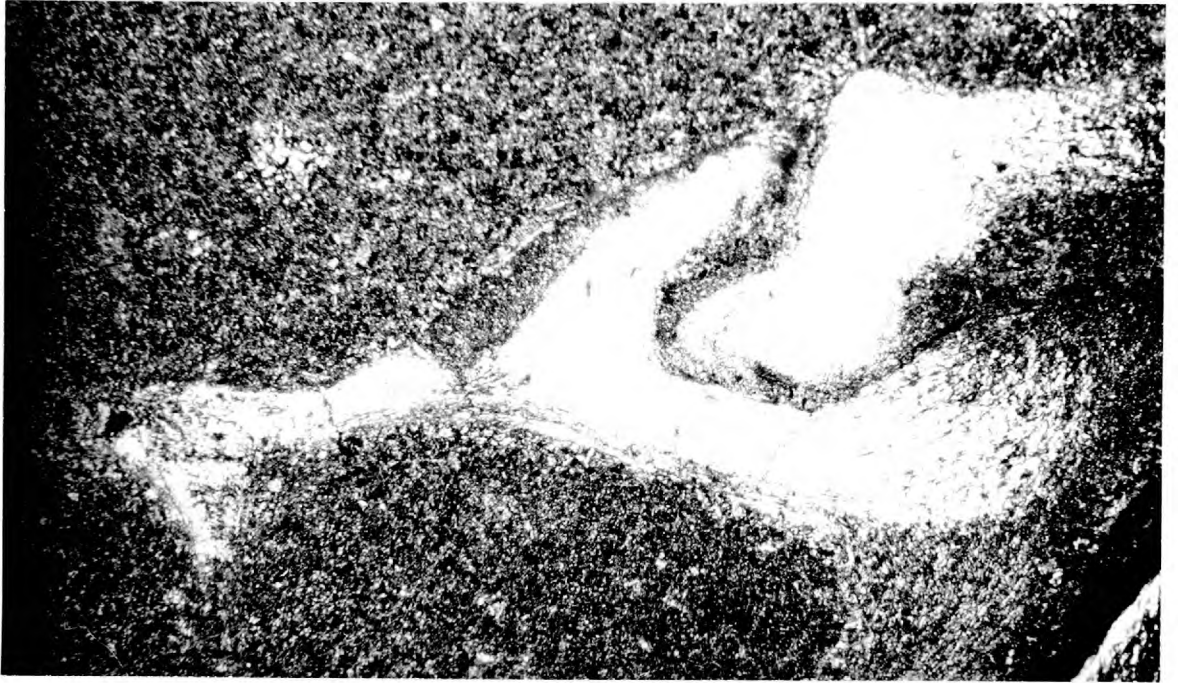
Personal collecting has confirmed the occurrence of 'Z'.elliptica in the Norian of Drnava, and the specimen figured by BITTNER (1890) as T.piriformis SUESS var. is probably also of this species. It is included in the synonymy above.

Dimensions of Figured Specimens:

	length	breadth	thickness
15/4	15.5	13.1	8.0
15/5	15.0	12.7	7.5
15/6	22.5	20.0	13.8
15/7	22.8	20.3	11.4
15/8	23.7	19.0	13.5

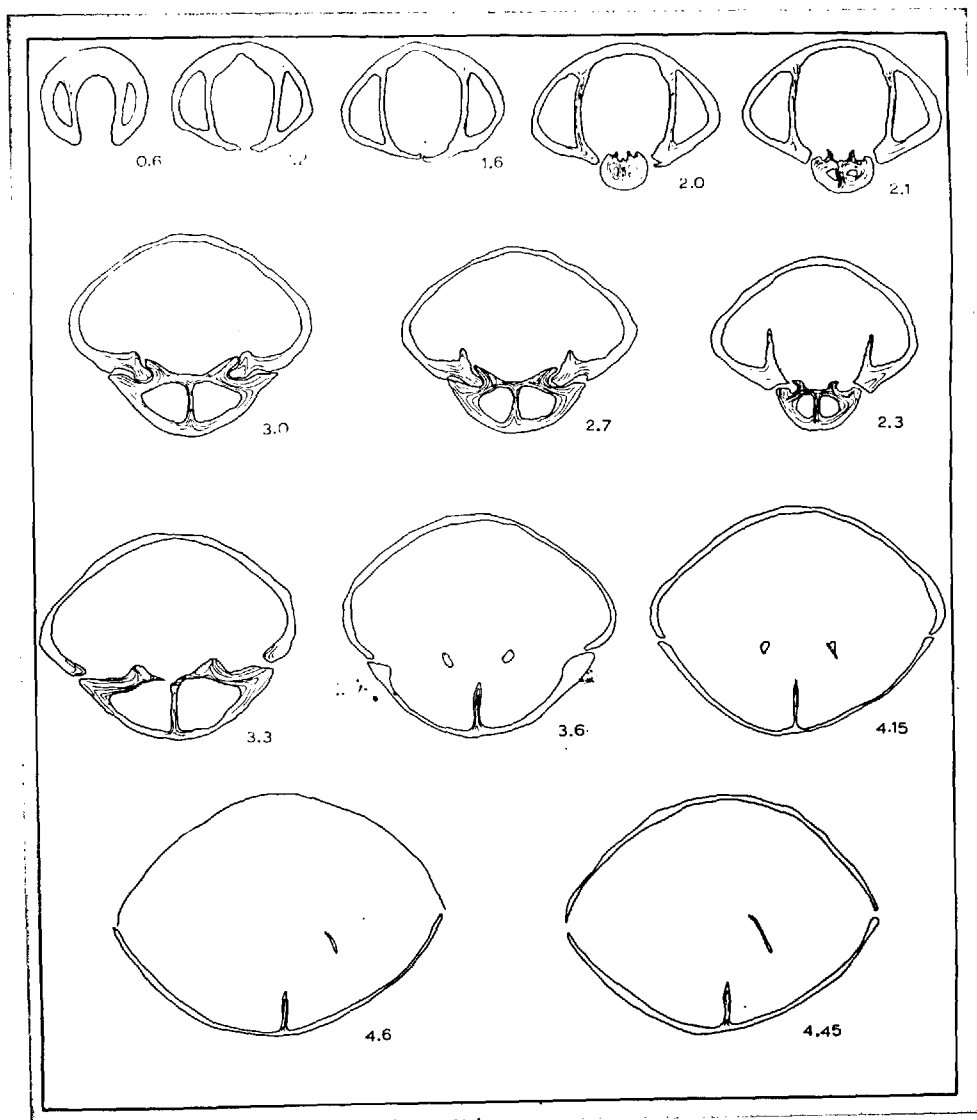
Material:

Kitzberg (type locality) - 10; Drnava - 3.



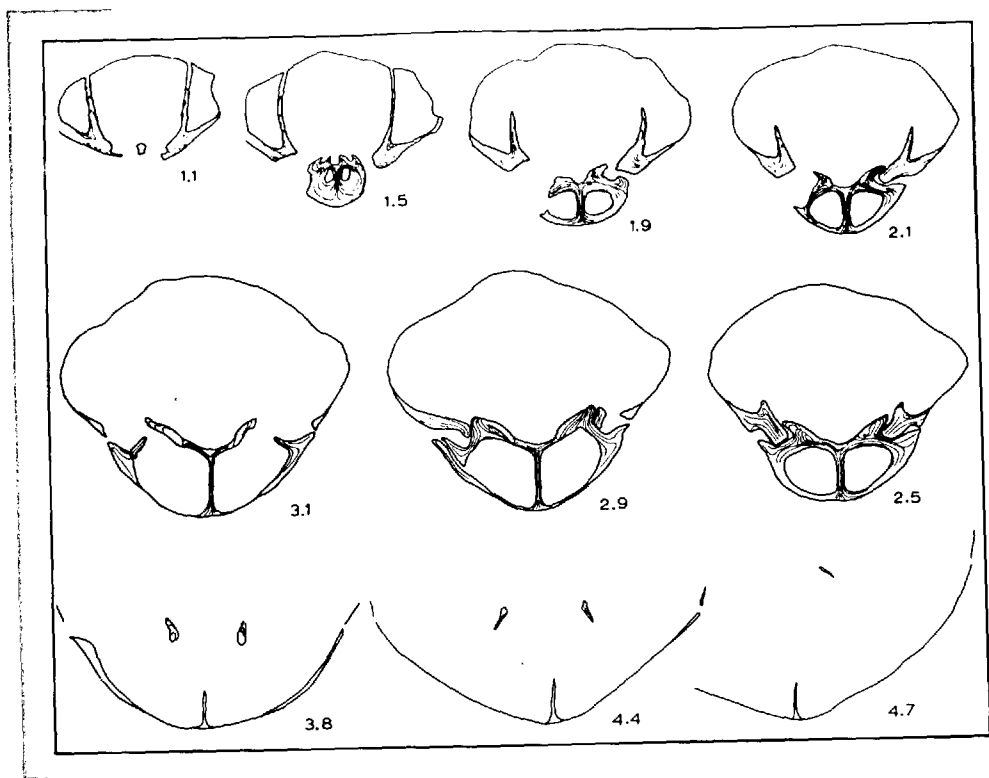
Text-plate S.14

Transverse section of the right hand part of the hinge plate of 'Zeilloria' elliptica, showing the deep socket, a tooth and the crural base lying on the inner socket ridge. Detail of section 3.0, text-fig. S.xlviii x15



Text-fig. S.xlviii

Serial transverse sections of Zeilleria elliptica (ZUGMAYER). Rhaetian; specimen from the Geol.Bundes.Vienna - 8 19/3 'Kössener Schichten. Rechtes Gehänge der Kaltenganges bei Wallegg, Kaiser N.W.hinab in den Kaltengang'. This locality lies in the Piesting Tal, Lower Austria. x5 Loop traceable to 4.7mm. Total length of specimen 15.5mm. PC.Nr.42.



Text-fig. S.xlix

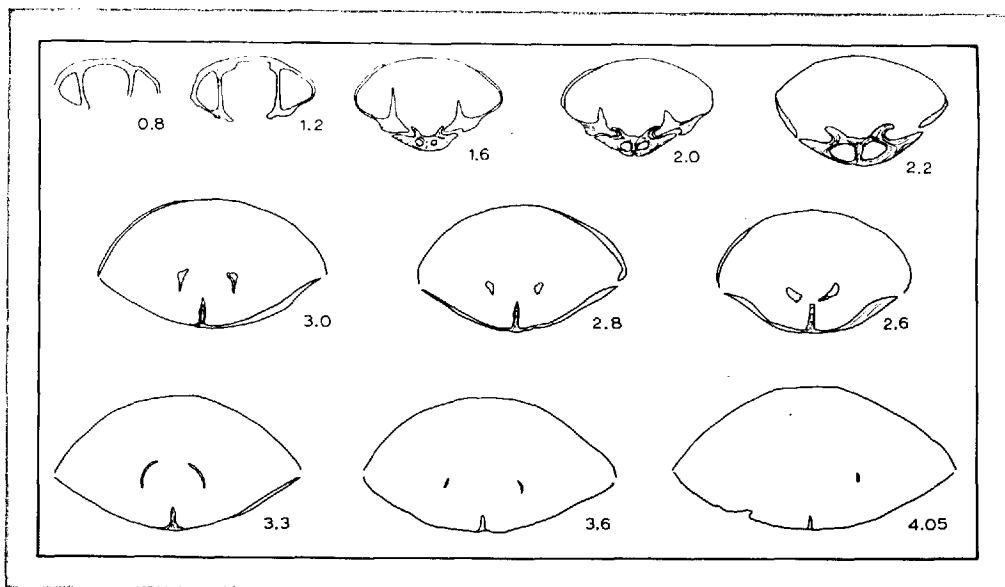
Serial transverse sections of Zeilleria elliptica (ZUGMAYER)
 Rhaetian; Kitzberg by Neusiedl, Lower Austria; 47°53'10''N.
 33°38'5''E. Locality indicated on Hohe Wandgebietes, Geol.Bundes.
 Vienna. x5 Loop traceable to 5.2mm. Total length of
 specimen 16.5mm. PC.Nr.57 Topotype.

'Zeilleria' cf. 'Z'.elliptica (ZUGMAYER), 1880

Plate 16, figs.1-4; text-fig.S.1

Remarks:

Ten specimens from Lahn by Lermoos, Austria, associated with Austriirhynchia cornigera, and one from the Hohe Mandling, Piesting Tal, Lower Austria, are both internally and externally reminiscent of 'Z'.elliptica. However they have a greater relative width and thus lack the ellipticity of outline from which that species gains its name. In particular young specimens are subcircular and contrast markedly with their opposite numbers. Additionally both valves are somewhat flatter than those of 'Z'.elliptica. The occurrence of a specimen in Piesting Tal far from Lermoos, suggests its distinctness as a species, but in view of the very few individuals involved in this variable group, it seems best to delay the creation of a new species until more localities have yielded specimens.

Text-fig. S.1

Serial transverse sections of 'Zeilleria' cf. 'Z'.elliptica (ZUGMAYER).
 Rhaetian; Lahn by Lermoos, Austria; 47°26'0''N. 28°31'0''E. 116 (Pr)
 Telfs. x4 Loop traceable to 4.2mm. Total length of specimen 13.2mm.
 PC.Nr.54

Dimensions of Figured Specimens:

	length	breadth	thickness
16/1	11.8	11.9	5.0
16/2	15.0	13.4	8.3
16/3	17.4	16.5	8.8
16/4	16.0	14.2	8.0

Material:

Lahn by Lermoos, Aust. - 10, T.77. Hohe Mandling, Piesting Tal,
forest path 630 - 670m. - 1, 16/3.

'Zeilleria' kitzbergensis sp.nov.

Plate 15 figs.1-3; text-fig.S.11

Holotype:

The specimen shown on plate 15, fig.2 is designated holotype. It is labelled 15/2 in the writer's collection and is to be deposited with a suitable museum.

Dimensions of Holotype:

Length 13.5mm, breadth 11.4mm, thickness 8.5mm.

Type Locality:

Kitzberg by Neusiedl, Piesting Tal, Lower Austria; 47 53'10''N. 33 38'5''E. Locality indicated on Hohe Wangebietes, Geol.Bundes.Vienna.

Range and Distribution:

Only known from the type locality.

Derivation of Name:

From Kitzberg, the site of the type locality.

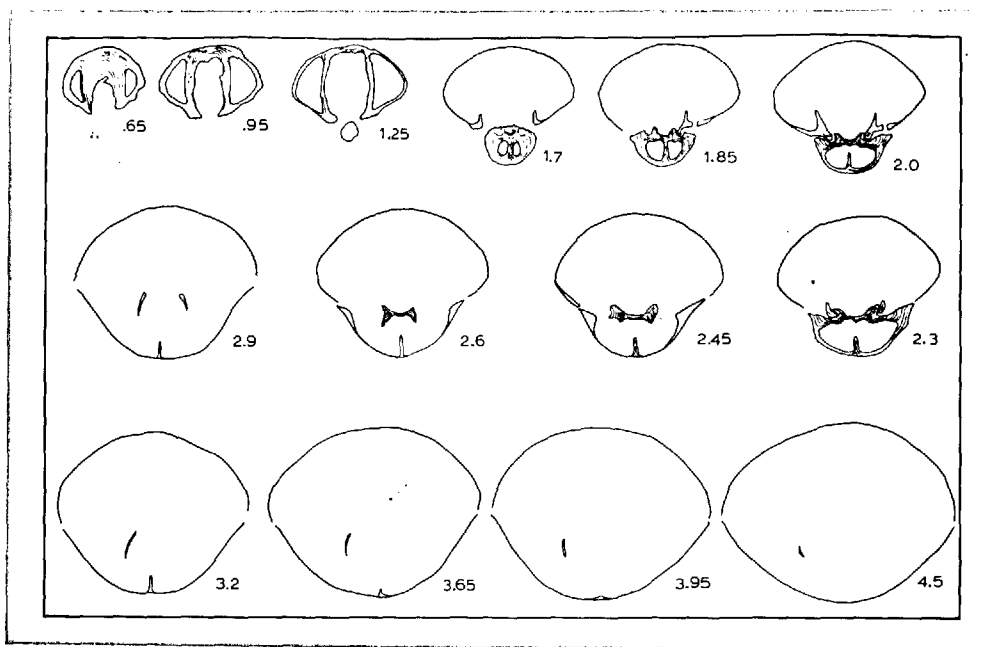
Diagnosis:

Small, robust zeilleriid; equibiconvex; outline rounded, slight anterior flattening. Anterior commissure barely flexed, margins of flexure marked on shell but no fold or sinus. Beak erect, bead ridges moderately rounded. Pedicle foramen mesothyrid in position. Delthyrial cavity thickened. Median septum present. Crural bases rounded, enclosed. Crural processes descendent. Full loop unknown.

Description:

'Zeilleria' kitzbergensis comprises small, equibiconvex, robust zeilleriids, smoothly rounded in outline with some anterior flattening in fully grown individuals. The anterior commissure is slightly and broadly flexed and the margins of the flexure are reflected on the anterior parts of the surface of both valves. The beak is erect, somewhat blunt, and accompanied by moderately rounded beak ridges. The pedicle foramen is small and mesothyrid in position.

The delthyrial cavity is thickened apically, and dental lamellae are present. The median septum is long but only briefly united with the flat inner hinge plate. No outer hinge plates are present and the rounded crural bases are embodied on the inner edge of the socket ridges.



Text-fig. S.1i

Serial transverse sections of 'Zeilleria' kitzbergensis sp.nov. Rhaetian; Kitzberg by Neusiedl, Lower Austria; 47°53'10''N. 33°38'5''E. Locality indicated on Hohe Wandgebietes, Geol.Bundes.Vienna. x4 Loop traceable to 4.65mm. Total length of specimen 12.0mm. PC.Nr.56. Topotype

The crural processes are descendent but the full loop was not present in the specimen ground and its form remains unknown.

Remarks:

Internally this species is closely similar to 'Z'. neusiedlensis but externally they have little in common, and both must await generic clarification until after further research.

Dimensions of Figured Specimens:

	length	breadth	thickness
15/1	13.8	13.1	9.7
15/2	13.5	11.4	8.5
15/3	12.8	10.0	7.0

Material:

Only six specimens are known , all from the type locality.

'Zeilleria' waldeggiana (ZUGMAYER), 1880

Plate 15 figs.5-7; text-fig.S.111

1880 Waldheimia waldeggiana ZUGMAYER, p.18, pl.2, fig.11.

1917 Waldheimia (Zeilleria) waldeggiana ZUGMAYER; GOETEL, p.122, pl.7, fig.11.

Holotype:

ZUGMAYER figured only one specimen and it is now preserved in the Pal.Inst.Univ.Vienna. It is refigured here on plate 16, fig.7.

Dimensions of Holotype:

Length 13.9mm., breadth 13.0mm., thickness 8.0mm.

Type Locality:

'Kaisersteffel' near Waldegg, Piesting Tal, Lower Austria. No specimens were found during collecting here.

Range and Distribution:

Rhaetian of the Northern Alps (Vienna area), Slovakia (Hybe), N.W.Rumania (Apuseni Mts.).

Diagnosis:

Small, subcircular zeilleriid. Beak low, broad; beak ridges sharp. Brachial valve very shallow. Anterior commissure almost rectimarginate; no fold or sulcus. Dental lamellae slender. Median septum joined with inner hinge plate. Crural bases round; crural processes descendent. Loop zeilleriform.

Description:

Zeilleria waldeggiana comprises small, broadly elliptical or subcircular zeilleriids, not apparently exceeding 15mm. in width. In lateral profile the valves are ventri-biconvex; transversely the pedicle valve is regularly convex and dominates the flatter brachial valve, particularly in the more circular specimens. The beak, with its remarkable broadness, is the most characteristic feature of the species, it is low, erect and barely disturbs the curvature of the outline. The beak ridges are sharp and long and clearly delimit the anacline area as far as the lateral margins. The position of the very small foramen was not to be seen on the material examined. The anterior commissure has a slight,

broad, flat dorsal flexure, and older specimens may show some flattening of the anterior outline. There is no trace of a sinus or fold.

The dental lamellae are slender and the laterally inserted teeth are equally delicate. Due to the flatness of the brachial valve the median septum is very low and apically the hinge plate lies on the valve floor. There are no outer hinge plates and the rounded crural bases lie on the socket ridges, giving rise to descendent crural processes. The loop, which is zeilleriform, extends for 60% of the total length in the ground specimen.

Remarks:

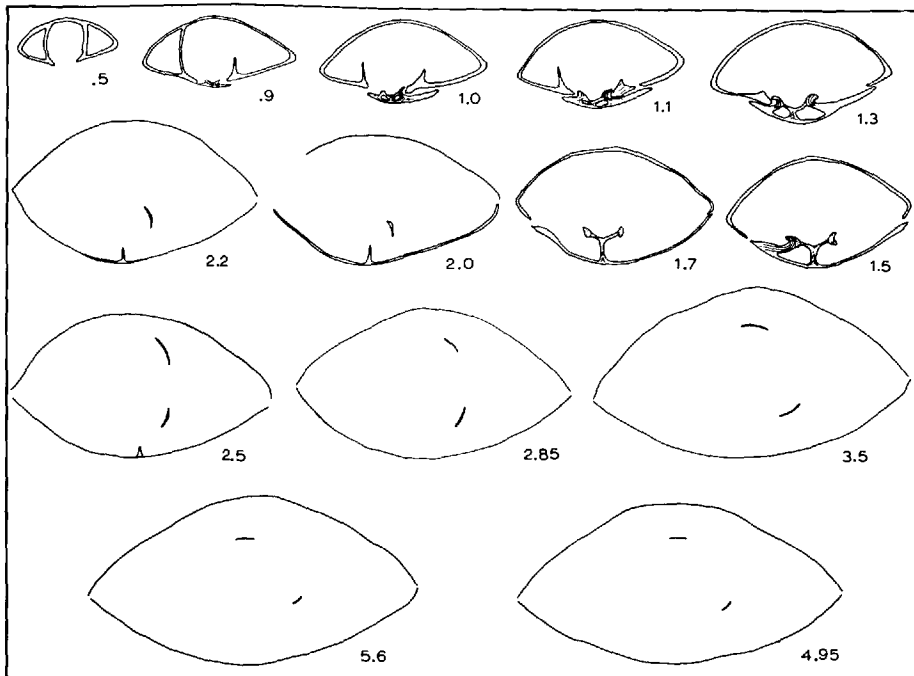
The transverse section given by ZUGMAYER (1880, pl.2, fig.11d.) is somewhat misleading and the structure of the cardinalia is not essentially different from that of typical zeilleriids as DAGIS (1965 p.195) thought might be the case. Only the flatness of the brachial valve causes the dielasmatic appearance of the hinge plate in the most posterior part of the valve.

'Z.waldeggiana is a rare species and has only been found in quantity at the type locality where it appears to be no longer obtainable. Only six specimens were discovered during extensive collecting in the region of the type locality, and its occurrence in both Rumania and Slovakia depends on single specimens, obtained personally in the first case, and by GOETTEL (1917) in the second.

GÜMBEL's name Spirigera nuciformis under which the specimens in the Geol.Bundes.Vienna were labelled, was not accompanied by a figure, but GÜMBEL (1861. p.401) described his species as having a 'sehr bestimmt ausgeprägte Doppelfalte', a description which clearly leaves 'Z.waldeggiana uncompromised.

Dimensions of Figured Specimens:

	length	breadth	thickness
15/5	14.4	13.5	17.5
15/6	11.3	10.2	6.3
15/7	13.9	13.0	8.0



Text-fig. S.lii

Serial transverse sections of 'Zeilleria' waldeggiana (ZUGMAYER). Rhaetian; specimen from the Geol.Bundes.Vienna - 4 Rot 19/3 labelled 'Spirigera nuciformis GUENB. Kössener Schichten. Rechtes Gehänge des Kaltengangs bei Wallegg, Kaiser N.W., hinabin den Kaltengang'. This is almost certainly refers to the type locality. (See Remarks for a note on the naming of these specimens.) x5 Loop traceable to 5.6mm. Total length of specimen 10.1mm. PC.Nr.48 Topotype.

'Zeilleria' neusiedlensis sp.nov.

Plate 16 figs.8-10; text-fig. S.liii

1880 Waldheimia norica SSS; ZUGMAYER, (partim) p.16, pl.2, fig.9

Holotype:

The specimen shown on plate 16, fig.9 is designated holotype. It is labelled 16/9 in the writer's collection and is to be deposited with a suitable museum.

Dimensions of Holotype:

Length 10.7mm., breadth 11.0mm., thickness 6.4mm.

Type Locality:

Kitzberg by Neusiedl, Piesting Tal, Lower Austria. 47 53'10''N. 33 38'5''E. Locality indicated on Hohe Wandgebietes, Geol.Bundes.Vienna.

Range and Distribution:

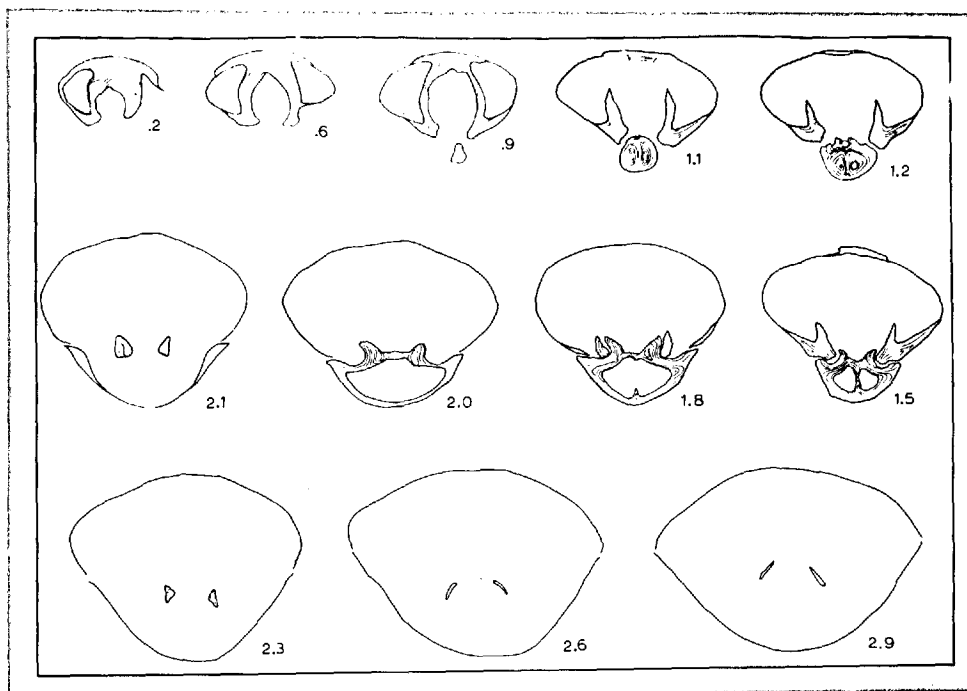
This species is known only from the Rhaetian in the neighbourhood of the type locality. ZUGMAYER's material is from 'Kaisersteffel' and 'Vorder Mandling' in collection.

Diagnosis:

Small zeilleriid; equibiconvex; subpentagonal outline. Brachial valve anteriorly sulcate, no fold whatever in pedicle valve. Beak erect, beak ridges sharp. Delthyrial cavity thickened, dental lamellae strong. Median septum present. Crural bases rounded, enclosed. Crural processes descendent. Form of loop unknown.

Description:

This species comprises small individuals apparently not exceeding 11mm. in width, equibiconvex, and with a markedly dominant brachial convexity in anterior view. In outline the valves are pentagonal, particularly in larger specimens. The anterior commissure shows marked angular deflections bounding a smooth, shallow median sulcation, and this is reflected on the surface of the brachial valve. There is however, no folding of the pedicle valve whatever. The beak is erect, broad and pointed, and accompanied by strong beak ridges delimiting a well developed area. The position of the pedicle foramen was not visible on the material examined.



Text-fig. S.1111

Serial transverse sections of 'Zeilleria' neusiedlensis sp.nov. Rhaetian; Kitzberg by Neusiedl, Piesting Tal, Lower Austria; 47°53'10''N. 33°38'5''E. Locality indicated on Hohe Wandgebietes, Geol.Bundes.Vienna. x4 Loop traceable to 3.0mms. Total length of specimen 9.9mms. PC.Nr.37 Topotype

Ventral thickening is present in the delthyrial cavity which is bounded by rather squat dental lamellae. A short median septum is present and united with the flat inner hinge plate. No outer hinge plates are present and the rounded crural bases are incorporated on the inner edges of the socket ridges. The crural processes are descendent, and narrow. Unfortunately the loop was not preserved in the ground specimen and it remains unknown.

Remarks:

The specimen illustrated by ZUGMAYER (1880) as a young 'Waldheimia' norica certainly belongs here. Despite his fig.9c showing a slight folding of the pedicle valve this is not evident on the specimen itself or any of many others labelled in the same manner in his collection.

Z.kysylrabataensis MOISSEIEV, a rare species in the Rhaetian of the Pamirs, is similar in outline and size to the present species but is easily distinguished by the sulcus in the pedicle valve, and by its flatness.

The distinctive nature of the growth of 'Z'.neusiedlensis if found in other species may well permit the separation of a new genus but for the moment the species is referred to the catch-all genus Zeilleria.

Dimensions of Figured Specimens:

	length	breadth	thickness
15/8	9.1	8.3	5.0
15/9	10.7	11.0	6.4
15/10	11.0	9.3	6.5

Material:

Seven individuals were collected at the type locality and about a dozen are preserved in the ZUGMAYER collection in the Pal.Inst.Univ.Vienna, from 'Kaisersteffel', and 'Vorder Mandling'.

Austrilleria gen.nov.Type species:Waldheimia norica SUESS, 1859 p.46Range and Distribution: (Type species only)Norian of Slovakia (Drnava), the Caucasus and Pamirs.Rhaetian of the Northern Alps, Slovakia, Rumania (Apuseni Mts.) and E.Iran.Diagnosis:

Large biconvex zeilleriids; folding opposite, beak ridges sharp, persistent. Pedicle foramen mesothyrid in position. Cardinal process present; crural bases wedge shaped, crural processes descendent. Median septum long, tall; loop long, zeilleriform.

Included Species:Only the type species is at present assigned to Austrilleria.Derivation of Name:

From Austria, where the type species is common.

Remarks:

Austrilleria is undoubtedly closely related to Zeilleria, the anterior emargination, the opposite folding, beak character and general external aspect of the type species are closely similar to typical members of that genus. However the significance of a bushy, well developed cardinal process within the Zeilleriidae is felt to be great enough to justify the creation of a new genus.

A topotypic specimen of Zeilleria quadrifida (LAMARCK), the type species of Zeilleria, kindly donated by Mr.H.C.PRUDDEN, was ground to confirm that no cardinal process is present in this species.

Austrilleria norica (SUESS), 1859

Plate 17, figs.1-9; text-figs.S.liv-S.lvi; text-plates S.15, S.16

- 1851 Terebratula indentata B.; SCHAFHAUTL, p.415, pl.7, fig.9
 1854 Terebratula cornuta SOWERBY; SUESS, (partim) p.10, pl.3, figs.1-5
 1857 Terebratula Schafh utli (T.identata, SCHAF.); STOPPANI, p.109
 1859 Waldheimia norica SUESS (T.cornuta SOW. SUESS) in HAUER, p.46
 1859 Terebratula Schafh utli WINKLER, p.20
 1861 Terebratula Schafh utli STOPP.; GUMBEL, p.401
 1863 Waldheimia norica SUESS; OOSTER, p.27, pl.10, figs.11-18
 1865 Terebratula norica SUESS; MARTIN, p.253
 1880 Waldheimia norica SSS.; ZUGLAYER, (partim) p.16, pl.2, figs.2-5
 1890 Waldheimia norica SUESS; BITTNER, p.279
 1906 Waldheimia norica SUESS; ARTHABER, pl.50, fig.1
 1917 Waldheimia (Zeilleria)norica SUESS; GOETEL, p.119
 1929 Dielasma sp., DOUGLAS, p.644, pl.44, fig.10
 1963 Zeilleria norica SUESS; DAGIS, p.197

Lectotype and Authorship:

The name Waldheimia norica first appeared in the minutes of a meeting of the Geol. Reichs. Vienna for the 15th. March 1859. HAUER is credited in the index with the authorship of a demonstration, but STUR appears to have been responsible for that part in which Waldheimia norica was included in a faunal list of Rhaetian fossils from Bistritz (now Bystrzy potok in Slovakia). In the absence of further information STUR would be the author. However, the use of SUESS's name after the nom.nov. was certainly intended to indicate that SUESS himself had revised his interpretation (1854) of T.cornuta SOWERBY and coined Waldheimia norica for the Rhaetian species. Therefore SUESS is maintained as the author of Waldheimia norica. This is in full accord with all later usage.

Terebratula Schafh utli WINKLER was also published in 1859, but whatever its order of priority it has been totally unused and if not a junior synonym it may be regarded as a nomen oblitum (ICZN Art.23b).

The originals of SUESS, 1854 pl.3 figs. 1,4,5, are preserved in the Geol.Bundes.Vienna, the remainder are presumed lost. That of fig.4 is here selected as lectotype and refigured on plate 17, fig.1; the original of fig.1 is also figured.

Dimensions of Lectotype:

Length 34.0mm., breadth 27.3mm., thickness 16.4mm.

Type Locality:

Kitzberg by Neusiedl, Piesting Tal, Lower Austria.

Range and Distribution:

As for the genus.

Diagnosis:

Elongate; anterior emarginate, folding strangulate. Cardinal process bushy. Otherwise as genus.

Description:

Austrilleria norica is a large, elongate, commonly equi-biconvex zeilleriid. Emargination of the anterior accompanied by greater or lesser sulcification and strangulate folding are characteristic, but wide variation occurs in the final aspect of the anterior. Similarly the size at which folding begins to develop differs markedly and shells 25mm. long may show no sign of it.

The beak ridges are sharp and long, and the beak itself erect and broad - a useful feature in distinguishing young specimens. The pedicle opening is small and mesothyrid in position. Clearly conjunct deltidial plates close the delthyrium.

Growth lines are prominent on the margins of mature individuals and late growth may result in considerable blunting of the profile (e.g. plate 17, fig.6).

The dental lamellae are slender and the delthyrial cavity is quite free of callus. The teeth are tangentially inserted into deep sockets. A prominent, bushy cardinal process occupies the apical portion of the hinge plate and may spill into the obsolete part of the sockets. Wedge shaped crural bases lie on the outer hinge plates and the strong inner socket ridges, and are clearly limited on their median edges. The crural processes are descendent, and the loop extends for 80% of the specimen length.

Remarks:

Although fully grown members of this species are unmistakable, immature individuals may be confused with both Z.austriaca and R.pyriformis in which case beak character is the most reliable guide to differentiation.

Despite its common occurrence in the Alps and Carpathians, A.norica is remarkably rare in the Soviet Union, only one specimen being known amongst the rich Caucasian Norian fauna and one from the Pamirs (DAGIS 1963).

Dimensions of Figured Specimens:

	length	breadth	thickness
17/1	34.0	27.3	16.4
17/2	25.5	20.5	12.1
17/3	28.8	22.0	16.4
17/4	25.9	20.0	13.0
17/5	36.0	26.4	17.8
17/6	29.3	23.5	17.5
17/7	16.1	14.0	8.0
17/8	17.9	14.0	8.1
17/9	30.8	24.0	17.0

Material:

'Mandling Wald', by Waldegg, Piesting Tal - 8, B.M.N.H., B 39200; Pfannkogel, by Hindelang - 4, B.M.N.H., B 39162; Ober Kaisersteffel, Piesting Tal - 7, T.78; Kitzberg by Neusiedl - 5, T.79; Hirtenberg, Triesting Tal - 2, T.80; Hohe Mandling, Piesting Tal, forest path 630 - 670m. - 4, T.81; Steinplatte by Waidring - 2, T.82; Hybe, Slovakia - 5, T.83; Val Frunsi, Ferice, Arieseni, Rumania - 2, T.84; Tarkaita, Moneasa, Rumania - 2, T.85; Rechtes gehänge der Kaltenganges bei Wallegg' Geol. Bundes. Vienna - 12, 8 rot 19/3.

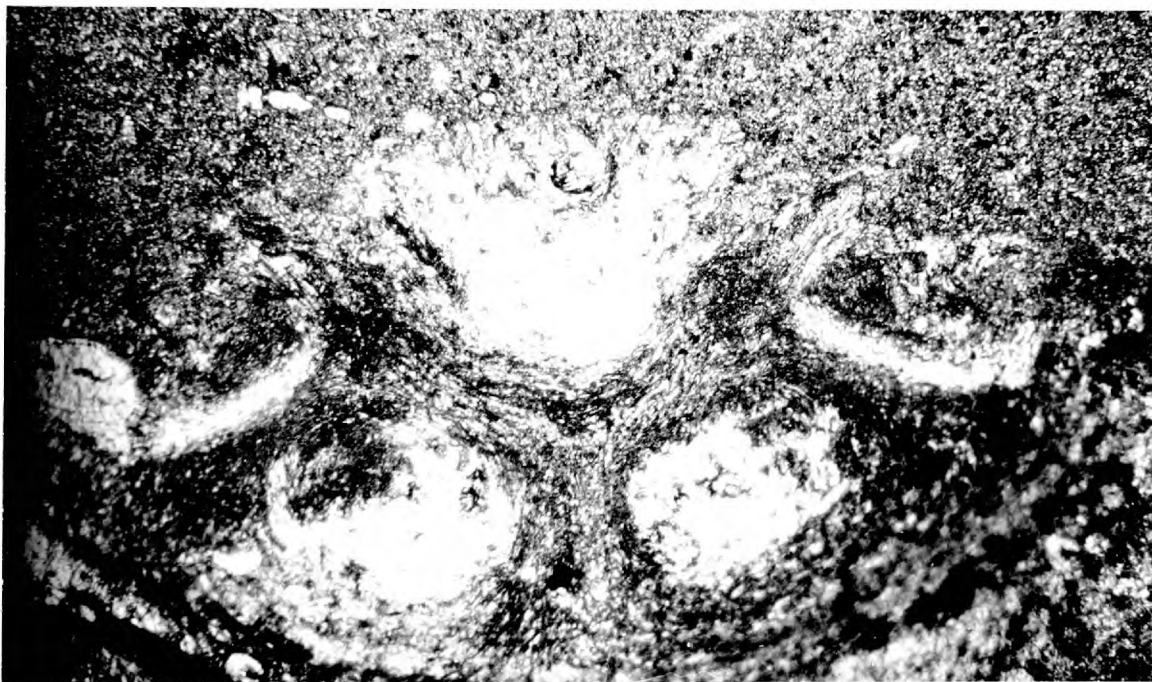
TEXT-PLATES S.15 and S.16
Austrilleria norica (SUESS)

Text-plate S.15

Transverse section of the umbo of Austrilleria
norica showing the bushy cardinal process lying on
the apical part of the hinge plate. Detail of sec -
tion 3.2, text-fig. S.1v x15

Text-plate S.16

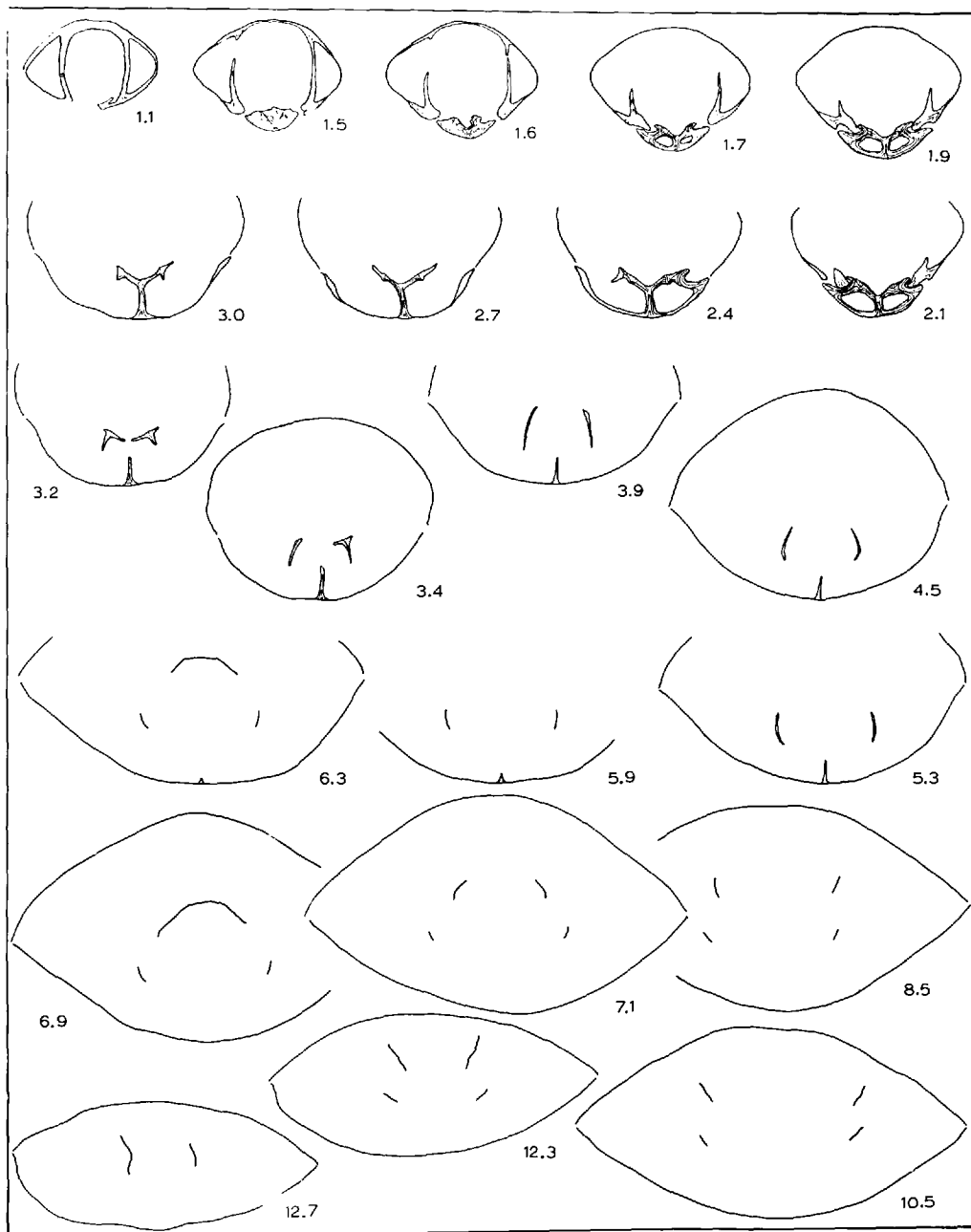
Transverse section of the right hand part of the
hinge plate of Austrilleria norica showing the crural
base lying on the inner socket ridge and the hinge
plate. Text-fig. as above, section 5.2 x50



Text-plate S.15

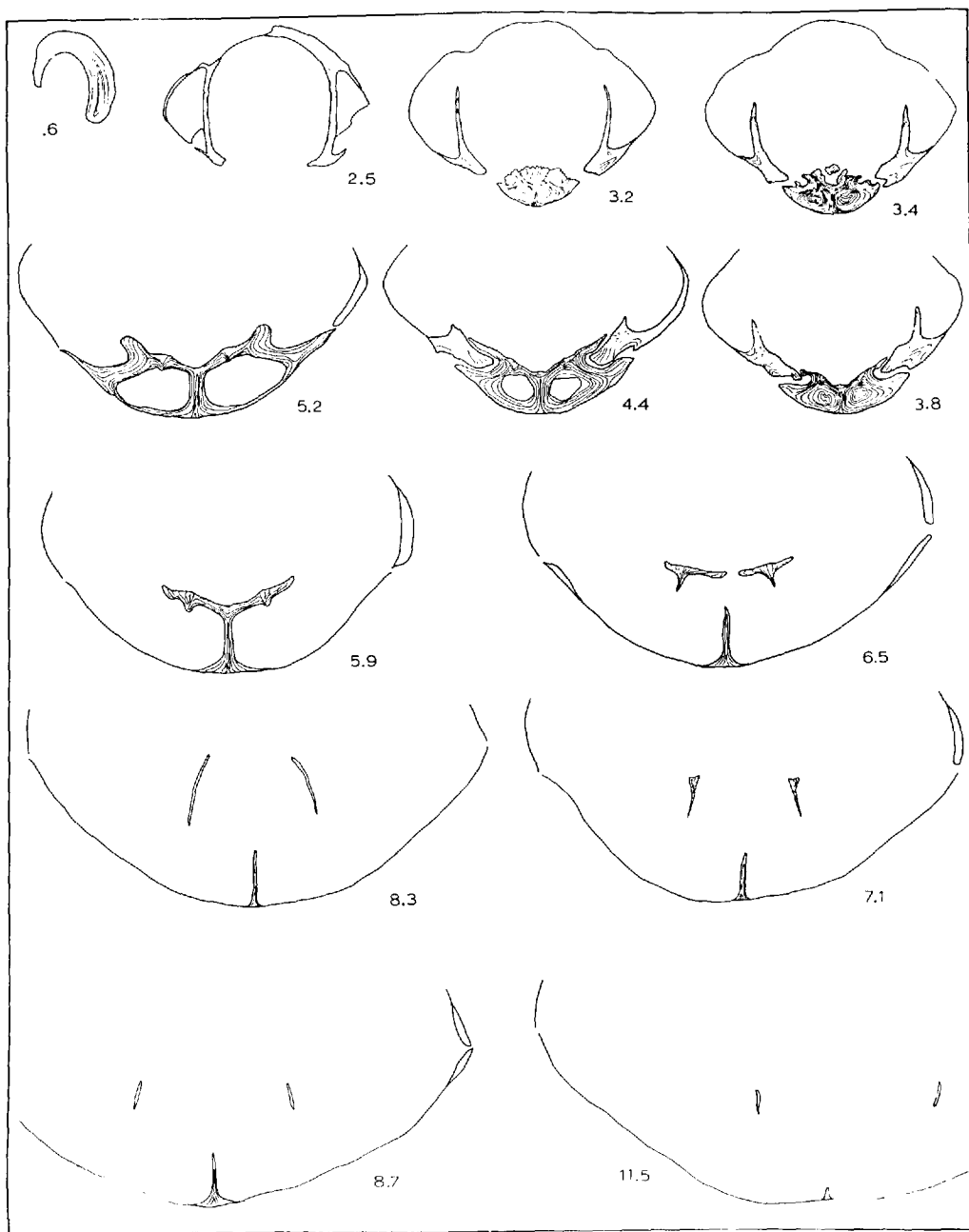


Text-plate S.16



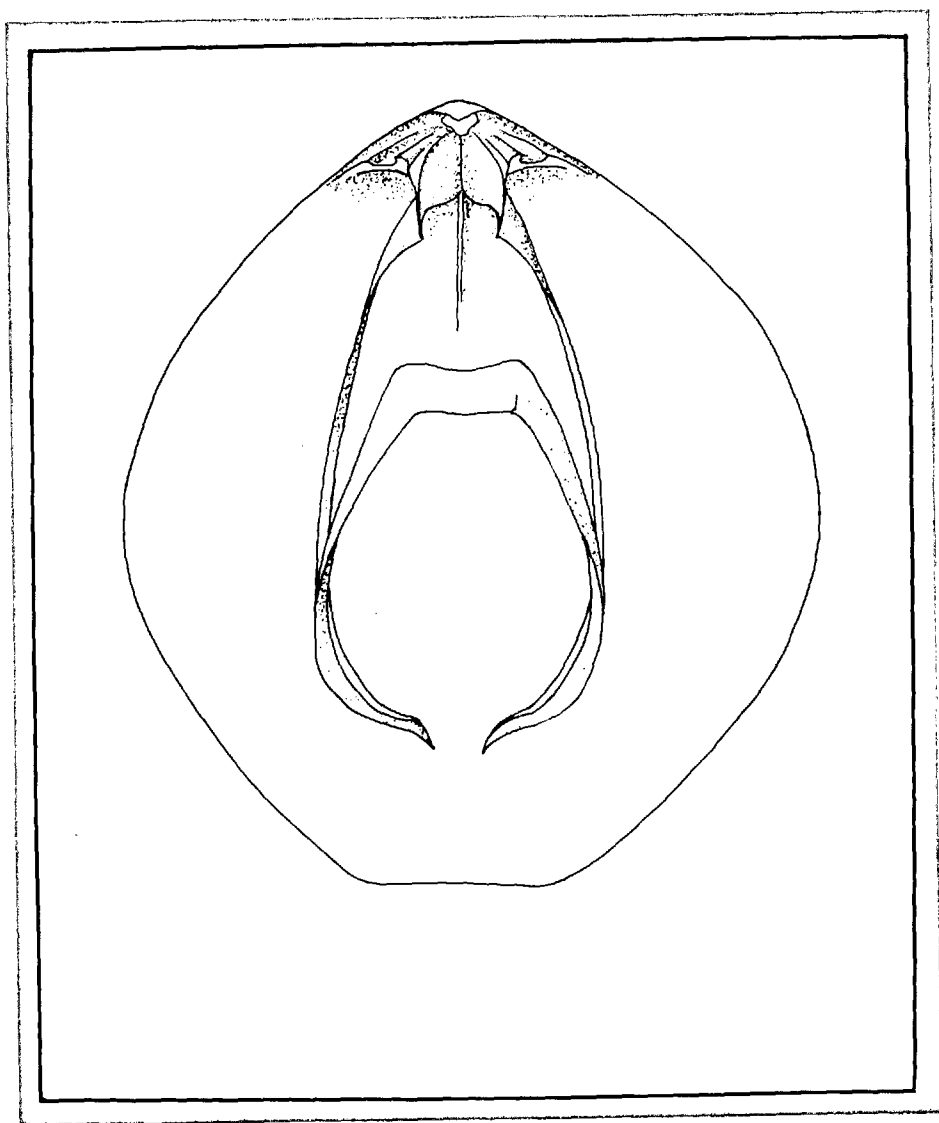
Text-fig. S.liv

Serial transverse sections of Austrilleria norica (SULESS).
 Rhaetian; specimen from the Geol.Bundes.Vienna - 8 Rot 19/3
 'Kössener Schichten, beim oberen Mandlingbauer in der Oed.
 Hintermannbauer N. Kitzberg N.' x4 Young specimen. Loop
 traceable to 14.1mms. Total length of specimen 16.6mms.
 PC.Nr.47



Text-fig. S.lv

Serial transverse sections of Austrilleria norica (SULESS).
 Rhaetian; Ascher, Miesenbach Tal, Lower Austria; 47°49'20''N.
 33°37'30''E. - Hohe Wandgebietes, Geol.Bundes.Vienna. Specimen
 from Geol.Bundes.Vienna, collected by Dr.B.PLÖCHINGER. x4
 Loop traceable to 13.3mm. Total length of specimen 28.9mm.
 PC.Nr.49.



Text-fig. S.lvi

Reconstruction of the loop of Austrilleria norica (SULESS).
Made from the sections shown in text-fig. S.liv. x

Superfamily Terebratulacea GRAY, 1840

Family Terebratulidae GRAY, 1840

Remarks:

The Terebratulidae is one of eight exclusively Mesozoic or Mesozoic-Cenozoic families of the Terebratulidina, and comprises eight subfamilies, five of which were proposed by MUIR-WOOD (1965) and are confined to the Cretaceous. Two of the remainder were erected by MAKRIDIN (1964) in an attempt to divide the plethora of nominal Jurassic genera in the Terebratulinae and remain unproved by other authors.

Despite the importance of the Terebratulidae in the Mesozoic their ancestry is still uncertain. In the Palaeozoic genera with a terebratuliform loop are placed in three families: the Dielasmatidae, the Heterelasminidae and the Labaiidae, and the character of the hinge plate is the only feature which can be used to guide the choice of one of these as the progenitor of the Terebratulidae.

In the Dielasmatidae and Heterelasminidae despite a variety of cardinal modifications the inner hinge plate appears never to have been entirely lost as it is in Terebratula. Rhaetina, the last known dielasmatid, still possesses the two disjunct inner hinge plates found in Dielasma in the Permian, and the related genera Fletcherithyris CAMPBELL and Arctothyris DAGIS from the Ladinian show a similar conservatism.

Only one family, the Labaiidae, has in addition to a terebratuliform loop, a hinge plate comparable with that in the Terebratulidae, and the union of the crural processes to form a ring in Labaiia (seen again in the Jurassic-Recent Cancellothyrididae) is probably of less significance than this resemblance. Therefore on present evidence Labaiia and related genera appear to provide the most probable root for the Mesozoic Terebratulidae.

Subfamily Triadithyridinae nov.

Diagnosis:

Smooth, biconvex terebratulids; anterior commissure plicate. Cardinal process prominent. Crura ventrally curved; descending branches short, arising directly from underside of crura.

Included genera:

Only Triadithyris DAGIS, 1963, from the Upper Triassic of Europe and the Soviet Union.

Remarks:

The Terebratulinae, as recognised by MUIR-WOOD (1965) comprises forty two genera. Eighteen of these were erected by BUCKMAN (1918) on somewhat esoteric external differences with no regard for internal morphology, even of the loop, and are of doubtful usefulness. Nevertheless, at least eleven of them have received recent descriptive recognition outside the all embracing Soviet and American Treatises, (see e.g. MAKRIDIN 1964; TULUWEIT 1964; ROUSELLE 1965). In addition Moisseievia MAKRIDIN, and Rhapidothyris TULUWEIT must be added to the subfamily.

Although MUIR-WOOD (1965) noted that this apparently very large subfamily was under review, the only classificatory regroupings have been carried out by MAKRIDIN (1964), who established the Lobothyridinae and the Loboidothyridinae for forms with a short and long terebratulid loop respectively. However, the difference is between 0.3 and 'less than 0.5 of the valve length' (MUIR-WOOD 1965 p.784) and its applicability remains to be confirmed, in particular their distinction from the type genus and subfamily is unclear. Jurassic Terebratulidae are at present being investigated by Dr.A.S.DAGIS (personal communication 1965).

Of the forty two genera listed by MUIR-WOOD only three are known from the Triassic: Plectoconcha COOPER from the Upper Triassic of western North America, Lobothyris BUCKMAN from the Carnian and Norian of the Soviet Union, and Triadithyris DAGIS described below. However, from its internal structure it is evident that Triadithyris cannot be regarded as having a subfamilial kinship with the genera in the Terebratulinae. In typical terebratulids, and also in the Dielasmatidae the crural

processes are ventrally directed from barely curved crura (see e.g. Rhaetina). In Triadithyris, in contrast to this, the crura are strongly curved ventrally and the short descending branches of the loop are direct continuations of dorsally descendent crural processes. This can be clearly seen in both the serial sections and reconstruction.

Further members of this subfamily will undoubtedly be found in the Triassic, rather than in the Jurassic where relatively thorough study has failed to reveal any species with a similar loop structure.

Genus Triadithyris DAGIS, 19631963 Triadythyris DAGIS, p.187.1965 Triadythyris DAGIS; MUIR-WOOD, p.905Type species:Terebratula gregariaeformis ZUGMAYER, 1880 p.13, pl.1, figs.26-29; OD.Range and Distribution:Norian Slovakia (Drnava), the E.Bulgarian Balkan Mts., Crimea, Caucasus and Pamirs.Rhaetian of the Northern Alps.Diagnosis:

Small, strongly biplicate. Beak low, suberect, beak ridges round. Foramen permesothyrid in position. Pedicle collar present. Cardinal process large, bilobed. No crural processes, crura bear descending lamellae only. Transverse band strongly arched.

Triadithyris gregariaeformis (ZUGMAYER), 1880

Plate 18, figs. 12-15; text-figs. S.lvii - S.lix; text-plates S.17, S.18.

1854 Terebratula gregaria SUESS, (partim) p.14, pl.2, fig.131879 Terebratula gregaria; STURZENBAUM, p.2881880 Terebratula gregariaeformis ZUGMAYER, p.13, pl.1, figs.22,26-291884 Terebratula gregariaeformis; BITTNER, p.1051890 Terebratula gregariaeformis ZUGM.; BITTNER, p.2781963 Triadithyris gregariaeformis (ZUGMAYER); DAGIS, p.188, pl.28, figs.1-9.Lectotype:

The originals of ZUGMAYER pl.1, figs.26-28 are preserved in the Geol.Buřdes.Vienna. That of fig.26 is here designated lectotype and refigured on pl.18, fig.14.

Dimensions of Lectotype:

Length 19.4mm., breadth 15.5mm., thickness 11.6mm.

Type Locality:

Kaisersteffel, Piesting Tal, Lower Austria. The writer has not been able to find specimens here.

Range and Distribution:

As for genus.

Diagnosis:

As for genus.

Description:

Typical members of this species are broad with a length - breadth ratio approaching 1:1; few specimens are longer than 20mms. The anterior commissure is episulcate, and the roughly equi-biconvex valves are boldly and sharply folded for about half their length. Very rarely the median sulcation of the commissure may be lacking and the nature of the folding is concomitantly affected. The beak is short and low, shows the common suberect - erect attitude, and is accompanied by blunt beak ridges. The foramen is round, permesothyrid in position and a pedicle collar accompanied by a symphitium are present. There are no dental lamellae and the strong teeth are tangentially inserted. The cardinal process is bilobed and luxuriant, filling the obsolete parts of the sockets and forming a prominent pit. The crural bases are strong features on the median edges of the very reduced outer hinge plates, (see text-plate S.17). The crura curve ventrally and the short descending lamellae are continuous with dorsally directed crural processes. The loop is terebratuliform with a strongly arched transverse band extends for 45% of the specimen length.

The brachial adductor muscle scars are pyriform in outline.

Remarks:

T.gregariaeformis was one of the first Mesozoic brachiopod species to be distinguished solely on account of its internal structure. ZUGMAYER (1880) separating it from Rhaetina gregaria on the basis of a polished section which showed it to lack the inner hinge plates of his 'Bipartitae' group of terebratulids. Both SUESS (1854) on establishing R.gregaria, and later STURZENBAUM (1879) had in fact confused the two species, but T.gregariaeformis can be distinguished by its greater

relative breadth, more angular folding, less produced beak, and the more regular transverse convexity of the pedicle valve.

This species is rare in the Rhaetian of the Northern Alps where it has only been recorded at the Steinernes Meer near Salzburg, and in the neighbourhood of the type locality in the Piesting Tal.

Dimensions of Figured Specimens:

	length	breadth	thickness
18/12	16.0	14.3	9.0
18/13	20.1	19.1	11.5
18/14	18.9	16.5	11.5
18/15	16.2	14.3	9.0

Material:

Drnava, Slovakia - c.200, T.66; Luda Kamchya valley, Bulgaria - 4, T.67; Kaisersteffel, (topotypes) Geol.Bundes.Vienna, 7 rot 19/3 - 12; Vorder Mandling - 1, T.68; Kitzberg - 2, T.69.

TEXT-PLATES S.17 and S.18

Triadithyris gregariaeformis (ZUGMAYER)

Text-plate S.17

Transverse section through the bilobed cardinal process of Triadithyris gregariaeformis, showing the invasion of the obsolete portions of the sockets and the twofold division of the socket plates.

Detail of section 2.7, text-fig. S.lxvii x60

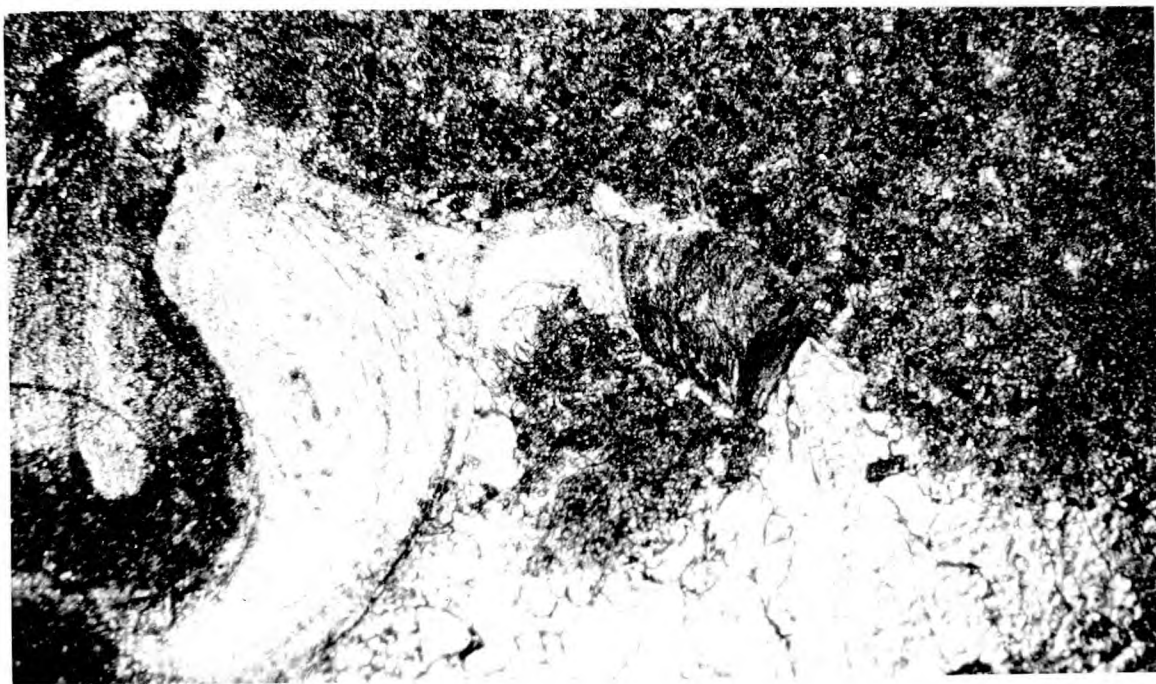
Text-plate S.18

Transverse section of the left hand socket of Triadithyris gregariaeformis, showing the tooth, massive socket ridge, reduced outer hinge plate and crural base (dark). Text-fig. as above, section

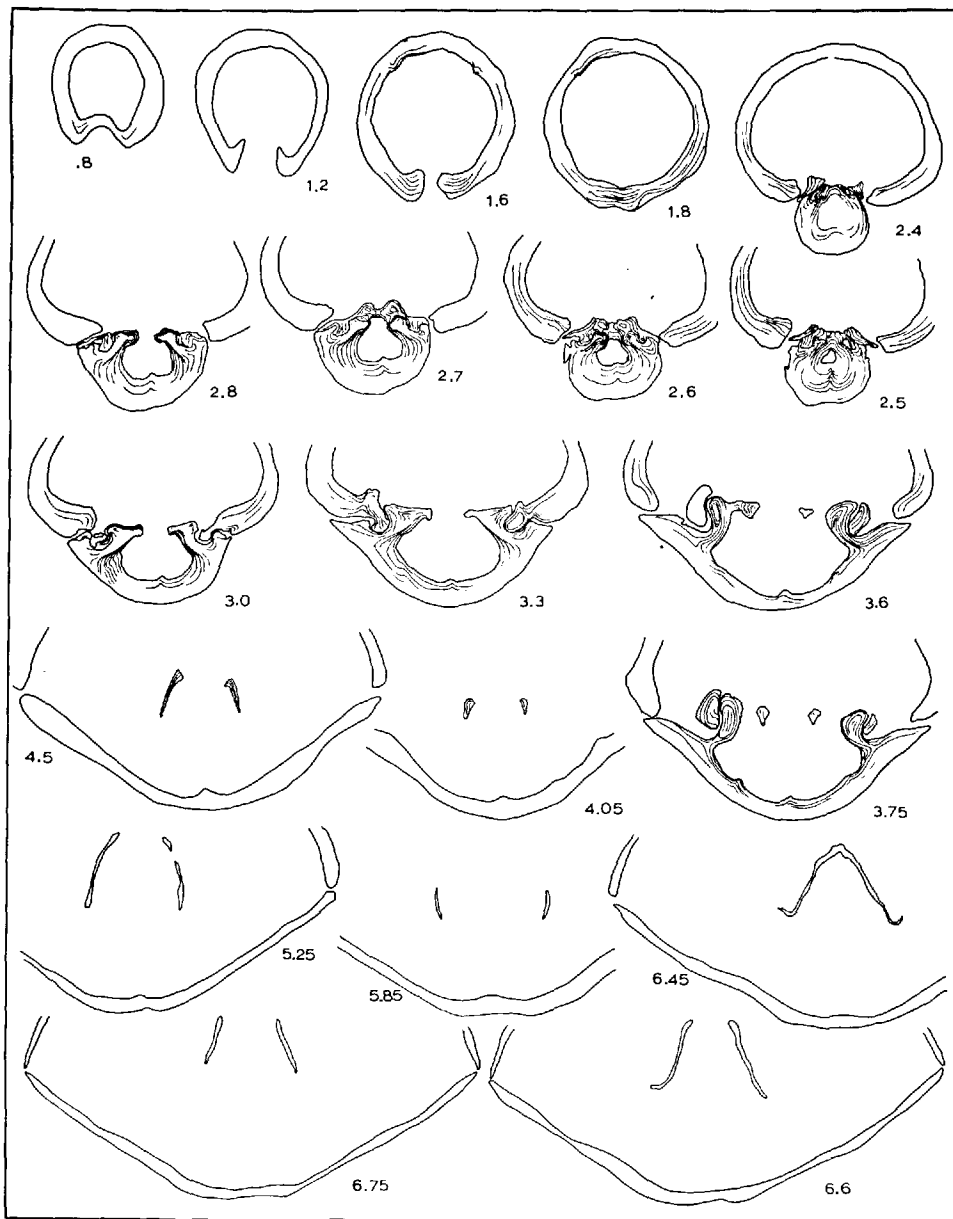
3.6 x75



Text-plate S.17

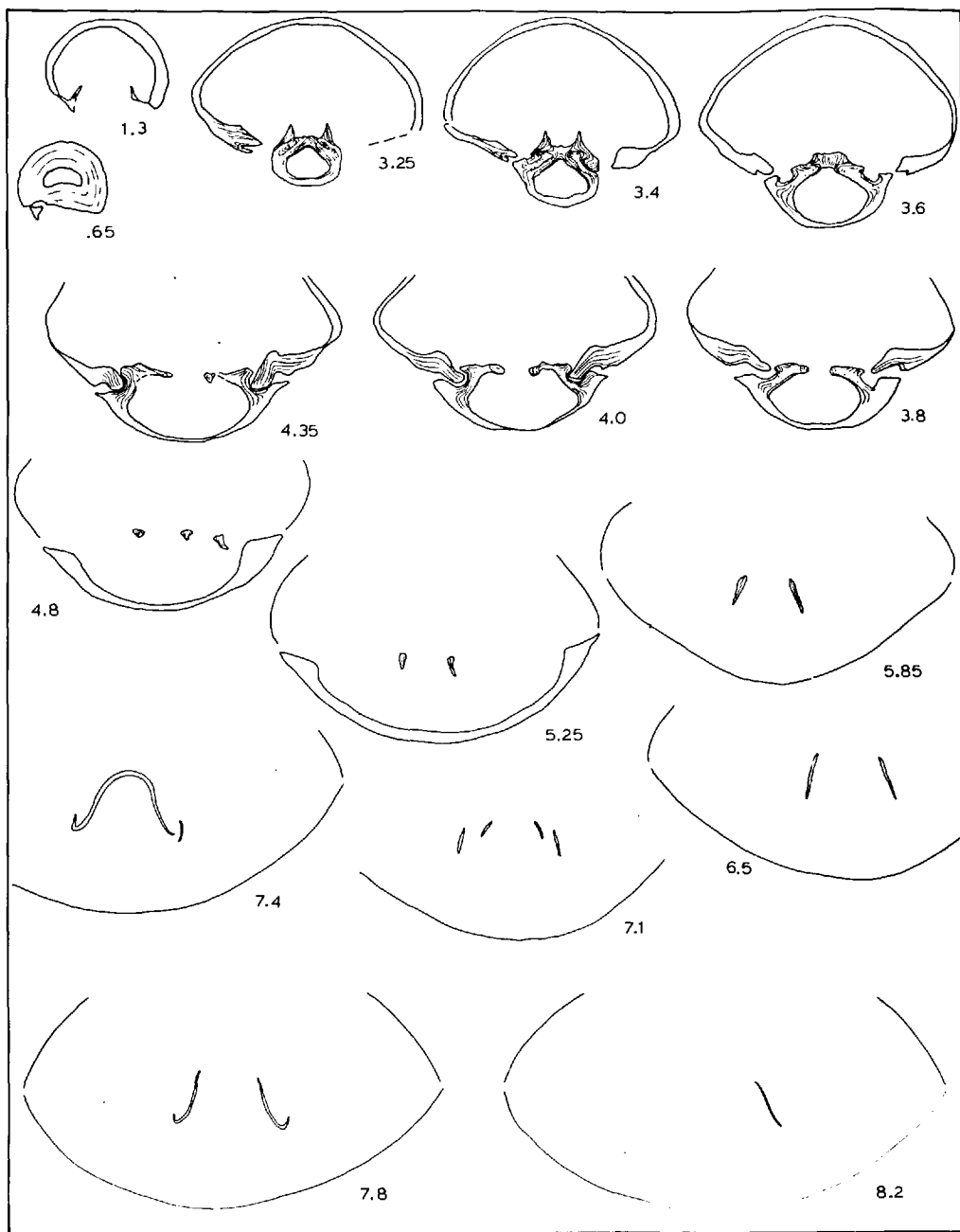


Text-plate S.18



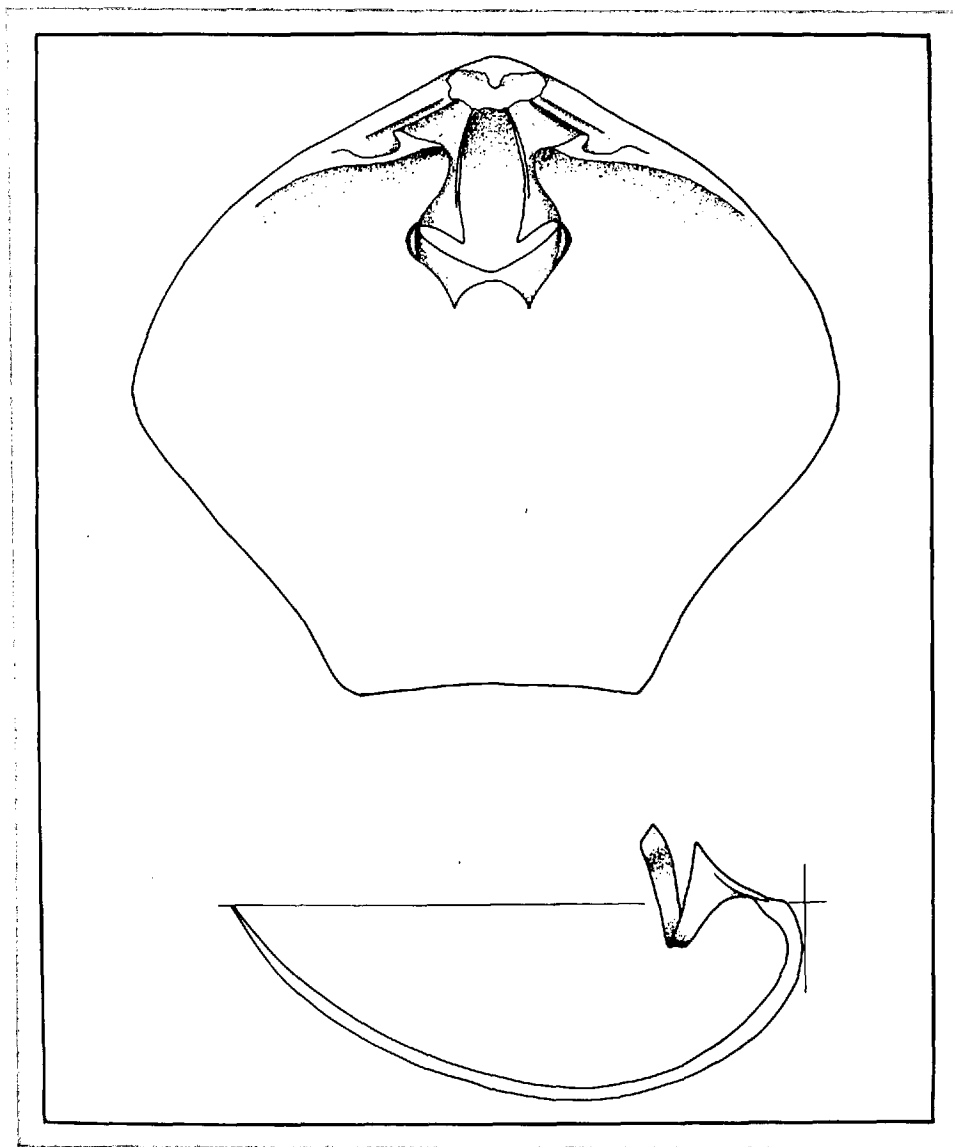
Text-fig. S.lvii

Serial transverse sections of Triadithyris gregariaeformis (ZUGMAYER). Rhaetian; specimen from the Geol.Bundes.Vienna - 7 Rot 19/3 'Kössener Schichten. Rechtes Gehänge der Kaltenganges bei Wallegg, Kaiser N.W., hinab in den Kaltengang.' This locality lies in the Piesting Tal, Lower Austria, and is almost certainly the type locality. x4 Loop traceable to 6.9mm. Total length of specimen 15.1mm. PC.Nr.40 Topotype.



Text-fig. S.lvi

Serial transverse sections of Triadithyris gregariaeformis (ZUGMAYER). Upper Norian; Bleskovy pramen, Drnava, north west of Plesivec, S.Slovakia. Locality of BITTNER's (1890) specimens. x4 Loop traceable to 8.3mms. Total length of specimen 17.8mms. PC.Nr.41.



Text-fig. S.lix

Reconstruction of the loop of Triadithyris gregarinaeformis
(ZUGMAYER). Made from the sections shown in text-fig. S.lvii

x5

Both views show the ventral curvature of the crura into the
crural points and the descending lamellae arising directly
from them.

Suborder Terebratulidina WAAGEN, 1883
 Superfamily Dielasmatacea SCHUCHERT, 1913
 Family Dielasmatidae SCHUCHERT, 1913

Remarks:

The Dielasmatidae is the only terebratulid family known to cross the Palaeozoic-Mesozoic boundary, and as understood at present contains a predominance of Mesozoic genera. Apart from the type subfamily three others are recognised: the monotypic and Palaeozoic Centronelloideinae STEHLI, 1965, and the wholly Mesozoic Nucleatulinae MUIR-WOOD, 1965, and Juvavellinae BITTNER, 1896.

Subfamily Dielasmatinae, SCHUCHERT, 1913

Remarks:

The Dielasmatinae was founded by SCHUCHERT as a subfamily of the Terebratulidae to include Palaeozoic genera characterised by a short loop with a transverse band. Subsequent revision was carried out by THOMSON (1926) to exclude the Cryptonellinae on the basis of its undivided hinge plate; by SCHUCHERT (1929) who raised the subfamily to family level, and CLOUD (1942). In addition THOMSON (1927) and DUGIS (1963) discussed its content and relationship.

Prior to 1956 however, agreement on a suitable classification for this group was hindered by lack of information about the type genus Dielasma KING. This was supplied by STEHLI (1956) and later the subfamily was amended by MUIR-WOOD (1965) to include genera 'having a centronellid loop in early growth stages but later becoming short terebratuliform', and with the inner hinge plates either separated and fused to the valve floor or joined along a low septum.

Although dental lamellae are present in the type genus, genera without them were included by MUIR-WOOD (1965) and also by STEHLI (1965) in his consideration of the Palaeozoic elements of the subfamily. However, K.S.W. CAMPBELL (1965 p.69) 'put more emphasis on the absence of dental lamellae than on the shape of the hinge plates', and withdrew the non-lamellate genus Hemiptychina from the Palaeozoic representatives

as the type of a subfamily within his new family the Gilledidae. Lacking dental lamellae Gilledia is superficially strongly reminiscent of the Triassic genus Rhaetina, but it shows no centronellid stage in the development of the loop as was revealed in Rhaetina by DAGIS (1958). CAMPBELL stressed the fundamental importance of this difference. Therefore there is no conflict over the position of Rhaetina. The bulk of the Palaeozoic dielasmatinids have dental lamellae and their presence or absence within the subfamily as defined on the nature of the loop, may well be a useful feature in attempting to distinguish Triassic lines of descent; Fletcherithyris CAMPBELL is lamellate whereas Arctothyris DAGIS and Rhaetina are not. The writer would, however, hesitate to use dental lamellae as radically as CAMPBELL suggested.

Considerable flexibility in the nature of the cardinalia within the Dielasmatinae was introduced on the reinstatement in the subfamily by CAMPBELL (1965) of Beecheria. Following its inclusion by LICHAREV (1960), STEHLI (1965) had placed it in the Heterelasminidae attaching familial significance to the division of the outer from the inner socket ridges. CAMPBELL however demonstrated this to be without even generic importance, but did suggest that following further investigation a Beecheria stock might be isolated as a subfamily.

Even allowing Beecheria in the subfamily, it does not seem possible to follow MUIR-WOOD (1965) and include Adygelloides or Zugmeyeria in the Dielasmatinae. Both lack inner hinge plates and the writer concurs with DAGIS (1963) who established a new family for them - the Zugmeyeridae (nom. correct pro Zugmayeridae DAGIS, 1963, p.71). It is perhaps unfortunate that DAGIS chose the Rhaetian Zugmeyeria as the type genus, for apart from two unillustrated reports one from Rumania (PREDA 1962), and the other by KÜHN (1942), that the writer has been unable to check and which must be considered doubtful in view of the difficulty of identifying the species externally, it has totally eluded collection since its original description by ZUGMAYER in 1880. On the other hand Adygelloides was ground and figured by DAGIS himself in the same publication. Nevertheless, since Adygelloides is undoubtedly close to Zugmeyeria (and may even be synonymous with it), the family may be used with confidence.

Following CLOUD's suggestion (1942), the Rhipidothyridae was proposed by DAGIS (1965) as the ancestor of the Dielasmatidae in opposition to the Cranaenidae favoured by STEHLI (1956a).

Genus Rhaetina WAAGEN, 1882

- 1880 Gruppe A (Bipartitae), ZUGMAYER, p.8
 1882 Rhaetina WAAGEN, p.334
 1963 Rhaetina WAAGEN; DAGIS, p.142
 1965 Rhaetina WAAGEN; MUIR-WOOD, p.769

Type species:

Terebratula gregaria SUESS, 1854 p.14, pl.2, figs.14,15; OD.

Range and Distribution:

Norian of the Caucasus, Crimea and Pamirs.

Rhaetian of the Northern Alps, Western Alps, Southern Alps, Lombardy Alps, Slovakian and Rumanian Carpathians, Turkey and Iran.

Liassic of the Northern Alps.

Rhaetina will certainly prove to include many species from the Middle and Upper Triassic at present described in the catch-all genus, Terebratula. R.pyriformis is already doubtfully known in the Carnian.

Included species:

Eight species have so far been described in the genus:

R.gregaria SUESS - the type.

R.pyriformis SUESS, 1854, p.13, pl.3, figs.6-8

R.turcica BITTNER, 1891, p.105, pl.1, figs.6-8

R.taurica MOISSELEV, 1932, p.598, pl.1, figs.14-17

R.robinsoni MOISSELEV, 1947, p.78, pl.9, fig.4

R.beskessensis DAGIS, 1963 p.153, pl.23, figs.7-9

R.elliptica DAGIS, 1963 p.155, pl.24, figs.1-5

R.caucasica DAGIS, 1963 p.159, pl.24, fig.6, pl.25, figs.1-3

The writer is doubtful about the distinction of R.turcica, R.taurica and R.robinsoni and these species are discussed below.

Diagnosis:

Small to medium sized; elongate oval to subpentagonal; may be biplicate. Pedicle foramen epithyrid in position. Loop centronellid in early growth stages, later becoming terebratulid. Inner hinge plates may unite over low dorsal septum. Dental lamellae absent.

Rhaetina gregaria (SUESS)

Plate 19, figs.1-8; text-figs.S.lx-S.lxxii

- 1845 Terebratula biplicata SOWERBY; ZEJSNER, pl.6, figs.8-13
- 1851 Terebratula biplicata; SCHAFHÄUTL, p.415
- 1852 Terebratula biplicata SOWERBY var. rotunda, ZEJSNER, p.201
- 1853 Terebratula biplicata; SCHAFHÄUTL, p.318
- 1854 Terebratula gregaria SUESS, (partim) p.14, pl.2, figs.14,15
- 1856 Terebratula biplicata, ZEJSNER, p.137
- 1859 Terebratula Paueri WINKLER, p.22, pl.2, fig.8
- 1861 Terebratula gregaria SUESS; STOPPANI, p.88, pl.18, figs.1-14
- 1861 Terebratula grossulus ? SUESS; STOPPANI, p.90, pl.18, figs.17-19
- 1861 Terebratula gregaria SÜSS; GÜMBEL, p.400
- 1863 Terebratula gregaria SUESS; OOSTER, p.5, pl.1, figs.1-6
- 1863 Terebratula pyriformis SUESS; OOSTER, p.6, pl.1, figs.7,8
- 1863 Terebratula gregaria SUESS; DESLONGCHAMPS, p.64, pl.37, figs.1-3
pl.8bis. figs.1-6
- 1863 Terebratula dipla SCHAFHÄUTL, p.348, pl.70, figs.1-6
- 1863 Terebratula indentata SOWERBY; SCHAFHÄUTL, (partim) pl.70, fig.7
non text p.347
- 1864 Terebratula Schafhaeutli STOPPANI; DITTMAR, p.149
- 1864 Terebratula gregaria SSS; RENEVIER, p.45
- 1865 Terebratula gregaria SUESS; MARTIN, p.254
- 1867 Terebratula gregaria SUESS; DUMORTIER, p.79, pl.13, figs.9-12
- 1869 Terebratula gregaria SUESS; QUENSTEDT, p.418, pl.50, figs.67-9
- 1871 Terebratula gregaria SUESS var. rotundiformis, TOULA, p.440
- 1871 Terebratula gregaria SUESS var. trigonalis, TOULA, p.440
- 1878 Terebratula gregaria; LEPSIUS, p.240
- 1879 Terebratula cf. gregaria UHLIG, p.304, pl.5, figs.9-13
- 1880 Terebratula gregaria SSS.; ZUGMAYER, p.10, pl.1, figs.1-11
- 1884 Terebratula gregaria SUESS; PARONA, p.366, pl.11, fig.3
- 1885 Terebratula gregaria SUESS; HALS, p.24, pl.1, figs.1-15, pl.2, fig.7
- 1889 Terebratula gregaria SUESS; GMEYER, p.15, pl.2, figs.20-24
- 1895 Terebratula gregaria SUESS; FUCINI, p.191, pl.7, fig.15

- 1891 Terebratula turcica BITTNER, p.105, pl.1, figs.6-8
 1892a Terebratula turcica m.; BITTNER, p.78, pl.4, fig.1-3
 1908 Terebratula gregaria SUESS; ARTHAUBER, pl.49, figs.11,12
 1909 Terebratula gregaria SUESS; TRAUTH, p.66, pl.2, figs.3,4
 1917 Terebratula gregaria SUESS; GOETTEL, p.111, pl.7, figs.5-8
 1926 Terebratula gregaria SUESS; MOISSEIEV, p.748, pl.23, figs.1-3
 1929 Terebratula gregaria SUESS; DOUGLAS, p.644, pl.44, fig.9
 1929 Aulacothyris sp., DOUGLAS, pl.44, fig.10
 1938 Rhaetina pamirensis n.sp. MOISSEIEV, p.38, pl.1, fig.3
 1947 Rhaetina robinsoni n.sp. MOISSEIEV, p.78, pl.9, fig.4
 1947 Rhaetina turcica (BITTNER); MOISSEIEV, p.79, pl.9, fig.1
 1962 Rhaetina gregaria (SUESS); ALLASINAZ, p.331, pl.24, figs.1-3
 1962 Terebratula gregaria SUESS; PREDÄ, p.64, pl.1, fig.8
 1963 Rhaetina gregaria (SUESS); DAGIS, p.143, pl.21, figs.14-19
 1963 Rhaetina turcica (BITTNER); DAGIS, p.148, pl.22, figs.6-16
 1963 Rhaetina robinsoni MOISSEIEV; DAGIS, p.150, pl.23, fig.6
 1963 Rhaetina gregaria (SUESS); BELLONI, p.411, pl.27, figs.1-3

Lectotype:

SUESS's originals were formerly in the Geol.Bundes.Vienna, but are now lost (Prof.R.SIEBER, verbal communication 1965). Of his three figured specimens, one, fig.13, is here judged to belong to Triadithyris gregariaeformis (ZUGMAYER) and its choice as lectotype would destroy ZUGMAYER's species. Fig.15 is of an anterior view only therefore the original of figure 14 is here selected as lectotype.

Dimensions of Lectotype:

From SUESS's figure - length 28.Omms., breadth 24.Omms., thickness 12.Omms.

Type Locality:

SUESS gave the type locality as 'Mandling Wand bei Wallegg'. This locality is marked on the Hohe Wandgebietes, Geol.Bundes.Vienna, and specimens may still be obtained there from the debris of former vineyards.

Range and Distribution:

Norian of the Caucasus and Crimea.

Rhaetian of the French Western Alps, Swiss Vaudoise Alps, Northern Alps, Lombardy Alps, Slovakia, Poland, Rumania and E.Iran.

Liassic of the Northern Alps, the Bergamo Alps and the Central Apennines.

Diagnosis:

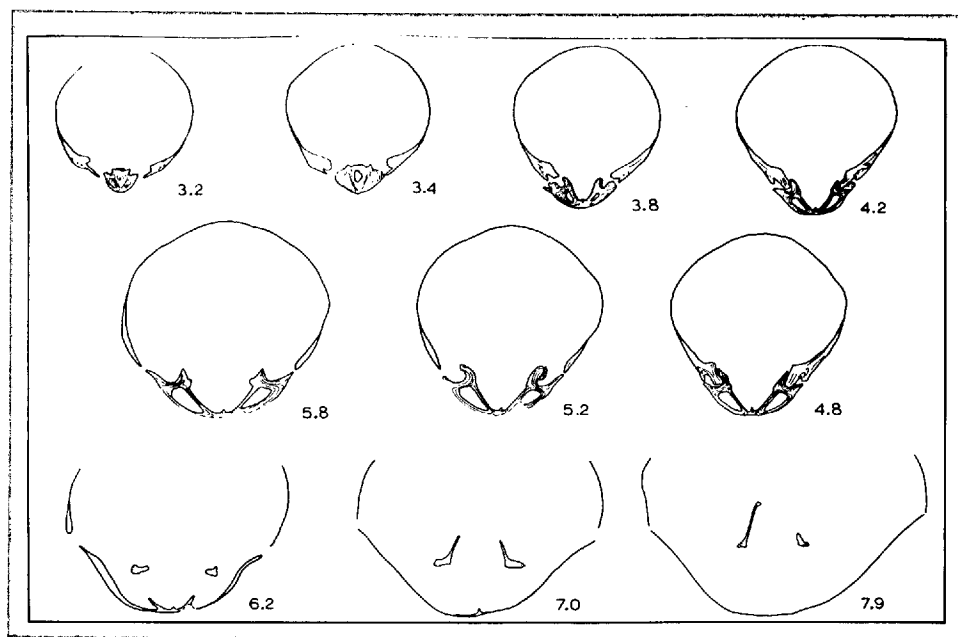
Moderately large, ovate-subpentagonal terebratulids. Anterior commissure sulcificate, folds and sulci strong in anterior part of valves. Pedicle foramen large, mesothyrid in position. Beak ridges rounded. Crural processes ascendent; transverse band medianly flattened.

Description:

Rhaetina gregaria encompasses a widely variable series of medium sized, biplicate, ovate terebratulids, externally reminiscent of very many Jurassic and Cretaceous species. Specimens from different localities may contrast markedly in size, but large individuals more than 30mm. long, such as that on plate 19, fig.1, are not common and are rarely found in the very large assemblages for which the species is notable; the specimens from Hindelang, particularly that of plate 19, fig.3, are more representative. Typical members of the species are ovate-pentagonal in outline with a prominent beak flanked by rounded beak ridges. Nevertheless the area is well developed and clearly discernible; the pedicle foramen is mesothyrid in position. The anterior commissure is sulcificate, and the valves are folded accordingly for about half their length. There is rarely any suggestion of lateral sulci bounding the pair of dorsal folds, but those bordering the median fold in the pedicle valve are clearly developed. Just as there is much variation in overall size from place to place so is there a considerable range in the development of folding: a collection of about two hundred specimens from Bodenschneid Gipfel by Schliersee contains none folded as strongly as is the rule at Hindelang and all other localities known to the writer. The vast majority of Bodenschneid individuals are markedly compressed with only gentle flexing, and often simple, broad plication of the anterior commissure. The normal variability of the species is excellently shown by HAAS (1885) in sixteen specimens.

A pedicle collar and a prominent, bushy cardinal process are present. There are no outer hinge plates and the inner hinge plates extend

obliquely from the sockets to the floor of the valve, where they flank a low median ridge, and may exceptionally unite on top of it (e.g. DAGIS 1963, text-fig.63). The two specimens figured by STOPPANI 1861 as a variety of T.gregaria differing in showing the trace of a median septum, and described as T.grossulus ?, are of this type. The crural bases lie along the inner edges of the socket ridges, and their processes are ascendent. The transverse band is medianly flattened.



Text-fig. S.1x

Serial transverse sections of Rhaetina gregaria (SUESS). From a loose block of Rhaetian limestone; Vorder Mandling, by Waldegg, Piesting Tal, Lower Austria. 47°52'20''N. 33°43'20''E. x3
Loop traceable to 9.3mm. Total length of specimen 23.5mm. PC.Nr.53
Topotype.

Remarks:

This is without doubt the commonest and most widely distributed of Rhaetian brachiopods. Following its distinction from the Upper Jurassic species T.biplicata with which it was confused by early geologists, it became recognised as an index fossil of the Alpine Rhaetian. However as TRAUTH (1909 p.66) pointed out, it has been recorded several times from supposed Liassic strata, and he cited the following authors: DUMORTIER 1867, UHLIG 1880, PARONA 1884, GEYER 1889, and FUCINI 1895, and himself recorded it from the Lower or Middle Liassic.

DUMORTIER regarded his material from the Haute Savoie (West Switzerland), as almost certainly from the 'infra-lias' (i.e. Rhaetian) despite including R.gregaria in the second part of his monograph which dealt with Liassic species. HAAS (1885) subsequently confirmed the level of these specimens.

All UHLIG's (1880) seventeen specimens from the western Alto Adige (N.W. Italy) came from one loose block without an accompanying fauna and cannot be regarded as certainly dated. Similarly, GEYER's record (1889 p.16) from the Liassic of Adneth (nr. Salzburg) is no longer acceptable following the redetermination of the relevant part of the 'Adnether Schichten' as uppermost Rhaetian (ZAPFE 1963 p.253). However the occurrence reported by GEYER in the Hierlatzkalk from Hierlatz, by Hallstatt (Upper Austria), that of TRAUTH in the Grestenerkalk by Hinterholz (nr. Gstadt on the Ybbs, Austria), PARONA from the Lower Lias of S. Roco di Adrara in the Bergamo Alps, and FUCINI from the Liassic of Monte Pisano (Central Apennines) seem credible. TRAUTH's material is probably still available in the Nat. Hist. Mus. Vienna, and FUCINI's may still be in the collections of the Univ. of Pisa; PARONA had only one specimen and did not give the place of its deposition. None of this material has yet been examined by the writer, but GEYER's originals (four of fifty he collected) from the Geol. Bundes. Vienna are refigured on plate 19 through the kindness of the Curator, Prof. R. SIEBER. The original of plate 2, fig. 23 shows clearly the traces of two inner hinge plates, and his specimens are undoubtedly dielasmatis. From GEYER's specimens (that of fig. 20, here plate 19, fig. 6, was his largest and is probably

unrepresentative) and from the figures of other authors it is only possible to conclude that they fall within the wide range of Rhaetinaa gregaria, and must, for the present, be included in that species. However, the Liassic at Hierlatz occurs in isolated, transgressive pockets on Triassic Dachsteinkalk and GEYER noticed that the preservation of his specimens of R. gregaria was different from that of the remainder of the fauna. He discounted the possibility of derivation from the underlying Dachsteinkalk because R. gregaria is apparently absent there. Even if GEYER was correct, the exact level of R. gregaria, and also Fissirhynchia fissicostata which accompanies it, should be investigated in the light of WIEDENMAYER's remarks (1963) on the condensation of the ammonite fauna there.

Just as the wide range of variation of R. gregaria makes it impossible to recognise a distinct Liassic species, so is it impracticable to separate the Turkish Norian species, Rhaetina turcica. BITTNER, himself, stressed the resemblance of the two species (1891 p.105) and distinguished them only through the supposed plumpness of R. turcica. DAGIS (1963 p.149) stated that the only 'sure criterion for distinguishing these species is the size' (N.L.L.transln.). However, variation makes this an inapplicable distinction and all the specimens figured by DAGIS can be matched in material from almost any of the numerous North Alpine localities. The much greater richness of R. turcica in comparison with R. gregaria which DAGIS's lists of material show, is easily understood as the ratio between differing locality collections of large and small R. gregaria. Therefore, Rhaetina turcica (BITTNER), as interpreted by DAGIS (1963) is included in the synonymy of Rhaetina gregaria (SUESS). Similarly, BITTNER's figures of somewhat thick individuals simply reflect a locality variant not greatly dissimilar to the specimens at Hindelang, and certainly their continued acceptance as representatives of a distinct species would give grounds for the erection of a host of 'species' in the Northern Alps. Therefore the original description of Terebratula turcica BITTNER is also introduced into the synonymy of Rhaetina gregaria (SUESS).

Rhaetina robinsoni MOISSEIEV, is recognised from only one Caucasian specimen, MOISSEIEV's original being refigured by DAGIS, and ~~there~~th seems very little doubt that it is simply an unusually elongate R.gregaria. Rhaetina robinsoni MOISSEIEV is therefore here included in the synonymy of Rhaetina gregaria (SUESS).

Dimensions of Figured Specimens:

	length	breadth	thickness
18/1	36.8	31.6	19.0
18/2	29.3	26.0	15.5
18/3	22.6	19.0	12.1
18/4	18.0	16.5	9.0
18/5	18.6	14.5	9.3
18/6	28.1	21.7	15.8
18/7	18.5	17.7	9.8
18/8	22.5	19.2	11.0

Material:

Ochsenberghütte by Hindelang - 40, T.86; loc.cit. - 16, B.M.N.H., B 39158; loc.cit. - 2, B.M.N.H., B 39161; loc.cit. - 3, B.M.N.H., B 39165; Hochalpkütte by Pfronten - 150, T.87; Bodenschneid Gipfel by Schliersee - 150, T.88; Waidhofen a. d. Ybbs - 120, T.89; Vorder Mandling, by Waldegg, Piesting Tal - 4, T.90; Kitzberg by Neusiedl, Piesting Tal - 6, T.91; Bystry potok, west of Ruzomberok, Slovakia - 40, T.92; Saddle north of Hlupy, Vysoke Tatry, Slovakia - 80, T.93; Mała Swinica by Zakopane, Poland - 90, T.94; Lejowa valley by Zakopane - 50, T.95; Strączyńska Alp by Zakopane - 60, T.96; Val Frunsi, Ferice, Arieșeni, Rumania - 20, T.97.

TEXT-PLATES S.19 and S.20

Rhaetina gregaria (SUESS)

Text-plate S.19

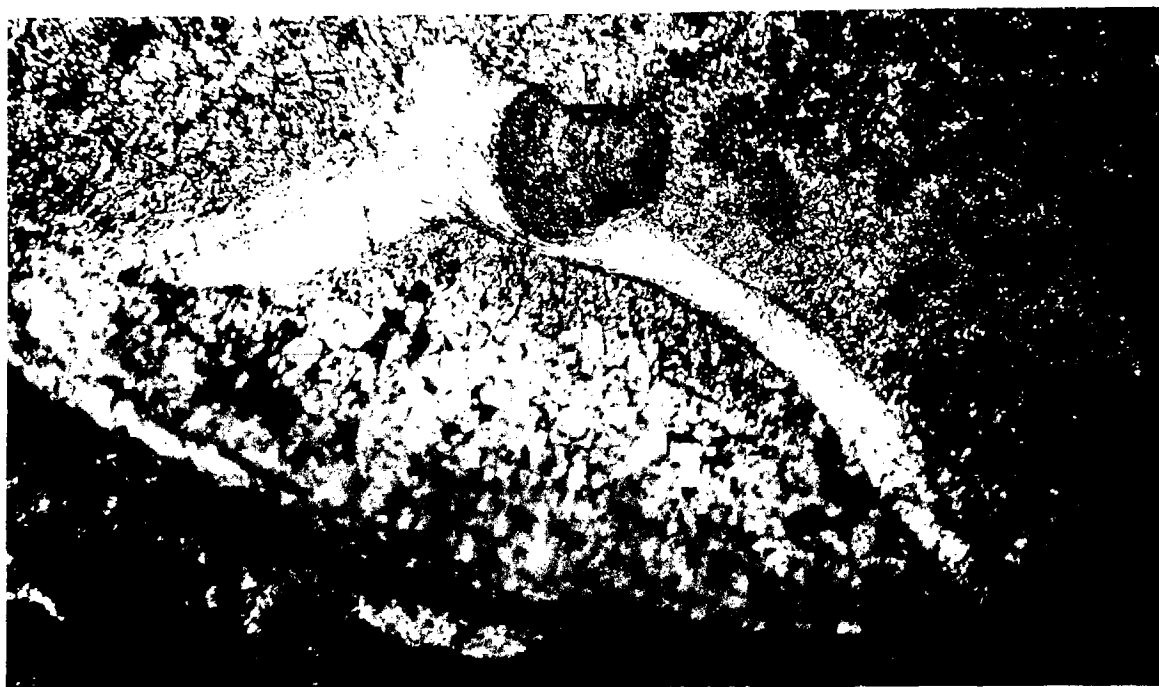
Transverse section through the brachial umbo of Rhaetina gregaria, showing the remains of the cardinal process lying between the oblique hinge plates, the socket plates with their strong inner socket ridges, and the crural bases. Specimen from Bystry potok by Gombas, west of Ruzomberok, Slovakia. Section at 3.15mms. x10

Text-plate S.20

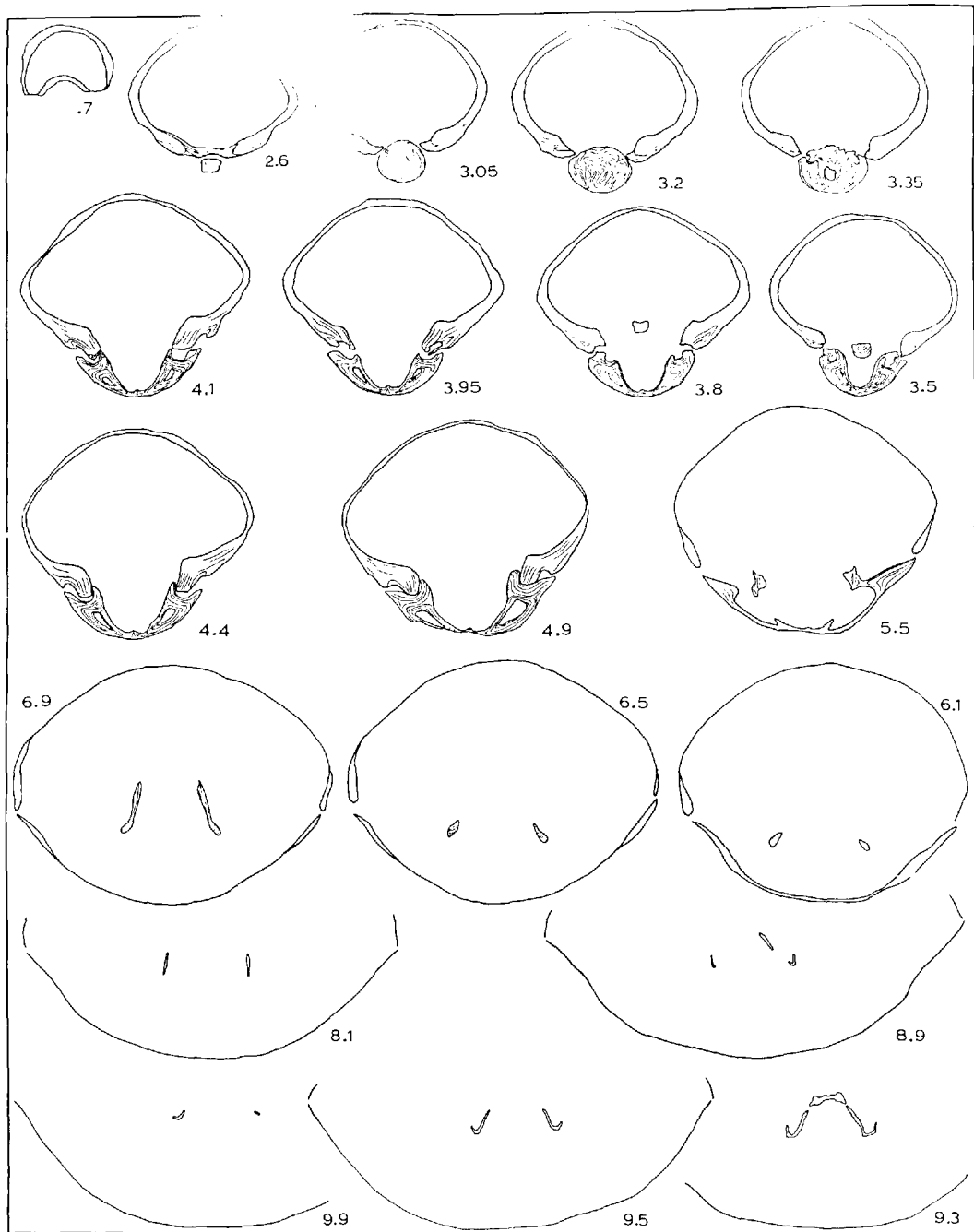
Transverse section of the left hand part of the hinge plate of Rhaetina gregaria ?ssp.nov., showing the anterior portion of the socket, the crural base (dark), the curved hinge plate and the median ridge. Detail of section 3.45 text-fig. S.lxiii x12



Text-plate S.19

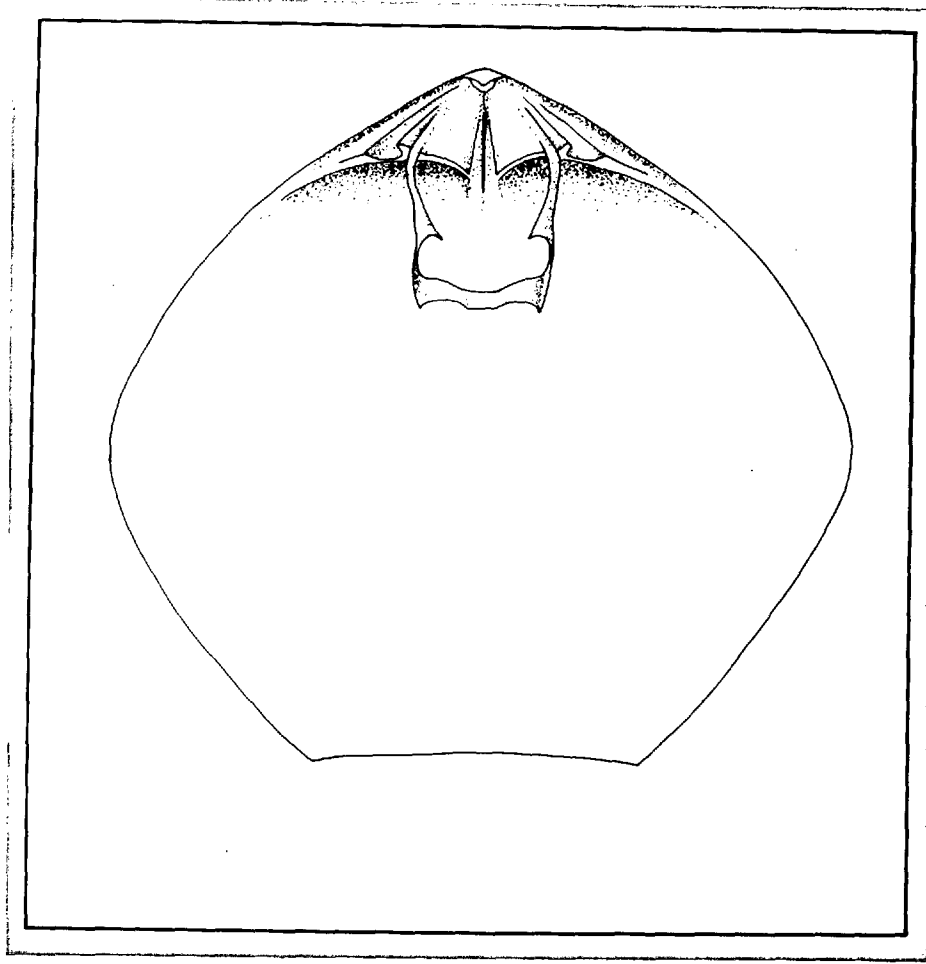


Text-plate S.20



Text-fig. S.lxi

Serial transverse sections of Rhaetina gregaria (SUSS).
 Rhaetian; Brem by Oberwössen, Bavaria - 91 St.Johann in
 Tirol. Specimen kindly donated from the collection of Prof.
 DEHM, Pal.Inst.Munich. x3 Loop traceable to 10.1mms. Total
 length of specimen 24.0mms. PC.Nr.43 Loop reconstructed
 in text-fig.lxii



Text-fig. S.lxii

Reconstruction of the loop of Rhaetina gregaria (SUESS).
Made from the sections shown in text-fig. S.lxi x5

Rhaetina gregaria ?ssp.nov.

Plate 19, figs.9-11; text-fig.S.lxiii; text-plate S.20

Description:

From a single locality in Bavaria several hundred specimens were obtained of a small Rhaetina apparently fully grown at 16mms. length, 14mms. breadth, and 9mms. thickness. In outline they are smoothly rounded with a low, broad beak and only a slight anterior flattening. Both valves are regularly convex in lateral profile and there is only a little median accentuation of the pedicle valve in anterior profile. The anterior commissure is gently sulciphate and this is reflected on the shell surface which also shows fine radial striations and marked growth lines.

The internal structure is the same as that of R.gregaria. The loop shows the same transverse flattening but is 50% of the total valve length in contrast to about 40%.

Remarks:

The concentration of growth lines near the anterior margin, the sulciphate of the anterior commissure, and the presence of folding, albeit shallow, for at least a third of the length of the valves, make it certain that the specimens are fully grown and not juveniles artificially concentrated. Therefore they may be considered as either stunted, as a subspecies of R.gregaria, or simply as a separate species.

Although the intimate association of a Rhaetina with the coral Thecosmilia is unusual, there is no evidence that it represented unfavourable living conditions for the brachiopod. In fact the richness of the locality indicates otherwise. In addition the only other accompanying brachiopod, Zugmayerella uncinata, is not noticeably small and certainly no smaller than at Hindelang where it occurs with typical R.gregaria. The difference in proportionate length of the loop also indicates individuality rather than overall reduction in size. Therefore stunting seems unlikely.

Two other localities where R.gregaria is found with Thecosmilia are known to the writer. Of these Val Spirola in the Lombardy Alps

consists of almost wholly of an exposure of massive limestone with vertical, unfragmented corals, and brachiopods (previously unknown there) are too rare to have any character as an assemblage. At Mała Swinica in the Polish Tatra, many of the thin bedded limestones interspersed with shale contain Rhaetina and fragments of Thecosmilia. The washing of the specimens down the profile makes accurate bed by bed collecting difficult and was not attempted by the writer. Although it is notable that the total collection from this locality is dominated by small specimens, those which are approaching maturity are still some 30% larger than those from Bavaria, and very few have a comparable plumpness, broadness of bead and roundness of outline.

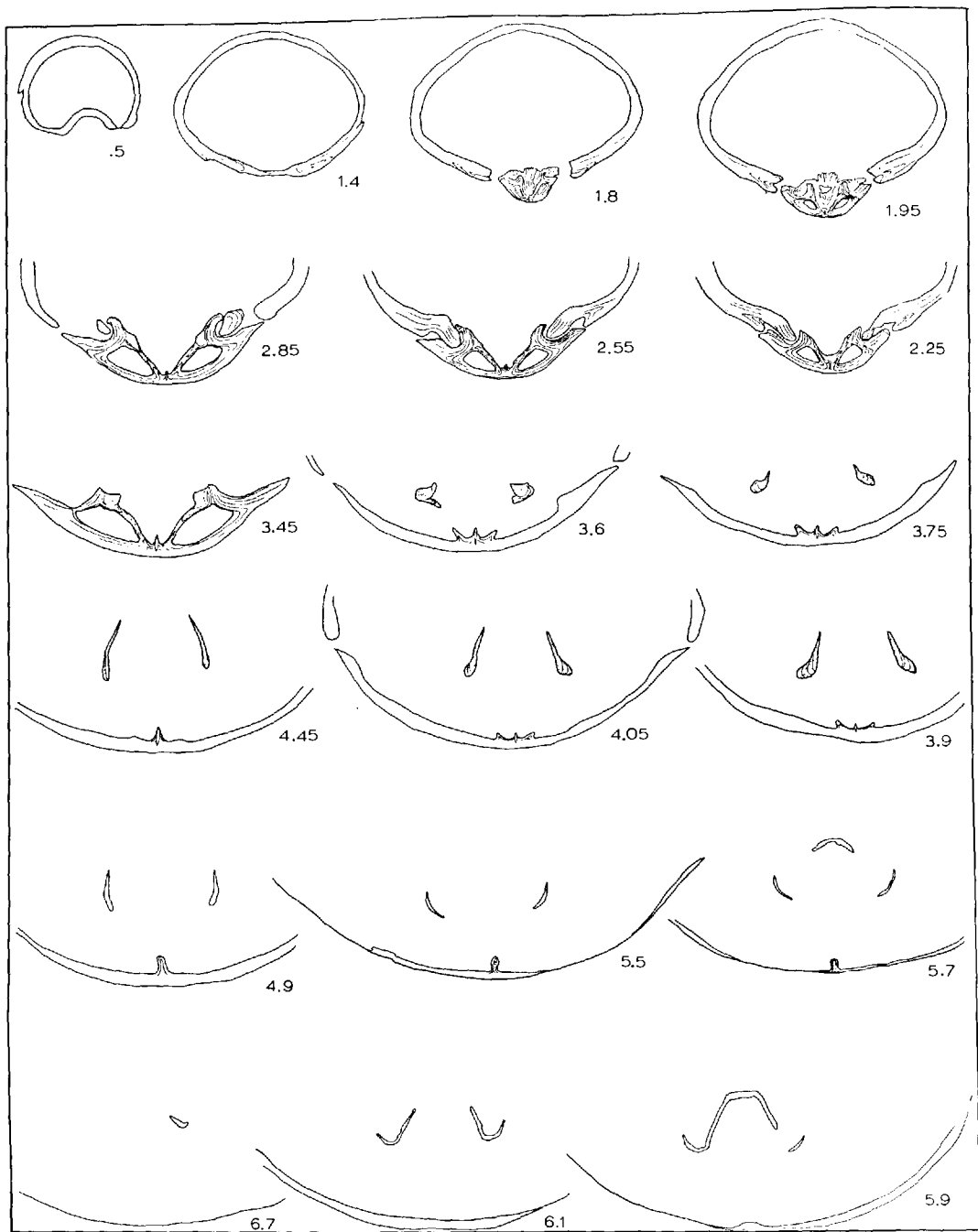
Therefore the Rhaetina described here may prove to have a distinct and consistent character not matched at other localities. However, the variation of R. gregaria is so great that it is inadvisable to establish a closely related species on the evidence of one collecting point alone. The creation of a local ecological subspecies or a separate species are both possibilities and further collecting is needed.

Dimensions of Figured Specimens:

	length	breadth	thickness
18/9	13.0	12.0	7.0
18/10	13.1	12.2	7.3
18/11	15.3	14.0	8.0

Material:

About 350 specimens from Ampelsbach by Achenkirch, Bavaria;
R/44825: H/52700. From the middle part of the Rhaetian succession just below Choristoceras marshi (see QUENSTEDT 1951).



Text-fig. S.lxiii

Serial transverse sections of Rhaetina gregaria
 ?ssp.nov. Rhaetian; Ampelsbach by Achenkirch, Bavaria;
 R/44825:H/52700 x4 Loop traceable to 6.8mm. Total
 length of specimen 14.3mm. PC.Nr.63

Rhaetina pyriformis (SUESS), 1854

Plate 18, figs.1-6; text-fig. S.lxiv

- 1854 Terebratula pyriformis SUESS, p.13, pl.3, figs.6-8
 1854 Terebratula horia SUESS, p.14, pl.3, fig.9
 1859 Terebratula pyriformis SUESS; WINKLER, p.22
 1861 Terebratula horia SUSS; GUMBEL, p.400
 1861 Terebratula pyriformis SUESS; STOPPANI, p.89, pl.18, figs.15,16
 1880 Terebratula pyriformis SUESS; ZUGMAYER, p.11, pl.3, figs.12-21
 ?1890 ~~Terebratula~~ aff. piriformis SUESS; BITTNER, p.157, pl.39, figs. 12-14
 1890 Terebratula piriformis SUESS; BITTNER, p.278, (partim), non pl.26, fig.1
 ?1892 Terebratula cfr. piriformis SUESS; BITTNER, p.21, fig.21
 1917 Terebratula pyriformis SUESS; GOETTEL, p.117, pl.7, figs.9,10
 ?1932 Rhaetina taurica MOISSEIEV, p.598, pl.1, figs.14-17
 1947 Rhaetina pyriformis SUESS, n.var.caucasica MOISSEIEV; p.77, pl.9, fig.7
 1947 Rhaetina skirdaensis MOISSEIEV, p.79, pl.9, fig.3
 ?1958 Terebratula pyriformis SUESS; MAHEL, p.145, pl.6, figs.1,2
 1962 Terebratula pyriformis SUESS; PREDA, p.64, pl.1, fig.1
 1963 Rhaetina pyriformis (SUESS); DAGIS, p.145, pl.22, fig.1-5
 1963 Rhaetina taurica MOISSEIEV; DAGIS, (partim) p.151, pl.23, figs.1,3
 non 1863 Terebratula pyriformis SUESS; OOSTER, p.6, pl.1, fig.7,8
 non 1863 Terebratula pyriformis SUESS; DESLONGCHAMPS, p.70, pl.8bis. figs. 7,8

Lectotype:

The originals of SUESS pl.3, figs.7 and 8 are preserved in the Geol. Bundes.Vienna, but fig.8 was only referred to as ?pyriformis and therefore the original of fig.7 is selected as lectotype.

Dimensions of Lectotype:

Length 59.1mm., breadth 45.7mm., thickness 31.5mm.

Type Locality:

Kitzberg by Neusiedl, Piesting Tal, Lower Austria.

Range and Distribution:

Norian of Slovakia (Stratenska hornatins), the Crimea and Caucasus.

Rhaetian of the Northern Alps and N.W. Rumania (Apuseni Mts.).

Probably the Carnian of the Northern Alps and the Bakony Forest (Hungary).

Diagnosis:

Large Rhaetina; anterior commissure broadly and flatly plicate; no sinus; weak, broad fold. Beak very prominent, pedicle opening large. Transverse band gently arched. Otherwise as genus.

Description:

Rhaetina pyriformis is a very large member of the genus, normally reaching 40mm., and exceptionally as much as 60mm., in length (e.g. SUESS 1854, pl.3, fig.7, and GOETEL 1917, pl.7, fig.9). In lateral profile the brachial valve is always less convex than the pedicle valve due to a broad slightly bowed, plication of the anterior commissure. A flat fold is commonly distinguishable, but no sinus is developed. In posterior view the convexity of the pedicle valve dominates the brachial valve, often very markedly in young specimens, in the same manner as seen in R. caucasica (see DAGIS 1963 p.161, pl.24, fig.6, and pl.25, figs.1-3). The hinge line is smoothly curved and the cardinal margins pass gently into the ovate outline of the shell. The beak is large, suberect, and has rounded beak ridges. The pedicle opening is mesothyrid in position. Growth lines are accompanied on internal casts by faint longitudinal striations.

Internally the structure is typical of the genus. The hinge plates are more widely separated on the floor of the brachial valve in the Austrian specimen figured here, than in the specimen figured by DAGIS (1963 fig.4), but this is quite normal internal variation.

Remarks:

There is no difficulty in distinguishing R. pyriformis from R. gregaria or from the Caucasian species, R. caucasica, R. elliptica and R. beskessensis. However, some confusion exists with R. taurica MOISSEIEV, and the holotype of this species appears to fall within the range of R. pyriformis. The specimen is from the Norian of the Crimea and is one of only five collected. Six years before he established R. taurica, MOISSEIEV (1927 p.749) recorded R. cf. pyriformis with four specimens from the same area. DAGIS (1963 p.222) repeats these records in general discussion but

does not consider R.cf.pyriformis in his synonymies. He lists about 150 specimens of R.taurica from the Caucasus, most of which are from one locality, but of the specimens he figures on pl.23 those of figs.1 and 3 appear to be R.pyriformis, and those of figs.2, 4 and 5, R.elliptica. Although DAGIS points out the obvious differences between R.taurica and several other Rhaetina species, he nowhere gives any means of distinguishing it from R.pyriformis. There are at present five species of Rhaetina reported from the Norian of the Caucasus (or four if it be accepted that R.turcica = R.gregaria, -see above) and so many closely related species of this genus from so restricted an area seems to the writer to be unlikely. Therefore Rhaetina taurica is questionably placed in synonymy with Rhaetina pyriformis; only further examination of the relevant Caucasian material can confirm this.

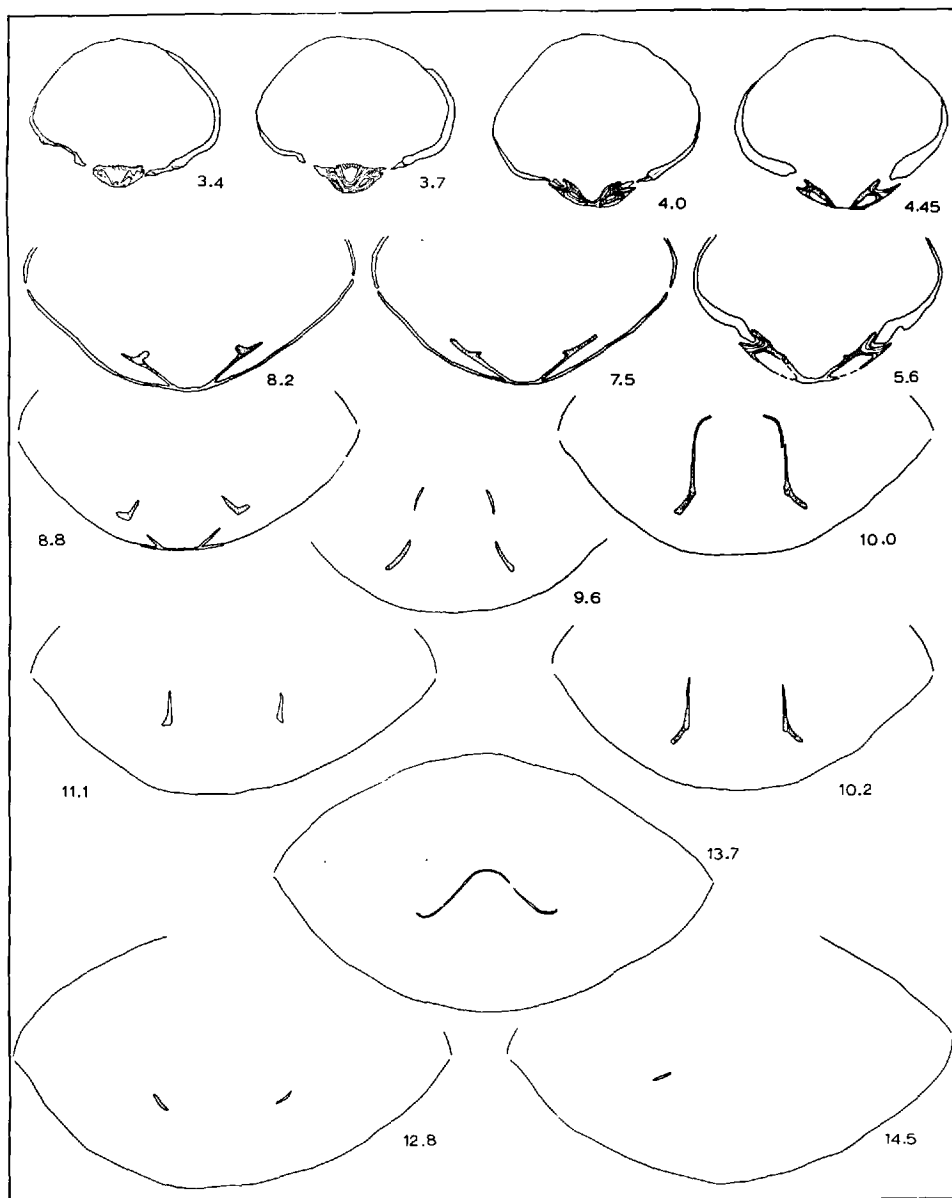
Rhaetina pyriformis is present in the Upper Norian of Drnava, although BITTNER's figure is probably of another species. In addition there are a number of figures of R.cf.pyriformis from the Carnian (see DIENER 1920, p.87, for a full list), and those given by BITTNER of a specimen from the upper part of the Carnian of the Bakony Forest, Hungary (1890 p. 157) and the middle part of the Carnian of the Vienna region (1892 p.21), seem to fall easily into R.pyriformis. Three specimens kindly loaned to the writer by Dr.M.GANEV from the ?Upper Carnian-Lower Norian of the East Bulgarian Balkans have supported the view that R.pyriformis is present at this level.

Dimensions of Figured Specimens:

	length	breadth	thickness
19/1	41.8	32.7	20.5
19/2	27.1	22.5	12.0
19/3	27.9	22.0	13.1
19/4	22.0	17.1	9.5
19/5	48.0	34.5	22.3
19/6	29.7	23.7	13.0

Material:

'Mandlingbauer in der Oed, .. Kitzberg N.' as plate 19, figs.1-3.
- 6, Geol.Bundes. Vienna, 5 rot 19/3; 'Kitzberg' - 6, Geol.Bundes. Vienna,
968; 'Mandling Wald' - 6, B.M.N.H., B 39202; Ober Kaisersteffel, Piesting
Tal - 3, T.70; Steinplatte above Waidring - 15, T.71; Hirtenberg, Triesting
Tal - 3, T.72; Kitzberg by Neusiedl - 5, T.73; Hybe, Slovakia - 6, T.74;
Val Frunsi, Ferice, Arieşeni, Rumania - 8, T.75; Tarkăița, Moneasa,
Rumania - 7, T.76.



Text-fig. S.lxiv

Serial transverse sections of *Rhaetina pyriformis* (SUESS). Rhaetian; Steinplatte by Waidring, Tirol; 47° 36'15''N. 12°34'30''E. Collected loose close to the point indicated on text-plate 1. Loop traceable to 14.6mm. Total length of specimen 34.2mm. PC.Nr.64

Other Terebratulida from the Rhaetian.Zugmeyeria rhaetica ZUGMAYER, 1880

- 1880 Terebratula rhaetica ZUGMAYER, p.13, pl.1, figs.30, 31
 ?1942 Terebratula (Zugmeyeria)rhaetica ZUGMAYER; KUHN, p.133
 ?1962 Terebratula rhaetica ZUGM.; PREDA, p.64

This small species, with dental lamellae, but lacking inner hinge plates, was described by ZUGMAYER from only two localities. Since then it has not been certainly recognised, for the external appearance is not diagnostic and neither KUHN nor PREDA sectioned material.

WAAGEN (1882 p.334) made the species the type of a new genus, Zugmeyeria, on the basis of ZUGMAYER's 'Cardinal-Schliff' (1880, pl.1, fig.23) and DAGIS (1963 p.171) used it as the type of his family, the Zugmayeriidae (nom.correct. above, pro Zugmayeridae DAGIS, 1963 p.171). This family was subsequently regarded by MUIR-WOOD (1965 p.768) as a junior subjective synonym of the Dielasmatinae. The writer is not in agreement with MUIR-WOOD's decision and it is further discussed in Remarks under Dielasmatidae.

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PLATE 1

Figs. 1-10. Fissirhynchia fissicostata (SUESS). x 1.5

1. Lofer Graben between KHssen, Aust. and Reit im Winkl, Bav. Specimen from quiet water environment showing oval shape and very small pedicle opening.
2. 'Rechtes Gehänge des Kaltenganges bei Wallegg, Kaiser N.W., hinab in den Kaltengang.' Geol. Bundes. Vienna. 6 rot 19/3.
3. Vorder Mandling by Waldegg, Piesting Tal. From coarse sandy limestone and showing protrusive beak. See also fig.10. Topotype.
4. Locality as fig.2.
5. Upper Norian of Drnava, S.Slovakia. The flatness of the brachial valve is notable in views b. and d.
6. Steinplatte by Waidring, (Stp. 1 on text-plate 1).
7. 'Brand', - Piesting Tal. Pal.Inst.Univ. Vienna, ZUGMAYER colln. Original of ZUGMAYER (1880), pl.4, fig.14.-var. applanata GUMBEL (1861).
8. Locality and source as fig.7. Original of ZUGMAYER (1880), pl.4, fig.17.- var. longirostris GUMBEL (1861).
9. Upper Norian, Drnava, S.Slovakia (as fig.5).
10. Vorder Mandling, Piesting Tal, (as fig.3).

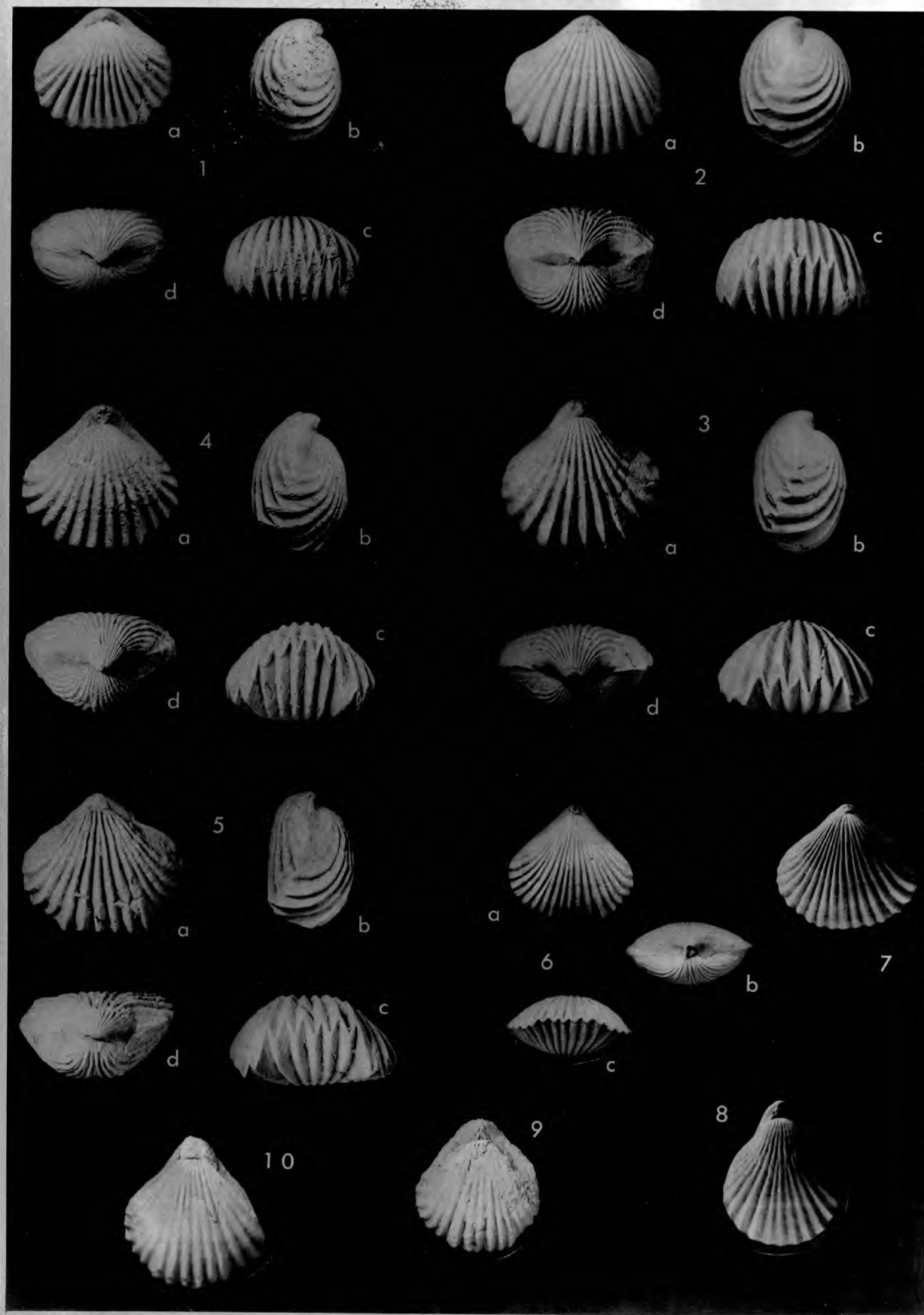


PLATE 2

Figs. 1-2. Fissirhynchia fissicostata (SUESS) x 1.5

1. Hierlatz by Hallstatt, Aust. Geol.Bundes. Vienna, 2907. Original of GEYER (1898), pl.6, fig.32.
2. Locality and source as fig.1

Figs. 3-7. Osmarella starhembergica (ZUGMAYER). x 1.5

- 3-4. 'Brand' - Piesting Tal, L.Aust. Pal.Inst.Univ. Vienna, ZUGMAYER colln. Originals of ZUGMAYER(1880), pl.4, fig. 19 - fig.4, lectotype and 21 - fig.3.
- 5-7. Locality as above. Topotypes.

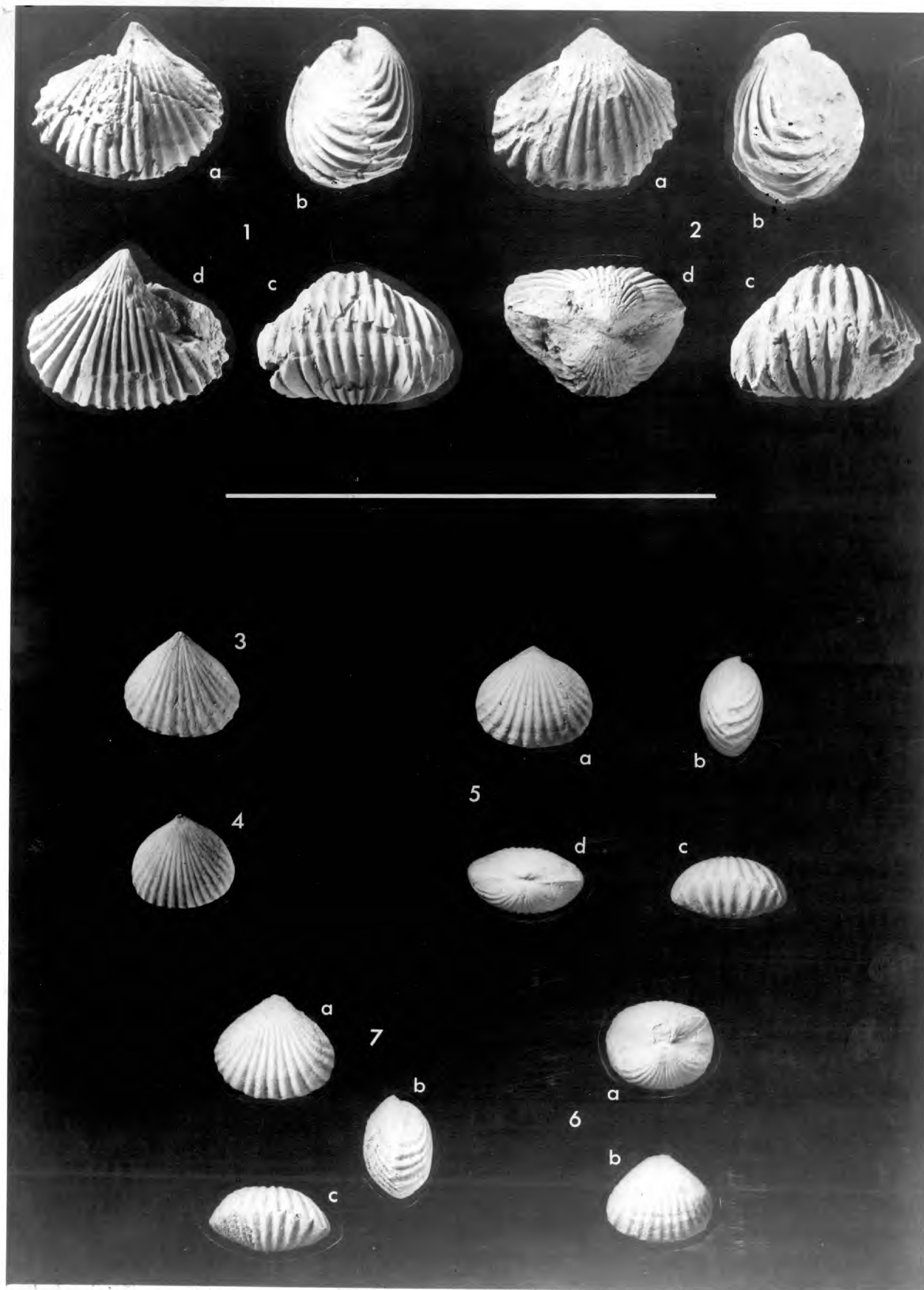


PLATE 3

Figs. 1-5. Gen.nov.A. sp.nov.A. x 1.5

'Marmorgraben bei Mittenwald', Bav. B.M.N.H.

B 24614. These are the only specimens known.

Figs. 6-7. Piarorhynchia cf. P.juvenis (QUENSTEDT)x 1.5.

6. Hohe Mandling, by Waldegg, Piesting Tal, L.Aust.

7. Ober Kaisersteffel also by Waldegg.

Fig. 8. Osmarella sp.nov.

Ober Kaisersteffel, by Waldegg, Piesting Tal, L.Aust.

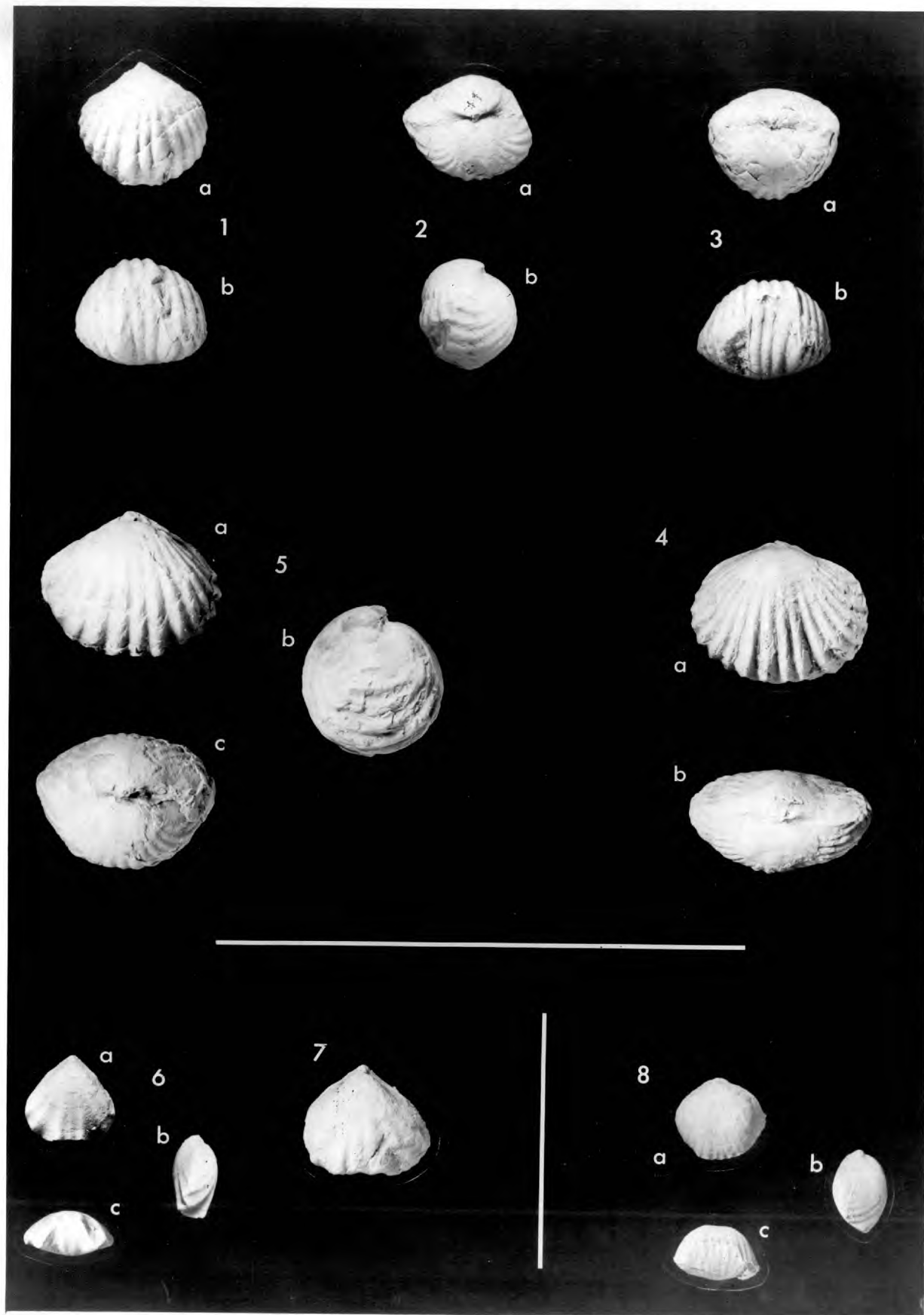


PLATE 4

Figs. 1-2. Gen.nov.A sp.nov.B x 1.5
Juchtenkopf by Pertisau, Achensee, Aust.

Figs. 3-5. Gen.nov.A sp.nov.C x 1.5
Lahnenwies Graben near Farchant, Bav.

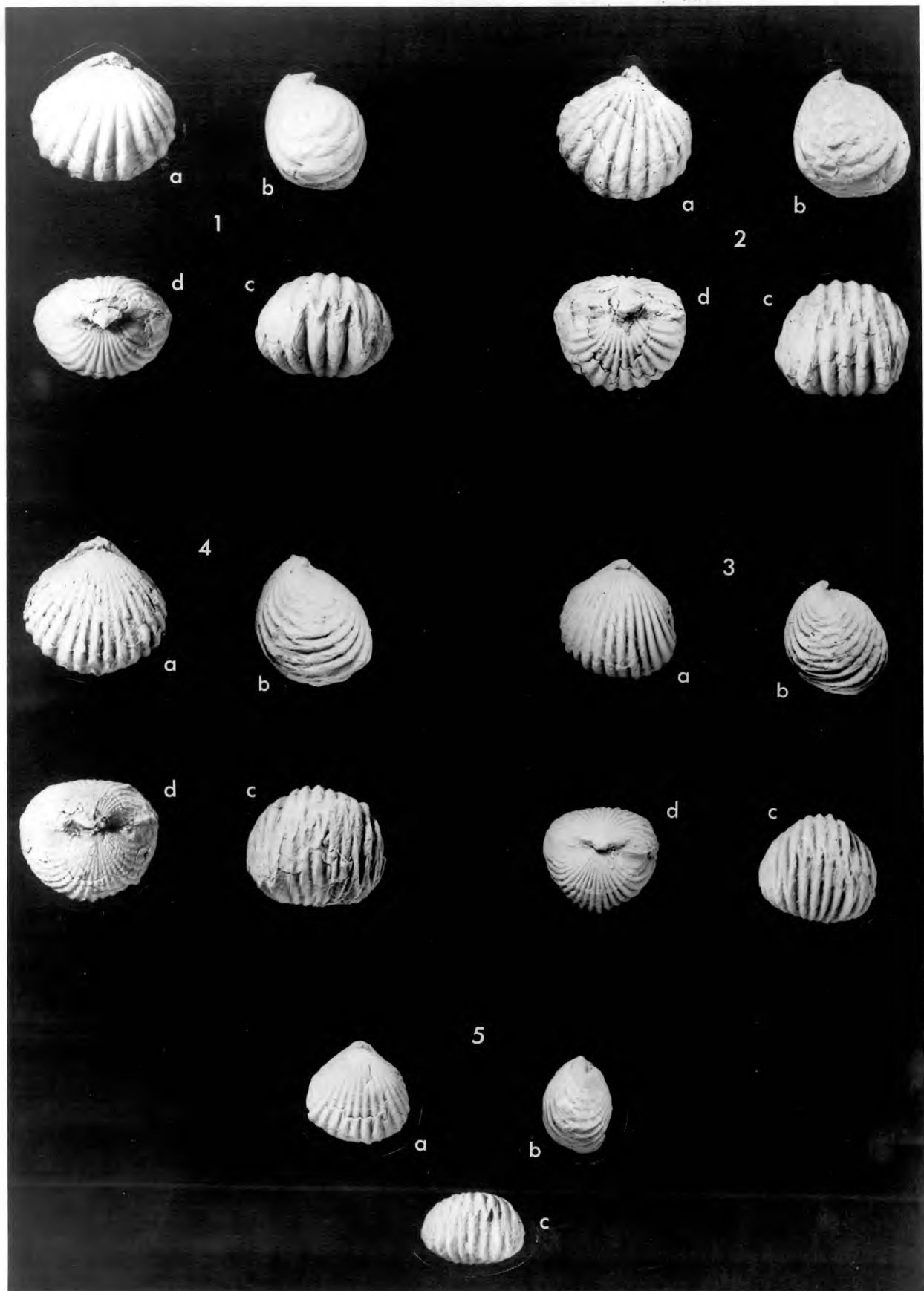


PLATE 5

Figs. 1-7. Austrirhynchia cornigera (SCHLAFHAUTL). x 1.5

1-2. Koth-Alpe, north of Bayerischzell, Bav. Topotypes.

3. 'Bistro' - now Bystry potok, west of Ruzomberok,
Slovakia. Pal.Inst.Univ. Vienna, ZUGMAYER colln.
Original of ZUGMAYER (1880), pl.4, fig.30 - 'Karpatische
Form'. x 2.

4. 'Kaisersteffel' - Piesting Tal, L.Aust. Pal.Inst.
Univ. Vienna. ZUGMAYER colln. Original of ZUGMAYER
(1880), pl.4, fig. 31. - 'Kössener Form'.

5-7. Axelstein by Jachenau, Walchen See.

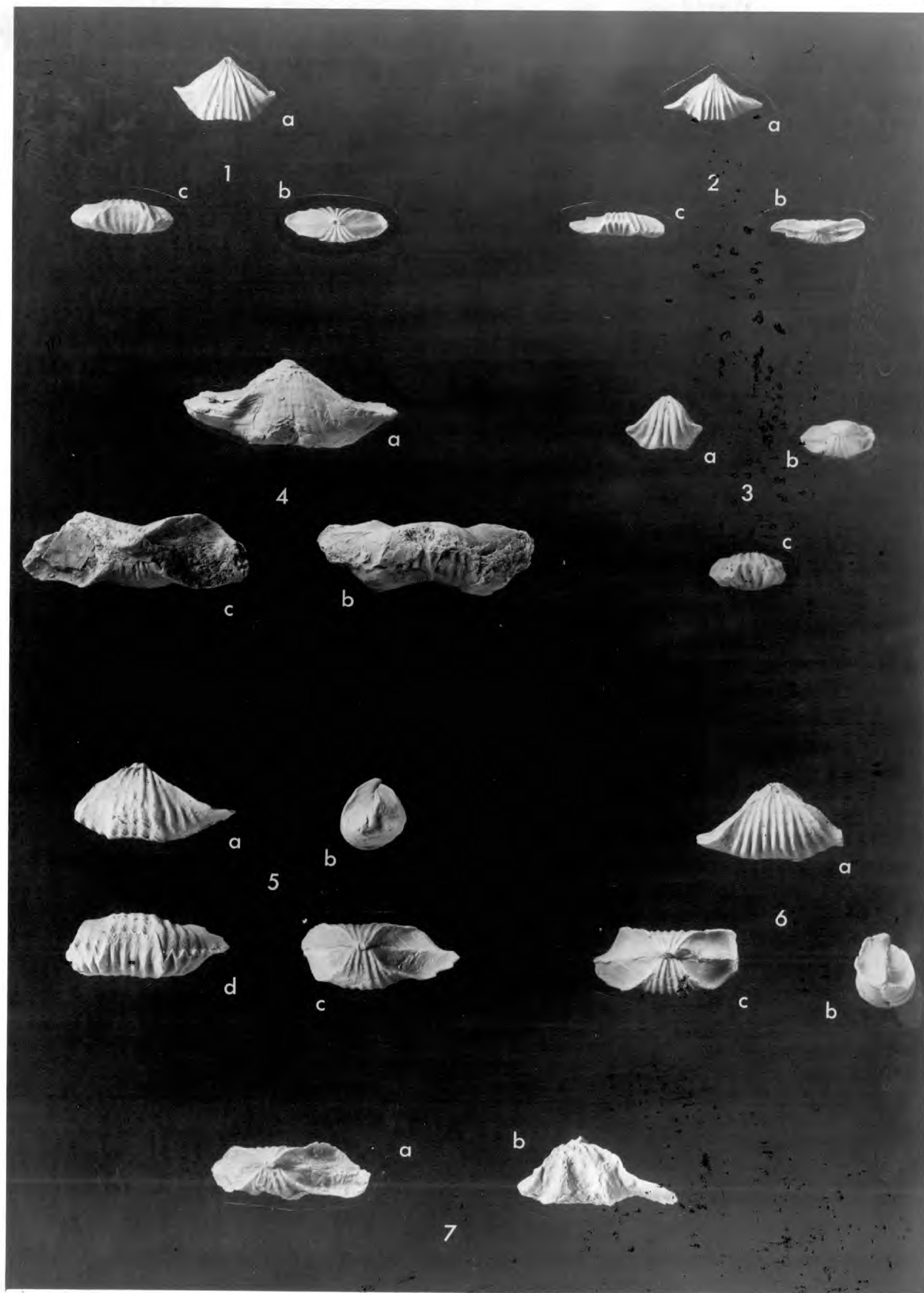


PLATE 6

Figs. 1-4. Calceirhynchia subrinosa (SCHAFHAUTL). x 1.5

- 1+3. Lofer graben between Küssen, Aust. and Reit im Winkl, Bav. Globose specimens from a probable colonial assemblage of about 250. Topotypes.
4. 'Weissloferbachgraben, bei Reit im Winkl'. Nat.hist. Mus. Vienna. D 3769. Very similar to lectotype. Topotype?

Figs. 5-6. ?Caucasorhynchia sp. x 1.5

5. 'Ober Weidring', Tirol, Aust. Nat.hist.Mus. Vienna. 1963 Nr.563/5. Possibly from the slopes of the Steinplatte reef.
6. 'Schwarzlofer Alm', by the Steinplatte reef as above. ZUGMAYER colln. Pal.Inst.Univ. Vienna.

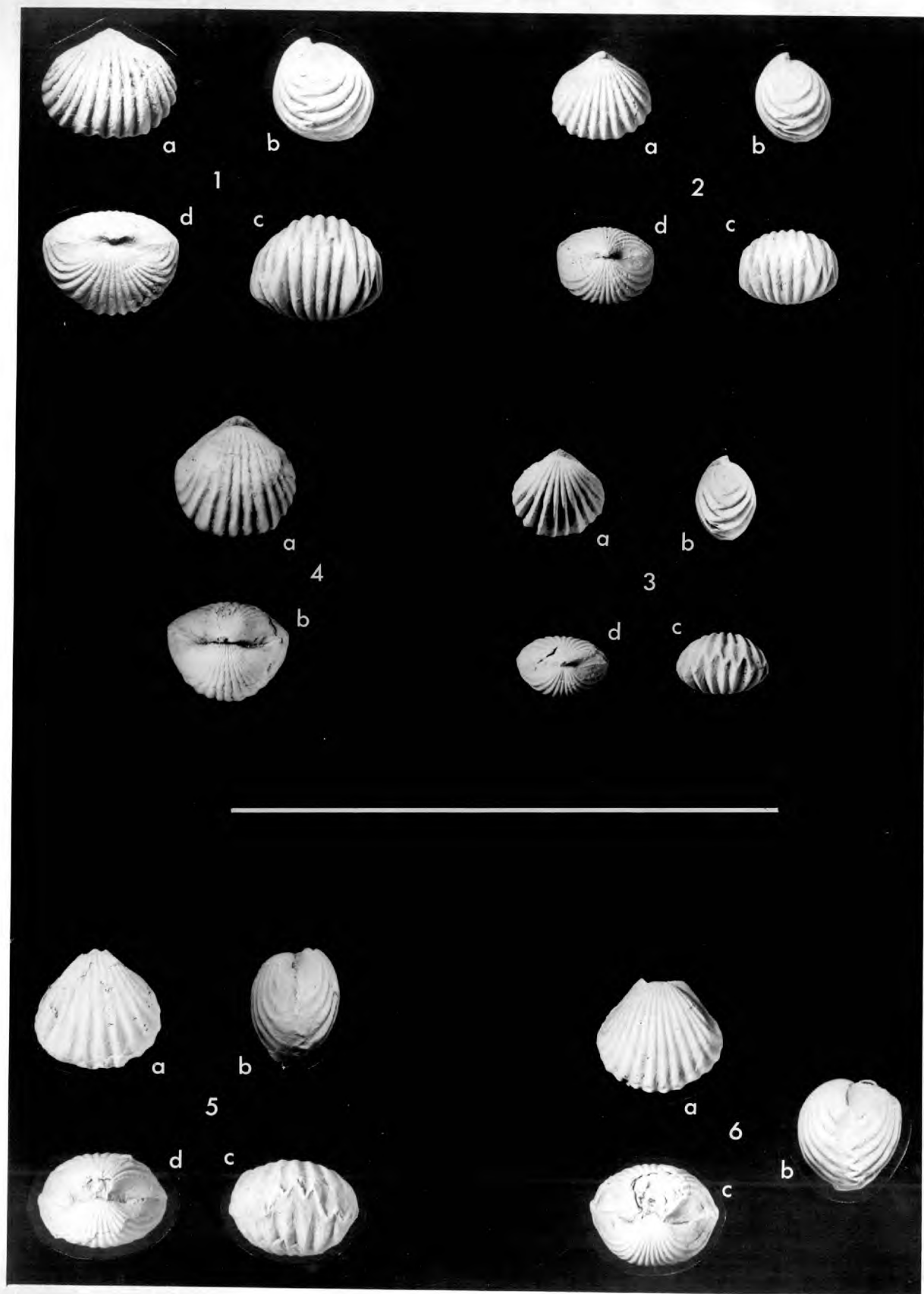


PLATE 7

Figs. 1-5. Calcirhynchia cf. C? pectiniformis (CANAVARI); TRAUTH
x 1.5

- 1-2. 'Mandling Wald' by Waldegg, Piesting Tal, L.Aust.
B.M.N.H., fig.1 - BB 43205; fig.2 - BB 43207.
3. Ober Kaisersteffel, by Waldegg, Piesting Tal, L.Aust.
4. Upper Norian, Drnava, S.Slovakia.
5. Source and locality as figs.1-2. BB 43206.

Figs. 6,7. Calcirhynchia cf. C. obtusifrons (SUESS). x 1.5

6. 'Brand' - Piesting Tal, L.Aust. Pal.Inst.Univ. Vienna.
ZUGMAYER colln. Original of ZUGMAYER (1880), Pl.4, fig.
29.
7. Upper Norian, Drnava, S.Slovakia.

Fig. 8 ?Calcirhynchia fringilla (BITTNER). x 1.5

Carnian, Oberseeland, S.Alps. Geol.Bundes. Vienna,
BITTNER colln. Holotype of BITTNER (1892), pl.4, fig.23.

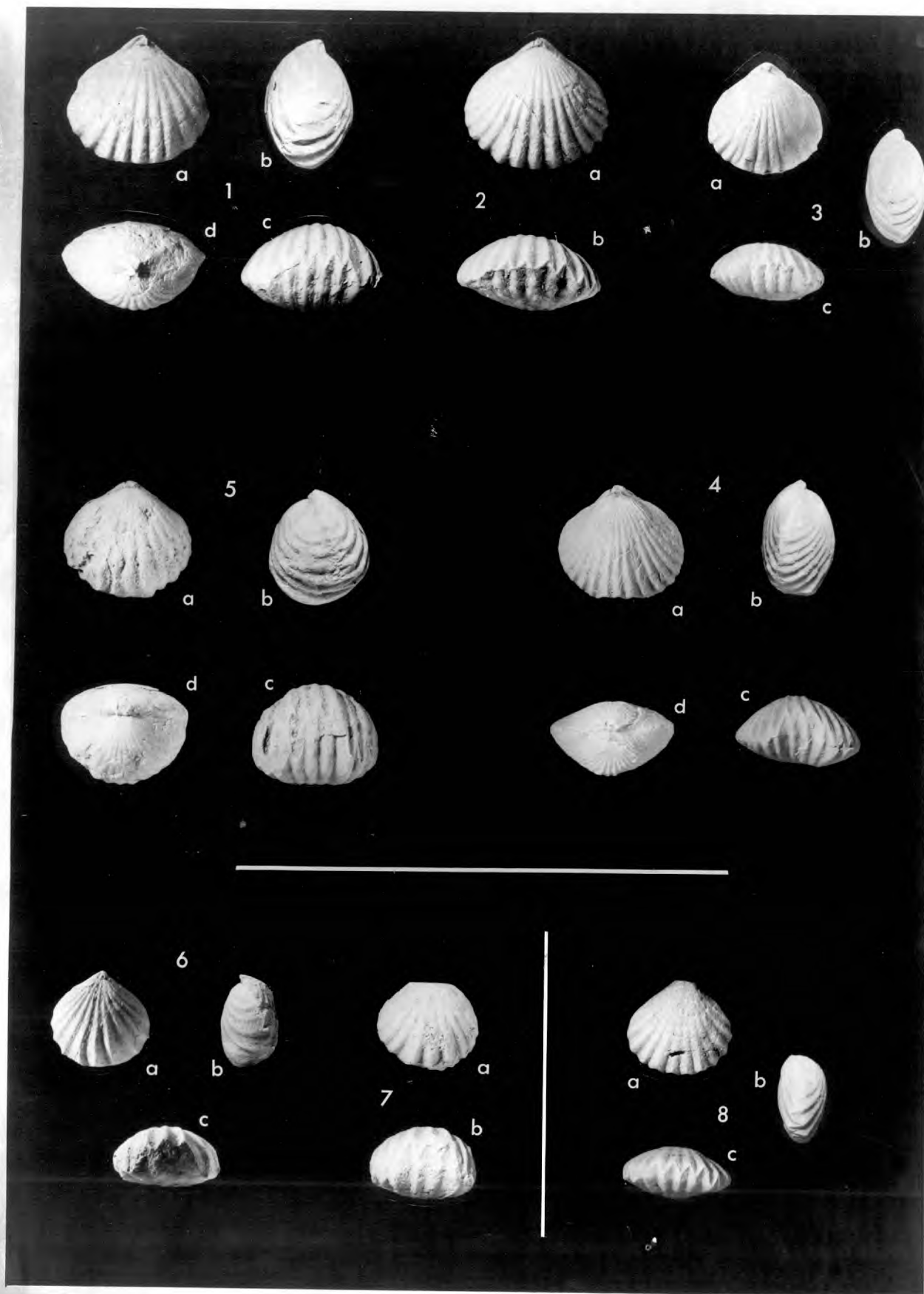


PLATE 8

Figs. 1-7. Vindobonella katzeri sp.nov. x 1.5

1-5. Originals of ZUGMAYER (1880), pl.4. Pal.Inst.
Univ. Vienna. ZUGMAYER colln.

1. 'Kaisersteffel' - Piesting Tal. L.Aust. - fig.24.
2. 'Vorder Mandling' - Piesting Tal. L.Aust. - fig.22.
3. Original preparation for fig.12.
4. Hindelang, W.Bav. - fig.26.
5. 'Kitzberg' by Neusiedl, Piesting Tal.
6. Paratype showing muscle scars. Locality as fig. 7.
7. 'Hirtenberg unweit südlich des Kalkofens am rechten
Triesting Ufer, links vom Fussteig nach Enzesfeld'.
Geol.Bundes. Vienna, 3 rot 9/5. Holotype.

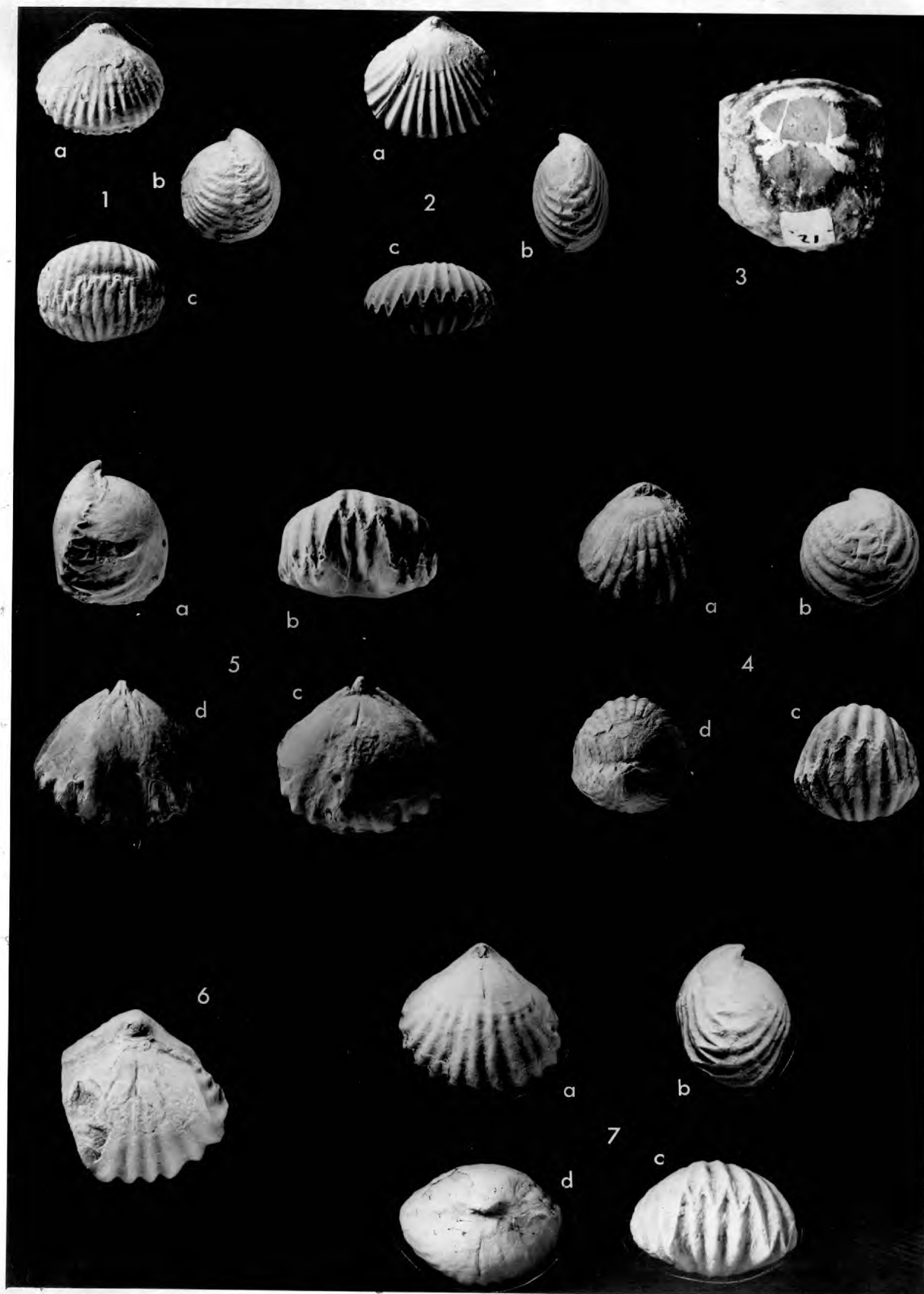


PLATE 9

Figs. 1-8. Vindobonella katzeri sp.nov. x 1.5

1-4. Hybe, by Liptovsky Mikulas, Slovakia. Locality of GOETEL (1917). Series of specimens from a single block. Collected, and kindly lent, by Dr.M.SIBLIK. Fig.4 shows notably extensive ribbing.

4-8. 'Rechtes Gehänge des Kaltenganges bei Wallegg, Kaiser N.W., hinab in den Kaltengang.' Geol.Bundes. Vienna, 9 rot 19/3.

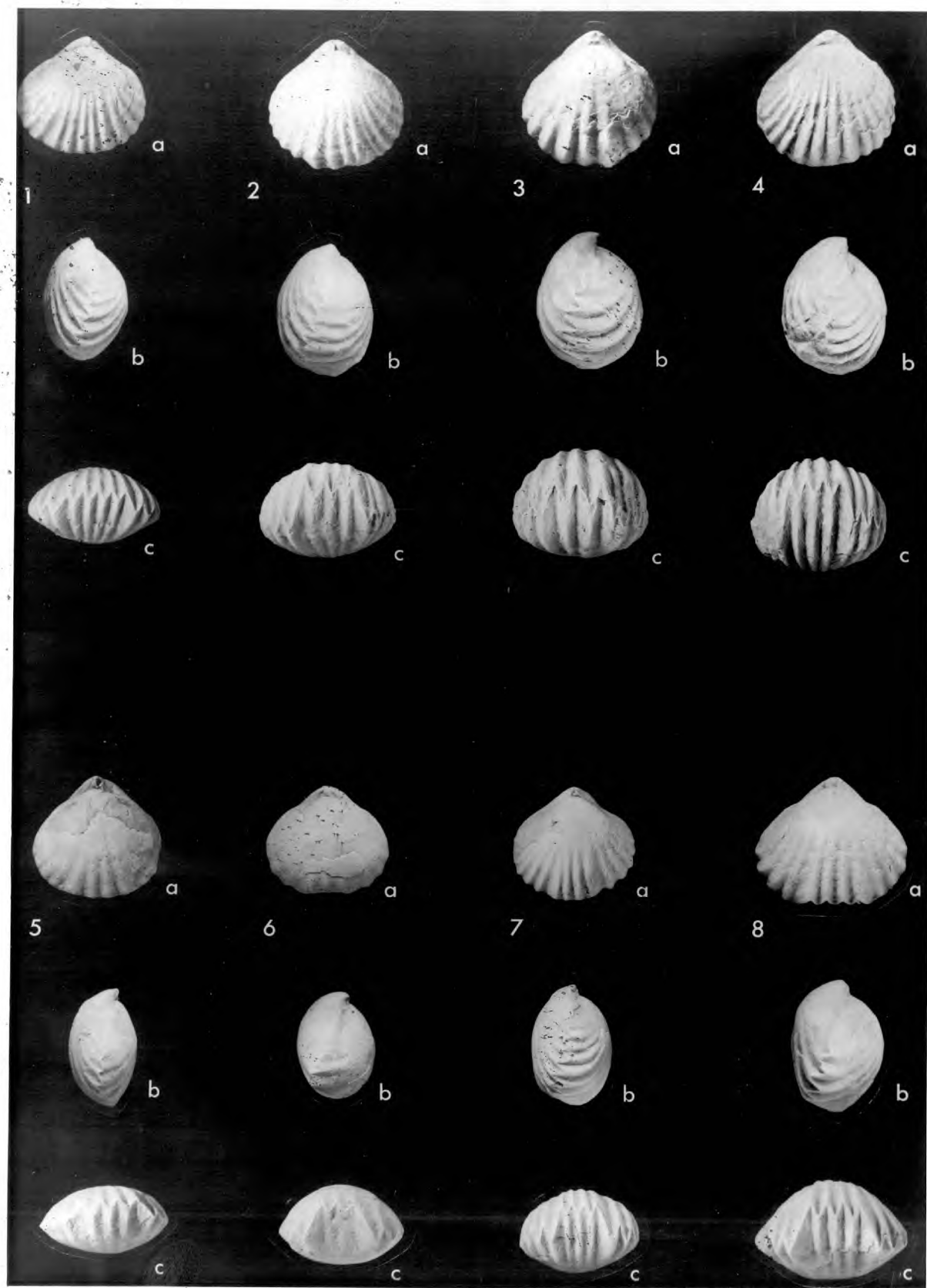


PLATE 10

Figs. 1-4. Carapezzia geyeri (BITTNER) x 1

1. Ober Pirkach, Drau Tal, S.Alps. Original of BITTNER
(1898), pl.12, fig.6. Lectotype. Geol.Bundes. Vienna, 3276.
- 2-3. Topotypes. Juveniles.
4. Topotype showing pallial markings. Geol.Bundes. Vienna.

Figs. 6-7. Mentzeliopsis cf. M.meridialis DAGIS. x 1

Marmor Graben by Mittenwald, Bav.

Fig. 5. Oxycolpella sp.nov. x 1

Hybe, by Liptovsky Mikulas, Slovakia.

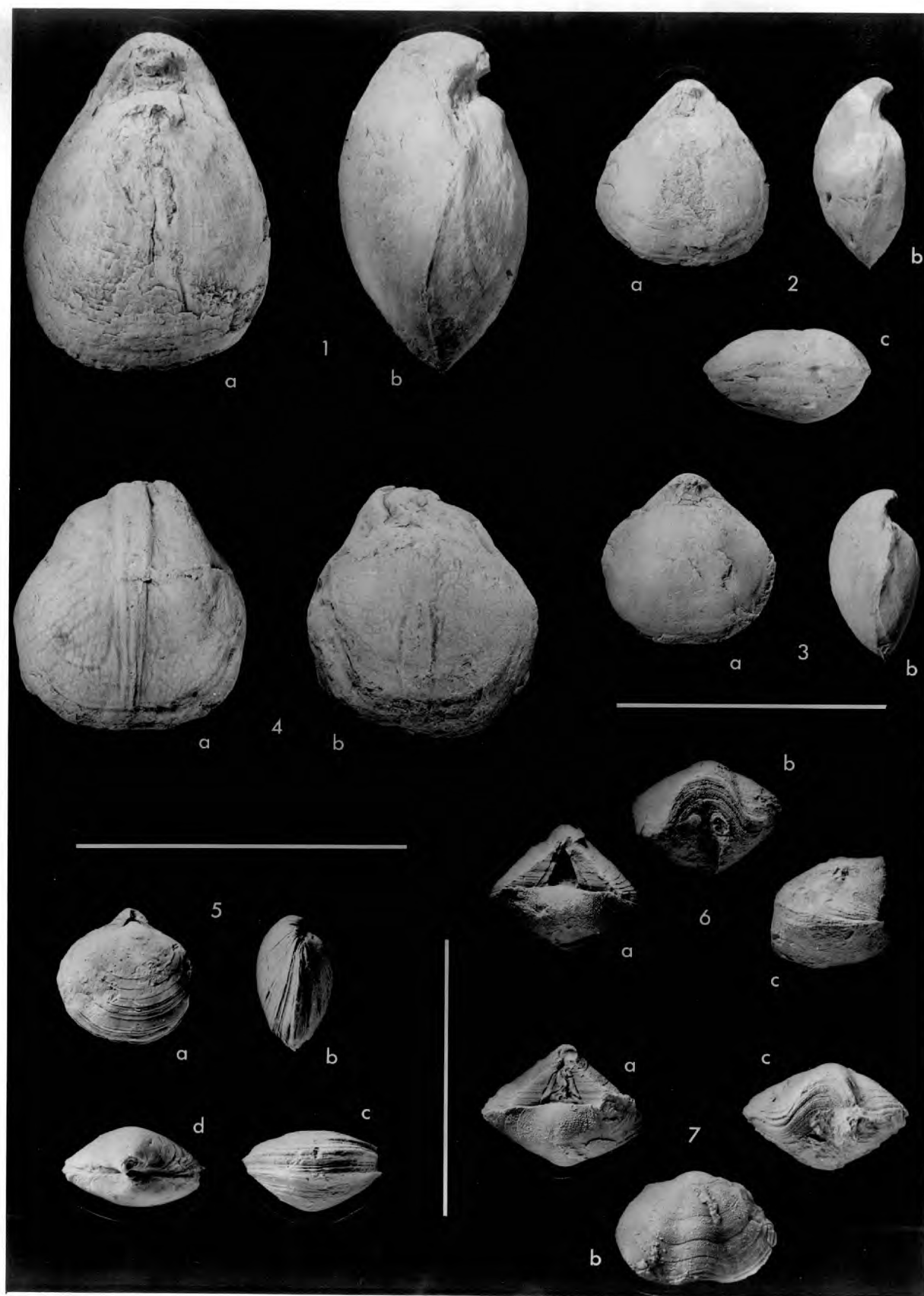


PLATE 11

Figs. 1-3. Sinucosta emmerichi (SUESS). x 1

1. 'Kitzberg' - by Neusiedl, Piesting Tal, L.Aust.
Pal.Inst.Univ. Vienna. ZUGMAYER colln. Original of
ZUGMAYER (1880), pl.4, figs.1-3.
2. Hybe, by Liptovsky Mikulas, Slovakia.
3. Kitzberg, as fig.1. Pal.Inst.Univ. Vienna.
ZUGMAYER colln.
4. Vorder Mandling, Piesting Tal, L.Aust.

Figs. 5-7. Laballa suessi (ZUGMAYER). x 1

5. Ober Kaisersteffel, Piesting Tal, L.Aust.
- 6-8. Hirtenberg, Triesting Tal, L.Aust. (Fig. 7c is
inverted).

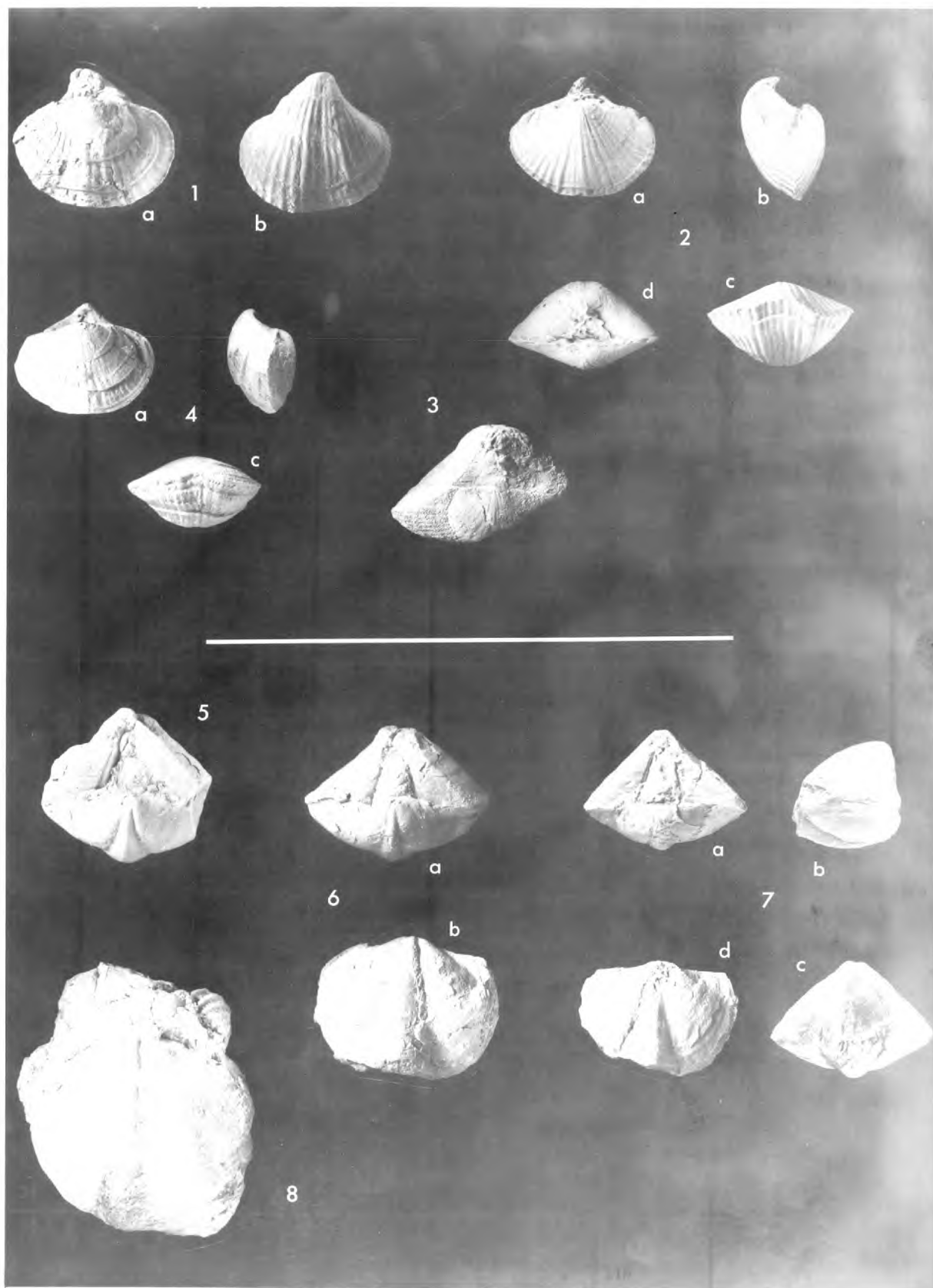


PLATE 12

Figs. 1-2. Zugmayerella koessenensis (ZUGMAYER). x 1

1. 'Kitzberg' - by Neusiedl, Piesting Tal, L.Aust.
Pal.Inst.Univ. Vienna, ZUGMAYER colln. Original of
ZUGMAYER (1880), pl.3, fig.2. Lectotype.
2. Locality as fig.1, Pal.Inst.Univ. Vienna, ZUGMAYER
colln. Original of ZUGMAYER (1880), pl.3, fig.3.
Juvenile. Syntype.

Figs. 3-6. Zugmayerella uncinata (SCHAFHAUTL). x 1

3. 'Bistrot' - near Bystry petek, Slovakia, Pal.Inst.Univ
Vienna, ZUGMAYER colln. Original of ZUGMAYER (1880), pl.3
fig.1.
4. Axelstein by Jachenau, Bav. See also text-plate S.9.
5. 'Kaisersteffel' - by Waldegg, Piesting Tal, L.Aust.
Pal.Inst.Univ. Vienna, ZUGMAYER colln. Original of
ZUGMAYER (1880), pl.3, fig.6 - Spiriferina austriaca
SUESS. See text-plate S.9.
6. Wildfellalm by Spitzingsee, Aust.

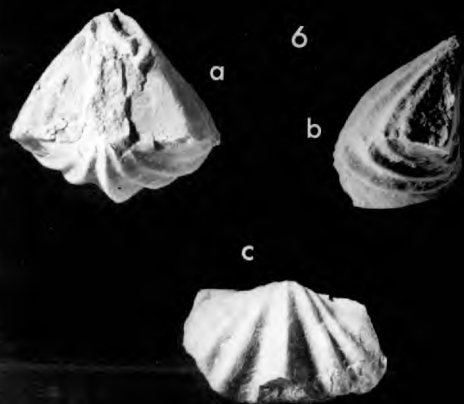
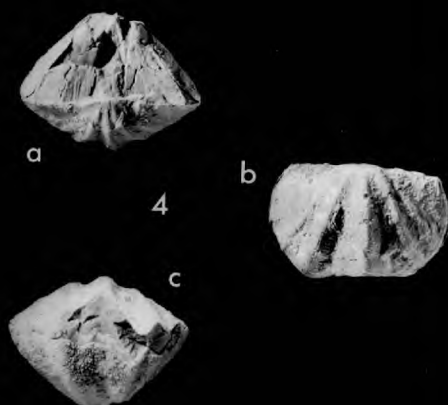
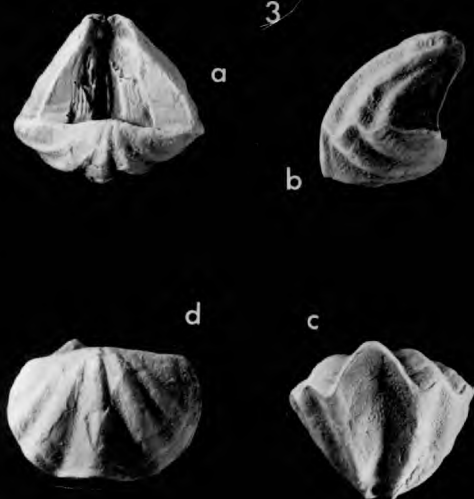
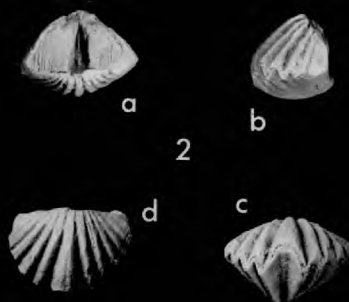
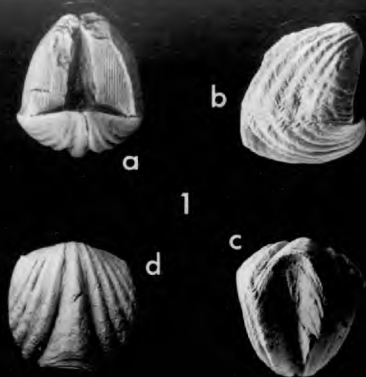


PLATE 13

Figs. 1-5. Oxycolpella oxycolpos (SUESS). x 1

1. 'Kössen' - Lofer Graben between Kössen, Aust. and Reit im Winkl, Bav. Geol.Bundes. Vienna, 1074.
Original of SUESS (1854), pl.1, figs. 1-4. Lectotype.
2. Locality as fig.1. Topotype.
3. Locality and source as fig.1. Original of SUESS (1854), pl.1, figs.5-7. Syntype.
4. Locality as fig.1. Topotype.
5. Marmor Graben by Mittenwald, Bav.

Figs. 6-8. Neoretzia superba (SUESS). x 1

6. 'Brand' - Piesting Tal, L.Aust. Pal.Inst.Univ. Vienna, ZUGMAYER colln. Original of ZUGMAYER (1880), pl.4, fig.6.
7. Hirtenberg, Triesting Tal, L.Aust. Topotype.
8. Upper Norian, Drnava, S.Slovakia. Topotype of BITTNER's (1890) species Retzia superbescens.

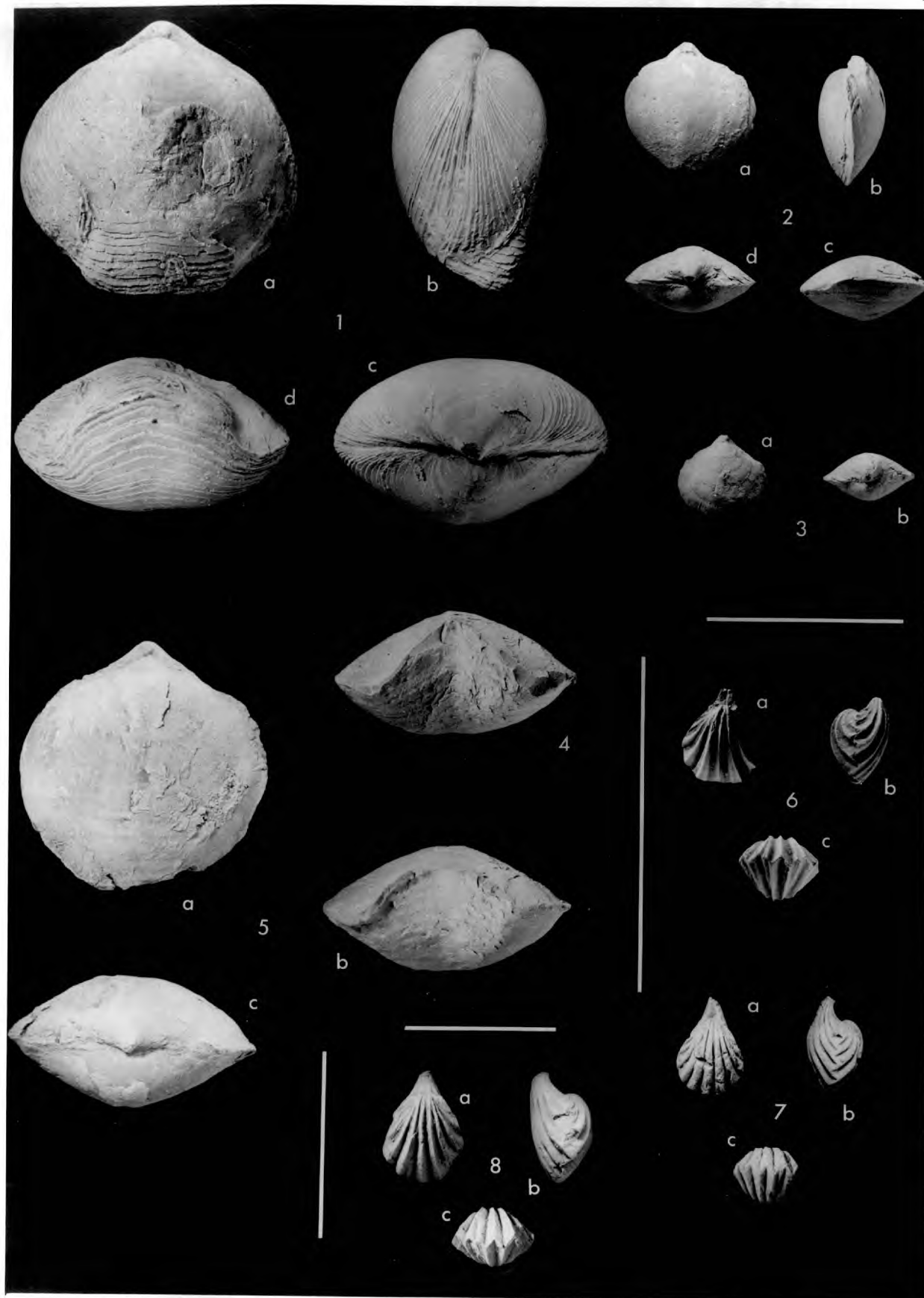


PLATE 14

Figs. 1-2. Mentzelia cf. M. glabra DAGIS. x 1
Hohe Mandling by Waldegg, Piesting Tal, L.Aust.

Fig. 3. ?Mentzelia praecursor (ZUGMAYER). x 1
'Kaisersteffel' - by Waldegg, Piesting Tal, L.Aust.
Pal.Inst.Univ. Vienna, ZUGMAYER colln. Original of
ZUGMAYER (1880), pl.4, figs.4,5. Holotype.

Figs. 4-8. 'Zeillera austriaca (ZUGMAYER). x 1

4. 'Kaisersteffel' - by Waldegg, Piesting Tal, L.Aust.
Pal.Inst.Univ. Vienna. Original of ZUGMAYER (1880).
pl.2, fig.13. Lectotype.
5. Hirtenberg, Triesting Tal, L.Aust.
6. Brand, Piesting Tal, L.Aust. Pal.Inst.Univ. Vienna.
ZUGMAYER colln.
7. Locality as fig.6. Juvenile.
8. Locality and source as fig.6. Original of ZUGMAYER
(1880), pl.2, fig.12. x 1.5, 8c. x 1. Syntype.

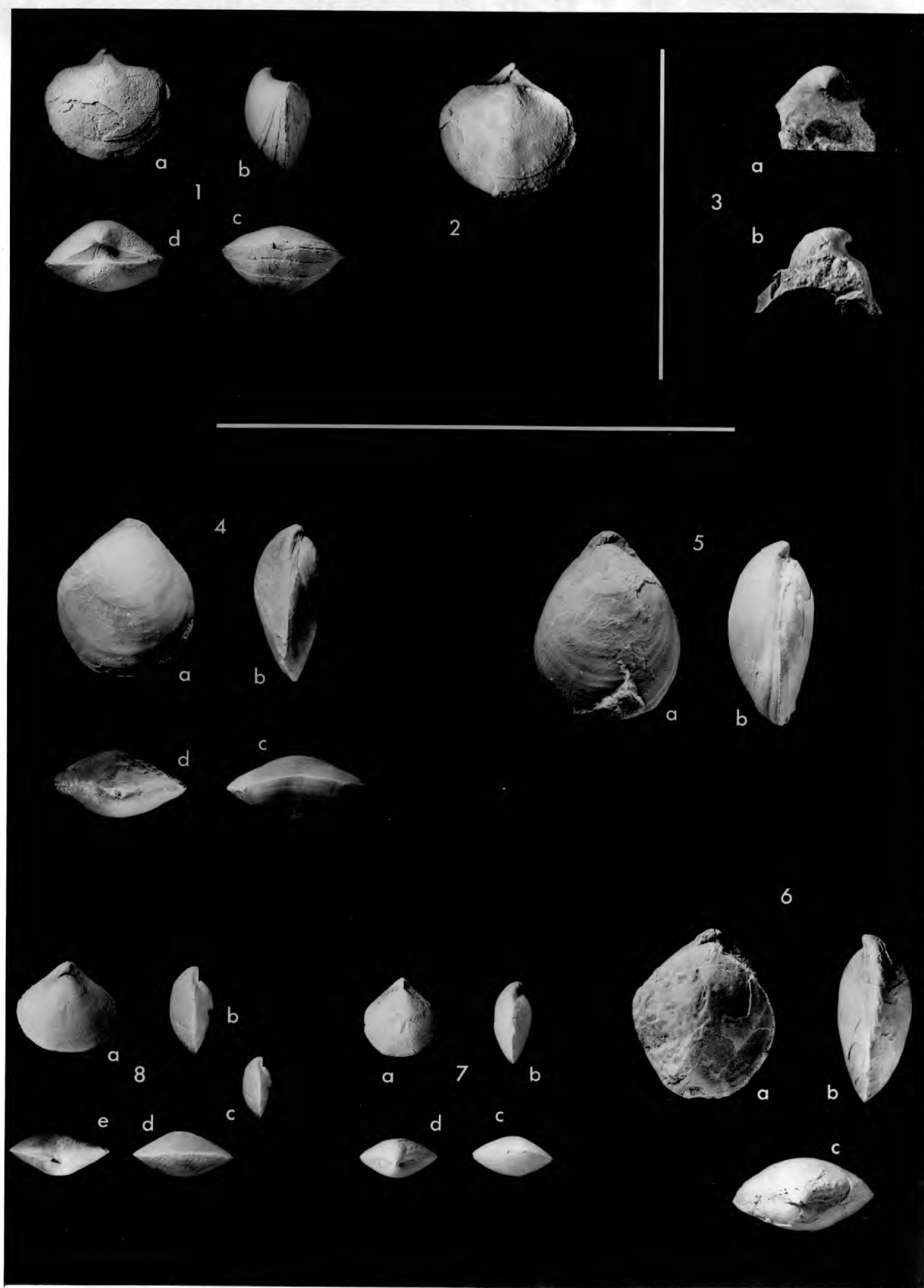


PLATE 15

Figs. 1-3. 'Zeilleria' kitzbergensis sp.nov. x 1.5
Kitzberg, by Neusiedl, Piesting Tal, L.Aust. Fig.2,
holotype; figs. 1,3 metatypes.

Figs. 4-8. 'Zeilleria' elliptica (ZUGMAYER). x 1.5

4. Ascher, by Miesenbach, Piesting Tal, L.Aust.
5. Kitzberg, by Neusiedl, Piesting Tal, L.Aust. Topotype.
6. Locality as fig. . Pal.Inst.Univ. Vienna, ZUGMAYER
colln. Original of ZUGMAYER (1880), pl.2, fig.6.
Lectotype.
7. Locality and source as fig.6. Original of ZUGMAYER
(1880), pl.2, fig.7. Syntype.
8. Locality and source as figs.6,7. Original of ZUGMAYER
(1880), pl.2, fig.8. Syntype.

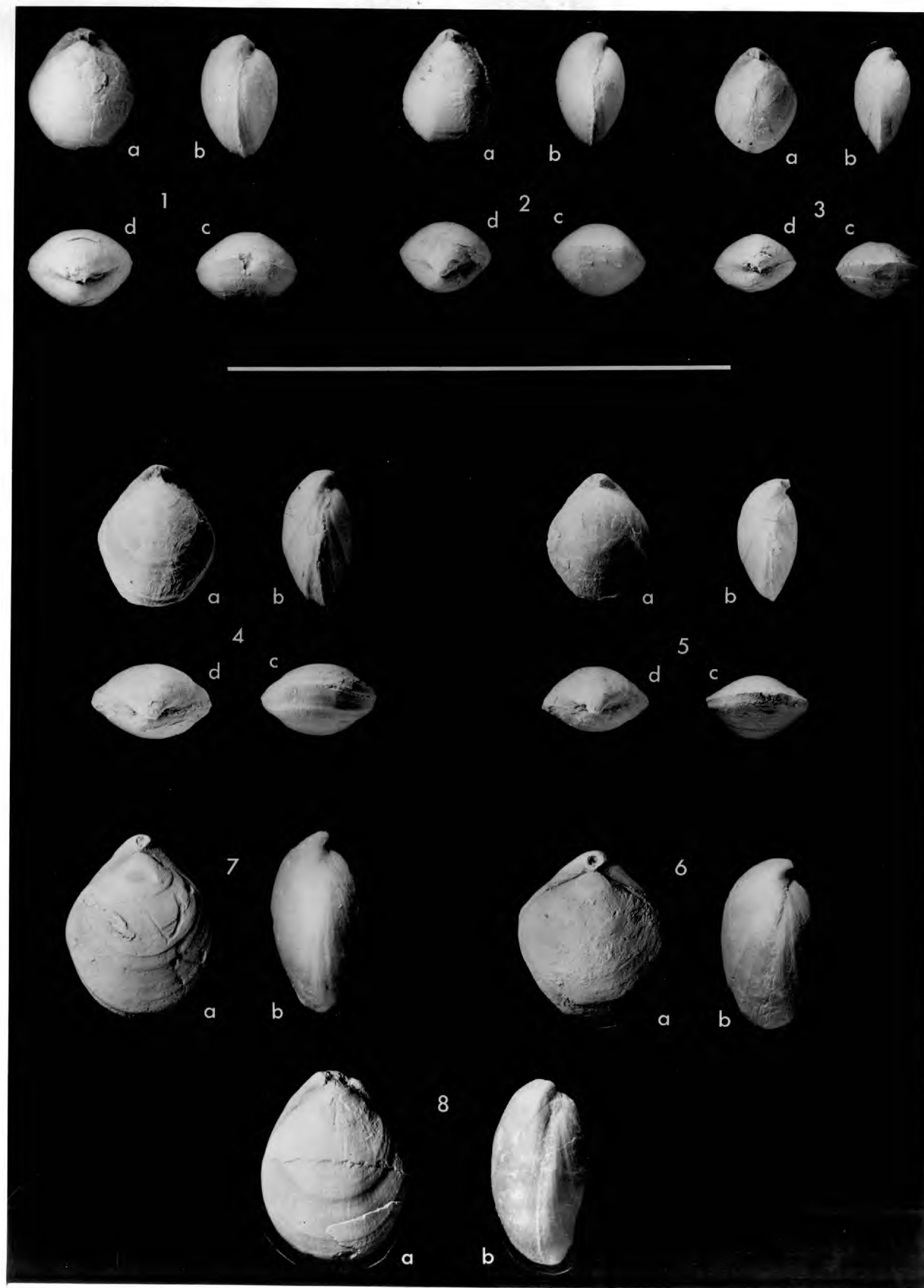


PLATE 16

Figs. 1-4. 'Zeilleria' cf. 'Z. elliptica (ZUGMAYER). x 1.5

1,2,4. Löhn, by Lermoos, Bav.

3. Hohe Mandling, Piesting Tal, L.Aust.

Figs. 5-7. 'Zeilleria' waldegiana (ZUGMAYER). x 1.5

5. Kitzberg, by Neusiedl, L.Aust.

6. 'Rechtes Gehänge des Kaltengangs bei Wallegg, Kaiser
N.W., hinab in den Kaltengang'. Geol.Bundes. Vienna,
4 rot 19/3. Topotype.

7. 'Kaisersteffel' - Piesting Tal, L.Aust. Pal.Inst.Univ.
Vienna, ZUGMAYER colln. Original of ZUGMAYER (1880),
pl.2, fig.11. Holotype.

Figs. 8-10. 'Zeilleria' neusiedlensis nov.sp. x 1.5

8. 'Kaisersteffel' - Piesting Tal, L.Aust. Pal.Inst.Univ.
Vienna. ZUGMAYER colln. Original of ZUGMAYER pl.2, fig.9
'Jugendform der W.norica'.

9-10. Kitzberg, by Neusiedl, Piesting Tal, L.Aust.
Fig.9 - holotype. Fig.10 - metatype.

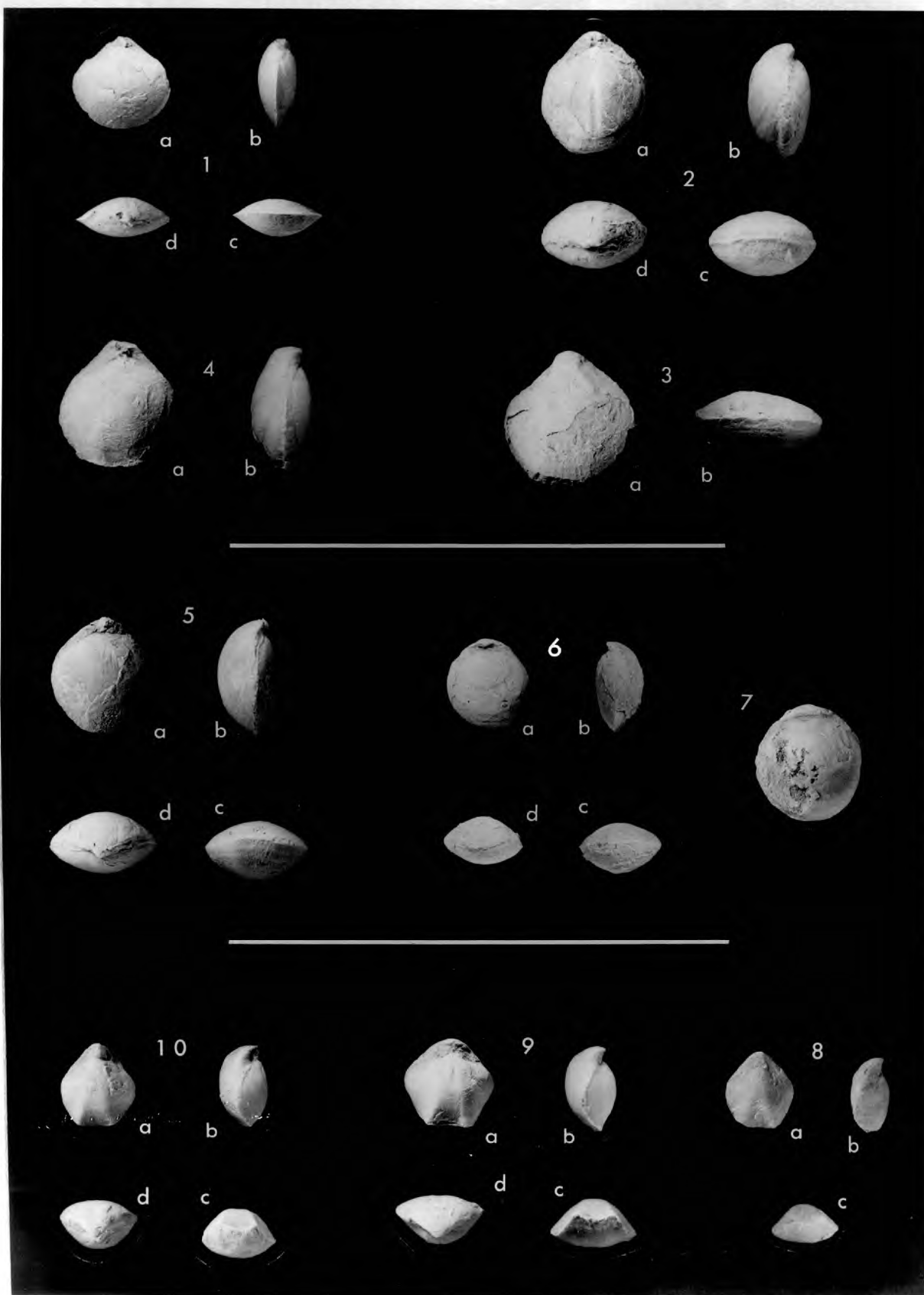


PLATE 17

Figs. 1-9. Austrilleria norica (SUESS). x 1

1. 'Kitzberg' - by Neusiedl, Piesting Tal, L.Aust.
Geol.Bundes. Vienna, 970. Original of SUESS (1854),
pl.3, fig.4. Lectotype.
2. Steinplatte, by Ober Weidring, Tirol, Aust.
3. Vorder Mandling, by Waldegg, Piesting Tal, L.Aust.
4. 'Kitzberg, Nordseite' - Piesting Tal, L.Aust. Geol.
Bundes. Vienna, 970. Topotype.
5. Hirtenberg, Triesting Tal, L.Aust.
6. Locality and source as fig.4. Topotype. Shows marked
anterior flattening.
7. Locality and source as fig.1. Original of SUESS
(1854), pl.3, fig.1. Juvenile.
8. Kitzberg by Neusiedl, Piesting Tal, L.Aust. Juvenile.
9. No locality known. Pal.Inst.Univ. Vienna, ZUGMAYER
colln. Original of ZUGMAYER (1880), pl.2, fig.2.

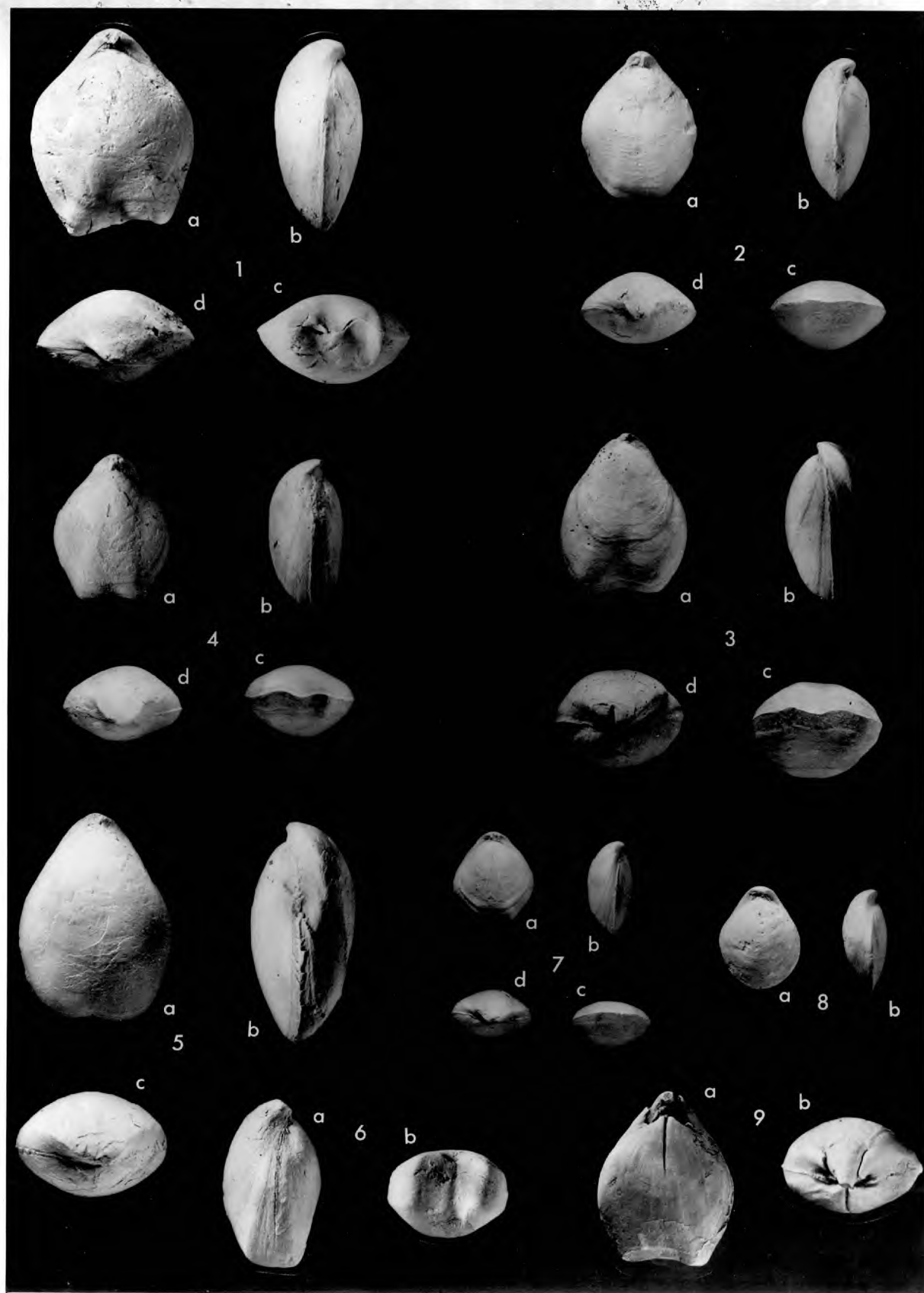


PLATE 18

Figs. 1-8. Rhaetina gregaria (SUESS). x 1

1. 'Kaiserstefel' - Piesting Tal, L.Aust. Pal.Inst.Univ. Vienna. ZUGMAYER colln. Original of ZUGMAYER (1880), pl.1, fig.2
2. Brem by Oberwässen, Bav. Specimen kindly donated from the collection of Prof. DEHM, Munich.
- 3-4. Ochsenberghütte by Hindelang, Bav.
- 5-7. Liassic, Hierlatz by Hallstatt, Aust. Geol.Bundes. Vienna, 2937. Originals of GEYER (1889), pl.2, figs. 20-24. Fig.5 - fig.23; fig.6 - 20; fig.7 - fig.22; fig.8 - fig.21.

Figs.9-11. Rhaetina gregaria ?ssp.nov. x 1

Ampelsbach by Achenkirch, Bav.

Figs. 12-15. Triadithyris gregariaeformis (ZUGMAYER) x 1

12. 'Rechtes Gehänge des Kaltenganges bei Wallegg, Kaiser N.W., hinab in den Kaltengang.' Geol.Bundes. Vienna, 7 rot 19/3.
- 13,15. Drnava, S.Slovakia. Locality of BITTNER's (1890), specimens.
14. 'Kaiserstefel' - Piesting Tal, L.Aust. Pal.Inst. Univ. Vienna, ZUGMAYER colln. Original of ZUGMAYER (1880), pl.1, fig.26.

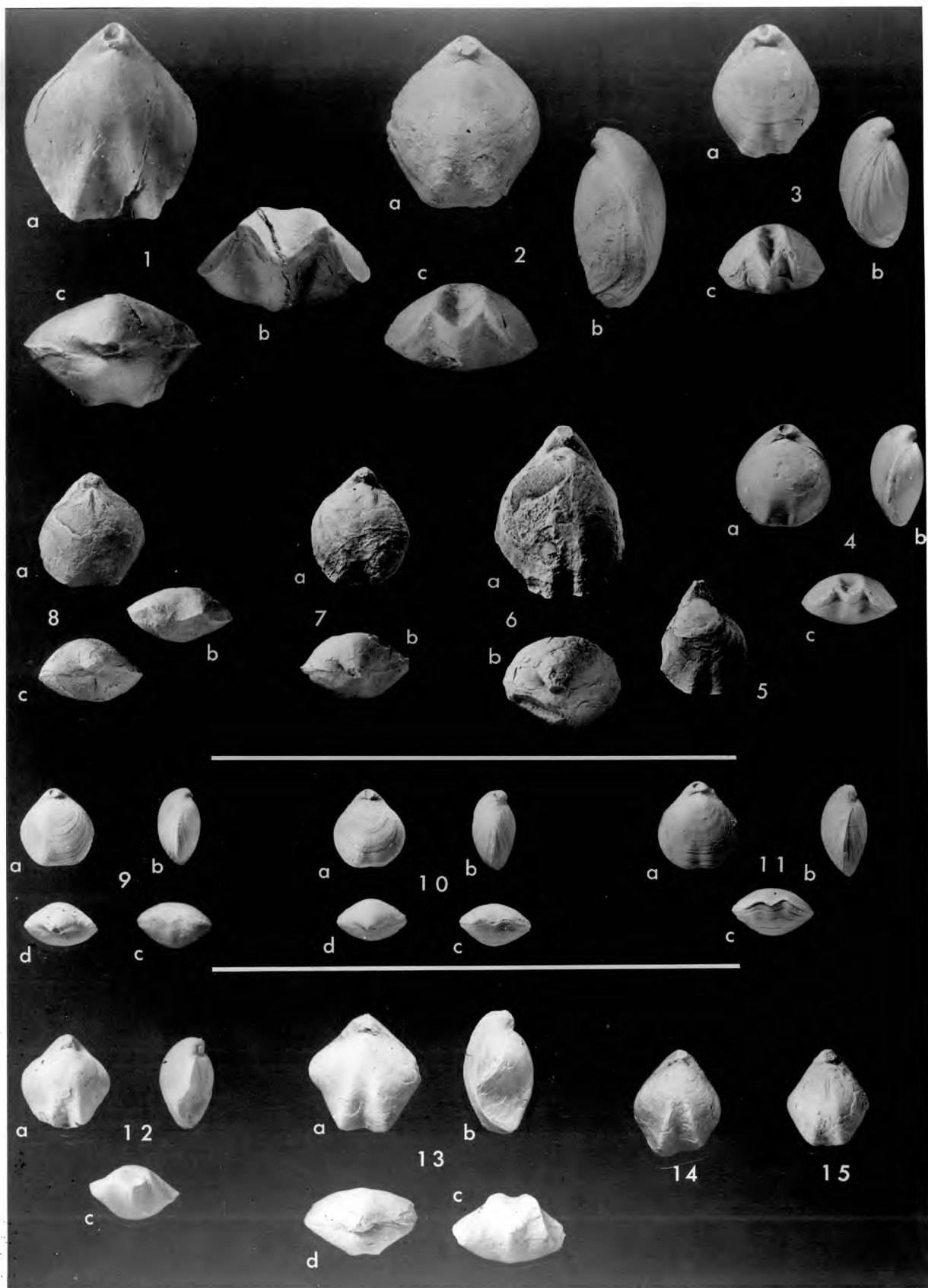
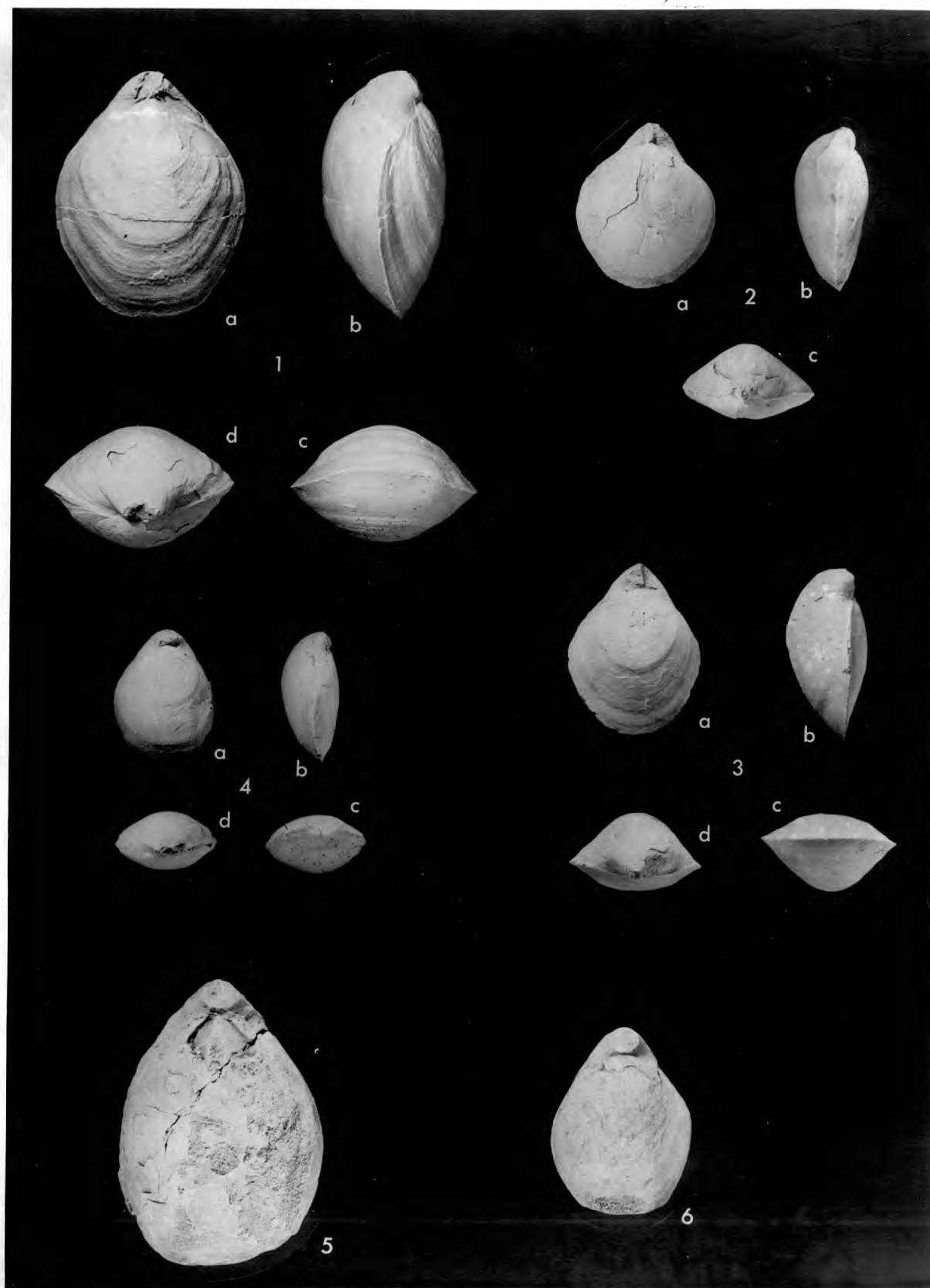


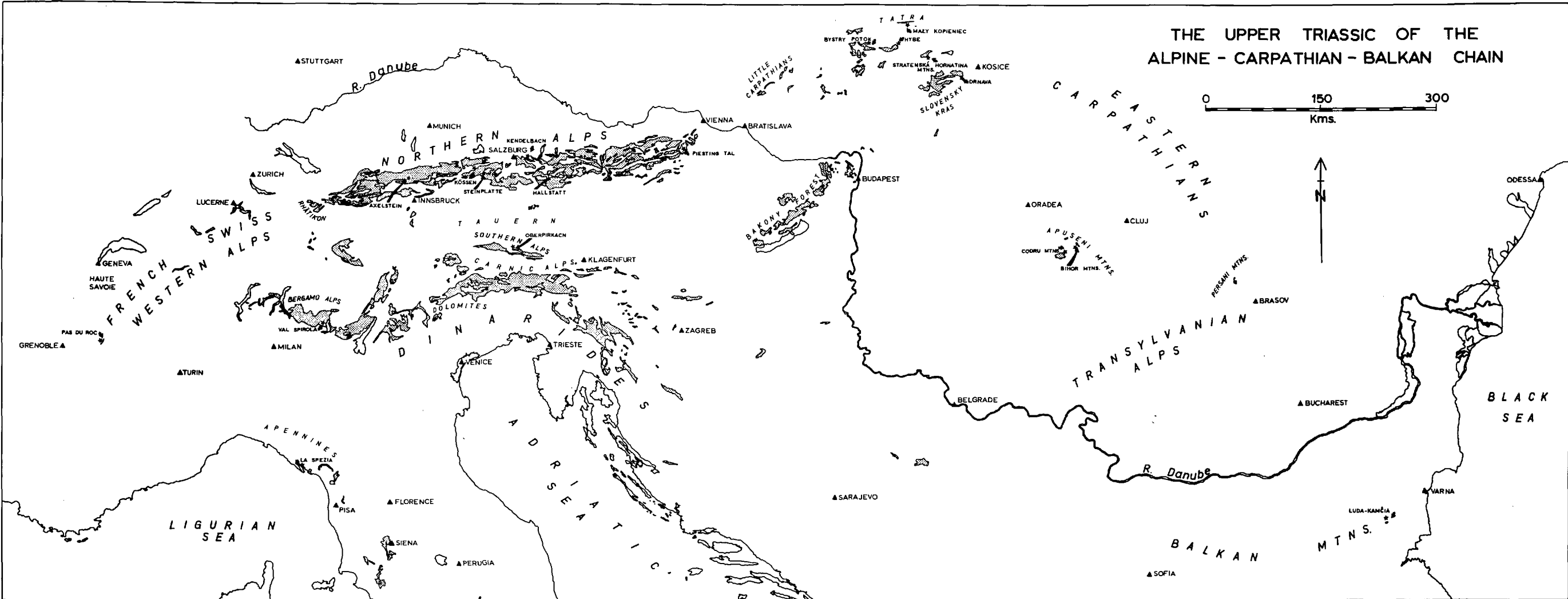
PLATE 19

Figs. 1-6. Rhaetina pyriformis (SUESS). x 1

- 1-3. 'Beim oberen Mandlingbauer in der Oed. Hinter -
mannbauer N., Kitzberg N.' - Piesting Tal, L.Aust.
Geol.Bundes. Vienna, 5 rot 19/3.
4. Kaisersteffel, by Waldegg, Piesting Tal, L.Aust.
5. 'Kitzberg Nordsäite' - Piesting Tal, L.Aust. Geol.
Bundes. Vienna, 969.
6. 'Enzesfeld' - Triesting Tal, L.Aust. Geol.Bundes.
Vienna, 933. Holotype of Terebratula horia SUESS,
1854, pl.3, fig.9.



THE UPPER TRIASSIC OF THE
ALPINE - CARPATHIAN - BALKAN CHAIN



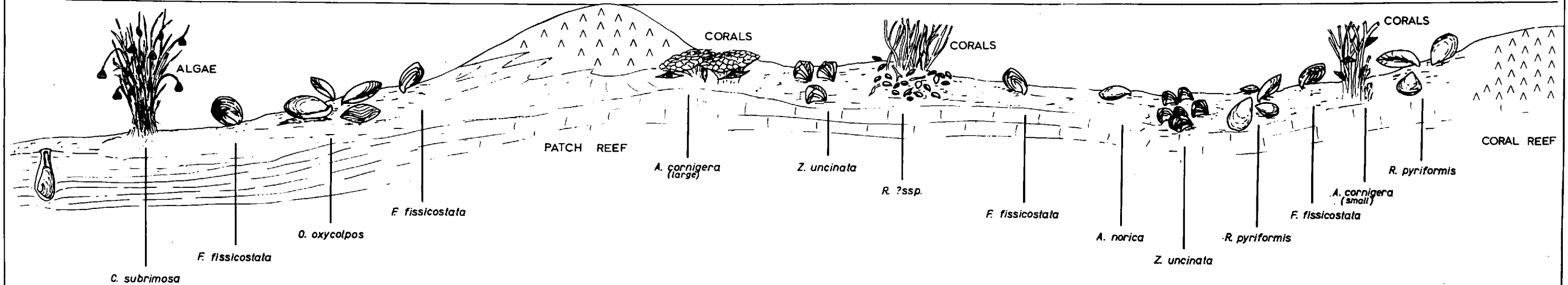
RHAETIAN BRACHIOPOD ASSOCIATIONS

LOFERBACH

AXELSTEIN

AMPELSBACH

STEINPLATTE



REEF AREA - WESTERN N. ALPS

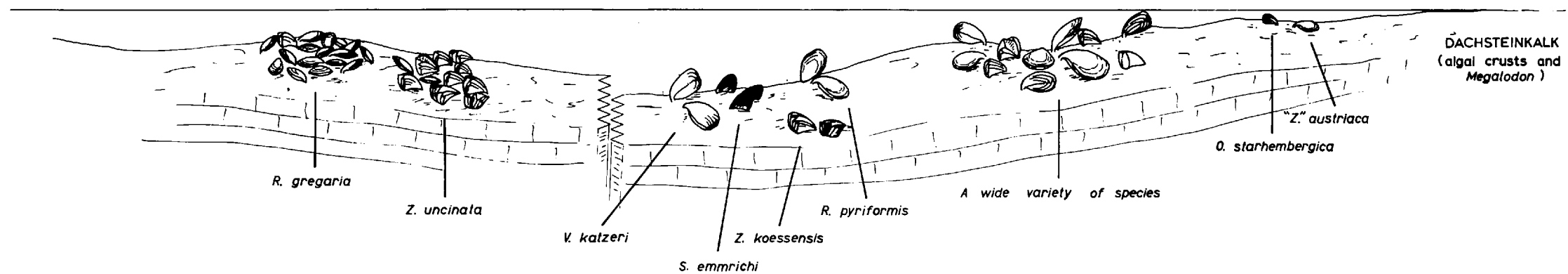
Waidhofen

Bystry Potok

Hybe

Ob. Kaisersteffel

Brand



NON REEF AREA - EASTERN N. ALPS AND CARPATHIANS